

It's not fair! Behavioral and neural evidence that equity
influences social economic decisions in healthy older
adults

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Abstract

Decision-making is a complex behavioral process that requires the integration of multiple cognitive and behavioral components. Little is known about how aging affects the ability to make complex economic decisions or whether the neural changes of aging impact decision-making. Older adults have age-related changes in emotional experiences and face demanding decisions at a time when their cognitive abilities are declining. Furthermore, age-related changes in decision-making are related to age-associated changes in brain regions that subserve decision-making. Therefore, the goal of this dissertation project is to examine the impact of aging on decision-making and its brain basis.

I examined self-report measures of risk behavior, and social and non-social economic decision-making in young (age range 21-45) and older participants (age range 65-85). Older adults reported that they engaged in impulsive or sensation-seeking behavior less frequently and were less willing to take social-risks as compared to the young. Older adults made fairer divisions of money and were more likely to reject unfair divisions of money during real social economic decisions leading to lower payoffs as compared to the young. However, younger and older adults showed similar patterns of economic decision-making in risk and time-delay tasks where there was no social component. To probe age-related differences in neural function that underlies older adults' preference for fairness, I examined behavioral and neural responses during functional magnetic resonance imaging (fMRI). Brain activity of the amygdala, anterior insula and dorsolateral prefrontal cortex (DLPFC) in younger and older participants was examined while they made decisions regarding generous, fair and unfair monetary offers from human and computer proposers in a social decision-making task, the Ultimatum Game. Older

adults rejected more generous and unfair, but not fair, offers than the young. The old had more brain activity in the anterior insula and DLPFC for generous and unfair offers, but not fair offers as compared to the young. Both young and old participants had greater activation of the amygdala to offers made by human as compared to computer proposers.

These studies suggest that aging modulates social economic decisions more than non-social decisions, and the old place more emphasis on fairness or equity than the young. Furthermore, these data indicate that older adults strive for equity, even to the point of refusing overly generous offers. This behavior is mediated by more activity in brain regions that are responsible for the integration and regulation of emotion during decision-making. I argue that the source of age-related differences in social decision-making lay in deficits of the deliberative (i.e., cognitive) system that causes older adults to rely on a rule-based decision strategy, which is supported by an enhancement of their affective (i.e., emotional) experiences.

Chapter 1:

General Introduction

Little is known about how aging affects the ability to make complex economic decisions or whether the neural changes of aging impact decision-making. Therefore, the goal of this dissertation project is to examine the impact of aging on decision-making and its brain basis. I focus here on the impact of socio-emotional interactions on economic decisions. In recent years, scores of older adults have lost billions of dollars through poor decision-making in investments that were unsuited to their needs, promoted in a misleading fashion, or simply had unclear risks (American Association of Retired Persons (AARP), 2006). While many situations, including choosing a health plan, selling a house, or spending retirement money, have elements of uncertainty, taking undue risks when making these decisions could spell disaster for the old. Older adults are particularly vulnerable since they are more likely to live on a fixed income. Many older Americans are at risk of outliving their retirement assets as they overestimate Social Security payouts, underestimate their postretirement expenses, and do not understand their longevity risk (Timmermann, 2005). In addition, older adults are more susceptible to misleading information about a product or situation that is unsuitable to their needs as compared to younger people (Denburg et al., 2007). The nature and mechanisms underlying these difficulties remain unclear but it is clear that age-related changes occur in brain regions known to underlie decision-making processes. The studies included in this project begins to elucidate the neural mechanisms of decision-making in aging. Two studies are reported here: Chapter 2 examines behavioral changes, and Chapter 3 examines the neural basis of age-related behavioral changes in economic decision-making.

To put these studies in context, here I review information about behavioral processes that influence social and non-social economic decision-making, theories and methods of decision-making, the neural basis of economic decision-making, age-related changes in decision-making and the effect that age-related changes in structure and function of the brain may have on decision-making.

Behavioral components of decision-making

Decision-making is a complex behavioral process that requires the integration of multiple cognitive and behavioral components. There are distinct stages decision-making that require cognitive evaluation (as reviewed in Ernst & Paulus, 2005). For example, when deciding the route to bicycle home from work, one may consider which route is fastest or safest, as well as elements such as traffic patterns and weather conditions. The assessment of decision options requires enumerating all possible options and weighing these options against our likes and dislikes. After the selection and execution of the decision, the outcome of the decision is catalogued and memory of that decision is updated for later use. Our goals (i.e., moral, financial, social etc.) guide decisions, and memory is critical for comparing current choices to previous, similar choices (Kristan, 2008).

Learning and memory (Rolls, 2008), attention (Rolls, 2008; Ernst et al., 2003) and executive functions (Bechara et al., 1997; Bechara et al., 2000a), are principal components of decision-making as shown by studies of human patients with cognitive dysfunction (Bechara et al., 1994; Brand et al., 2005; Brand et al., 2007) and healthy adults (Brand et al., 2008; Brand & Markowitsch, 2009). For example, in the Iowa Gambling Task (IGT), a 'real-world' decision-making assessment tool, people select cards from multiple decks: advantageous decks and disadvantageous decks (Bechara et al., 1994; Bechara et al., 2000b). At the start of the task they are unaware of the status of these decks and must learn which decks are 'advantageous' and 'disadvantageous' (Bechara et al., 2000b). Patients with

brain lesions or dysfunctions in crucial learning and memory regions, including the prefrontal cortex (Bechara et al., 1994; Bechara, 2001; Clark et al., 2008; Manes et al., 2002) and amygdala (Brand et al., 2007; Brand et al., 2005), do not learn to make the most advantageous decisions in the IGT and maintain preference for the disadvantageous decks as compared to healthy adults (Clark et al., 2008). Clark et al. (2008) suggest that poor decision-making in lesioned patients is “driven by the short-term benefits associated with risky decks, without regard for the longer-term negative consequences; a profile labeled ‘myopia for the future’ ” (Clark et al., 2008, pg 1312). The Game of Dice Task (GDT; Brand et al., 2005) evaluates executive functions such as categorization, goal-oriented behavior and cognitive flexibility. In the GDT participants must ‘guess’ which number will be thrown on a single die. Participants can choose different alternatives with different probabilities and payouts. For example, they can ‘guess’ that the number 4 will be thrown on the next trial, which is associated with a \$5 payout, or they can ‘guess’ that either the number 2 or 4 will be thrown for a \$2.50 payout. In practice, healthy adults typically begin by selecting the high-risk, high reward option (i.e., choosing one number) but quickly learn to change their strategy to the lower-risk, lower-reward condition (Brand et al., 2008). This task shows that people update and adapt their decisions over time by employing flexible cognitive strategies based upon memory and feedback from previous outcomes (Brand & Markowitsch, 2009).

It is well established that emotions play a key role in decision-making (Elster, 1998; Loewenstein, 2000; Peters et al., 2006). People evaluate decisions in a subjective manner and emotions influence these evaluations (Loewenstein & O'Donoghue, 2004; Naqvi et al., 2006; Slovic et al., 2007). The emotional content of decisions has two major features: valence and arousal. Valence represents negative or positive aspects of the decision, and arousal represents the strength of the

emotional content (Kensinger & Corkin, 2004). The role of emotional valence in decision-making is straightforward. Positive affect leads to increases in satisfaction, well-being, or value; negative affect leads to the opposite (i.e., dissatisfaction, ill-being, worthlessness; Zeelenberg et al., 2008; Inman et al., 1997; Mellers et al., 1999). Emotional arousal can either be acute or long-lasting (i.e., moods) both of which affect decision-making (Zeelenberg et al., 2008). Acute negative emotions (sadness, anger, etc) lead to specific shifts in decision-making outcomes. For example, sadness results in a propensity for high reward, high-risk responses (Raghunathan & Pham, 1999; Raghunathan & Pham, 1999), and anger during strategic bargaining games may lead to lower payouts (van Dijk et al., 2008). It has been hypothesized that once individuals are in a state of positive mood, they work to maintain this state, resulting in more conservative decision-making (Kennedy & Mather, 2007). Indeed, during instances of potential personal loss, a positive mood state results in less risk-taking than a neutral mood (Nygren et al., 1996). On the other hand, negative mood results in more pessimistic approaches (e.g., assuming a negative outcome; Williams et al., 2003) and avoidant decision behavior (Luce, 1998). Emotional regulation strategies can alter decision-making (Heilman et al., 2010). For example, using a cognitive strategy to down-regulate negative emotional feelings leads to a neutral mood and riskier decision-making, whereas a suppression strategy does not (Heilman et al., 2010). Thus, emotions can either disrupt or optimize decision-making.

Economic Decision-Making

The study of economic decision-making has been useful in probing both the cognitive and emotional factors that influence decision-making. Economic decisions involve comparing the values of different possible economic options and selecting the option that best meets one's goal. This can be straightforward, or a complex, highly nuanced process. Simple decisions that only differ in one

dimension (i.e., amount of reward) rarely produce much conflict (i.e., choosing between \$5 and \$10). More often, decisions are choices between options that differ on multiple dimensions. For example, deciding whether to accept \$5 today vs. \$10 next month requires an individual to consider both the amount of a reward and the time he/she is willing to wait to get a particular reward. Typically, individuals prefer a larger reward when the delay to reward is long. However, if a smaller, immediate reward comes substantially sooner, individuals will switch their reward preference (Ainslie, 1992; Green et al., 1993; Green et al., 1994b; Madden et al., 2003; Rachlin, 1989). These types of decisions are considered non-social economic decisions, as they are made without the influence or interaction with another individual. For example, deciding whether to spend \$10 on lunch today or saving one's money for a nice dinner out this weekend would be considered a non-social decision. More complex decisions require more cognitive resources (Wittmann et al., 2007; McClure et al., 2004) and are complicated by the decision context (i.e., non-social vs. social). For example, deciding how to split \$10 with another individual adds an emotional dimension to the decision, including personal views of fairness, trust and altruism (for review see Sanfey, 2007). These types of decisions are considered social decisions as they involve direct interaction with other individuals, which may influence the outcome of the decision. These decisions are considered to be more representative of 'real-world' decisions, as most decisions made on a daily basis have social context. For instance, deciding whether to lend your co-worker \$10 for lunch requires one to assess the non-social factors of the decision (i.e., Can I afford to give \$10?), but also requires assessment of the other person (i.e., Do I trust my co-worker to repay me this \$10?). For the purposes of this dissertation, the term 'social' refers to interactions between a decision-maker and another person. These interactions are social as the attitudes, orientations and behaviors of the decision-maker take the interests, intentions or needs of

the other person into account (irrespective of whether the decision-maker is aware of this coexistence). Thus, both non-social (i.e., reward, delay) and social (i.e., presence of another) factors can influence the decision-making process. This dissertation contrasts age-related changes in decisions made within a social context with those that are not.

Theories about and methods for assessing decision-making

Non-social economic decision-making

Standard non-social economic models of decision-making propose that decisions are completely self-interested and are made based upon rational evaluation of their consequences (Sanfey & Chang, 2008). These models assume that decision-makers are 'perfectly rational cognitive machines' (Sanfey et al., 2003) and choices are dependent solely upon reward and risk. Expected Utility theory proposes that people choose a course of action by determining the desirability or 'utility' of each decision's outcome (Bernoulli, 1954). People determine the value of each possible decision outcome, compare outcomes, and then select the decision with the best overall outcome (Kahneman & Tversky, 1979). Gambling tasks assess how well people estimate the expected value of alternatives. For example, a gamble with a 1 in 50 chance for \$100 has an expected utility of $[(1/50)*100]$, or \$2. Thus, in a choice between a guaranteed \$1 and this gamble, Expected Utility theory suggests that people should choose the more valuable outcome, the \$100 gamble. However, people tend to choose the more certain option (i.e., the guaranteed \$1), even though it has less utility or value (as reviewed in Weber & Johnson, 2009). Prospect Theory (Kahneman & Tversky, 1979; Tversky & Kahneman, 1992) builds upon the foundation of expected utility but also incorporates risk. These theories assume that people set a reference point (i.e., current income) for making a decision and consider lower outcomes as losses and larger outcomes as gains. Thus, for the gamble described above, a person's current

income and the risk or uncertainty about the gamble for \$100 would also factor into the decision. For example, someone that earns \$1000 per week may be more willing to choose the risky gamble for \$100 as opposed to someone who only earns \$50 per week because the guaranteed \$1 has more value to the second person. Thus, both risk and uncertainty about possible consequences and how the context, such as income status, influence how individuals approach the decision-making process (as reviewed in Weber & Johnson, 2009).

The Discounted Utility Model predicts how people make non-social decisions involving alternatives whose costs and benefits are distributed over time (Samuelson, 1937). For example, delay-discounting tasks measure an individual's preference when weighing a reward that is modified by a delay until receipt (i.e., \$5 now versus \$10 next week; Rachlin et al., 1991; Richards et al., 1999). Delay-discounting experiments present subjects with a choice between a standard larger-later reward (e.g., \$1000 delivered in 1 year) and an immediate reward whose magnitude is adjusted until the participant subjectively considers the two rewards to be of approximately equal worth (e.g., Green et al., 1994a). This point of equivalence is the indifference point for that particular delay interval. Indifference points obtained for different delays permit an empirical determination of the rate at which delayed rewards are discounted. Individual differences in cognitive ability are associated with steeper discounting rates (Shamosh & Gray, 2008). For example, poorer cognitive ability in younger adults, as measured by IQ, results in choices of smaller, more immediate rewards (Shamosh & Gray, 2008) and those with better cognitive ability are more likely to wait for the larger reward (Shamosh & Gray, 2008). In Chapter 2, I will assess the impact of aging on delay-discounting performance.

Social economic decision-making

Decisions change when the outcome involves another person, and models of social economic decision-making indicate that people do not act out of complete self-interest in these situations. In fact, the mere presence of another individual affects economic decision-making in a variety of ways (Fehr & Schmidt, 1999; Fehr & Gächter, 2000; Van Lange, 1999; Camerer, 2003; Sanfey et al., 2003; Bolton & Ockenfels, 2000). People make generous decisions even when interacting with non-relatives and strangers (Fehr & Fischbacher, 2003). For example, in the Dictator game, in which a person presents a stranger with a one-time anonymous monetary offer, people typically make equitable offers (Camerer, 2003), instead of keeping the entire sum of money for themselves. If people were purely self-interested they should keep the entire sum of money for themselves, however they do not. Prior knowledge about another person can also bias social decision-making. For instance, when participants interact with someone who is perceived to have 'positive moral character' they are more likely to be generous than when interacting with someone perceived to have 'negative moral character' (Delgado et al., 2005). The social component of these decisions may be just as influential to the decision-making process as non-social factors such as risk and reward.

Reciprocal fairness and inequality aversion are two prominent theories that attempt to explain deviations in self-interested behavior during social economic decision-making. In models of reciprocal fairness, decision-makers positively value kindness and negatively value antagonistic intentions of others (Rabin, 1993; Dufwenberg & Kirchsteiger, 2001; Falk & Fischbacher, 2005). This model implies that the intention of the person is known and that it has direct bearing on one's decision. The Trust Game measures trust and reciprocity that develops over multiple interactions with a partner (Berg et al., 1995). In the Trust Game, an investor and

a trustee are endowed with \$10. The investor can send all, some or none of his \$10 to the trustee. Every dollar sent by the investor is tripled. The trustee receives this amount and decides whether to send all, some or none back to the investor. The amount sent by the investor is considered a measure of trust while the amount returned by the trustee is a measure of trustworthiness. Investors send about 50% of the total sum on average, and trustees typically return the amount the investor sent (Berg et al., 1995). Classical economic models predict that the 'rational' strategy is for investors to send nothing since they would realize that a purely self-interested receiver has no intention of returning anything. However, reciprocal fairness better explains the behavior observed. For example, if the investor makes a poor decision that is viewed as negative (i.e., small amount) the trustee will reciprocate with an equally low return amount (if any). However, if the investor is generous, the trustee will likely be generous, indicating that the trustee reciprocates the positive intentions of the investor.

Models of inequality aversion suggest that people simply have disgust for unequal outcomes (Fehr & Schmidt, 1999). Inequality aversion manifests itself as the "willingness to sacrifice potential gain to block another individual from receiving a superior reward" (Fehr & Schmidt, 1999; pg 818). This model implies that people care about equity and attempt to maintain their social reputation by rejecting inequity. In an economics framework equity is the concept of fairness, such that the subjective valuation of a person's own share of some good is the same. The Ultimatum Game (UG) measures views about fairness by having two individuals determine how to divide a sum of money, typically in a one-time interaction (Guth et al., 1982). In the UG, two people are anonymously paired. One plays the role of a proposer and the other a responder. Both players are given all the rules of the game and instructed that the game will

be played once. The proposer is endowed with a sum of money (i.e., \$10) and divides the money between himself and the responder (e.g. \$5 for me; \$5 for you). The responder observes the offer and decides whether to accept or decline. If the offer is accepted, they both receive the corresponding amount (i.e., \$5), but if rejected, both players receive nothing (i.e., \$0). Proposers tend to offer close to 50% of the total available sum, and responders typically reject half of offers below 20% of the total sum. This UG data confirms that people will forgo a small financial reward (i.e., \$1) if they feel they are being treated unfairly by another person (Eckel & Grossman, 1996; Sanfey, 2007). Classical game theory suggests that the rational strategy is for the proposer to offer the smallest possible share and for the responder to accept any non-zero offer (Sanfey, 2007), but again, this behavior is not typically seen (Guth et al., 1982; Nowak et al., 2000; Sanfey et al., 2003). Inequality aversion best describes the decisions made by both the proposer and responder (Fehr & Schmidt, 1999). Since the proposers rarely keep more than half of the endowment for themselves, their decisions appear guided by either the desire be fair towards the responder or by knowing that the responder expects some level of equality in the offer. Furthermore, equality is important to the responders since they prefer receiving nothing, which is equal to what the proposer will receive in this scenario, to receiving a small share of the pie. In this case, rejecting the offer is in effect paying to punish the proposer for making an offer that deviates in equality. Reciprocal fairness is not typically considered a viable explanation in the UG since the game is only played once between two given players, thus reciprocation is not an issue.

Social interactions alter judgment and add a salient emotional component to decision games. For example, individuals with a positive facial expression (i.e., smile) were more likely to

be trusted, and thus given larger sums of money than individuals with a neutral expression, who were rated as less trustworthy (Berg et al., 1995). In addition, anger is associated with the rejection of low unfair offers in the UG (Pillutla & Murnighan, 1996; Xiao & Houser, 2005). In fact, rebuffing unfair offers is a mechanism by which people assert and maintain their social reputation (Nowak et al., 2000) and the negative emotions evoked by unfairness can lead people to do so even knowing that they are sacrificing considerable financial gain (Sanfey, 2009; Rilling et al., 2008). In Chapters 2 and 3, I will focus on the UG as the social decision-making task and assess the impact of aging on fairness in social economic decision-making.

The neural basis of economic decision-making

The decision-making circuit (Figure 1) is comprised of the prefrontal cortex, [dorsolateral (DLPFC), ventromedial (VMPFC), & orbital (OFC)], the anterior region of the insular cortex and 'subcortical' (i.e., amygdala, nucleus accumbens, striatum) brain structures (Fellows, 2004). Animal models (Cardinal et al., 2001; Mobini et al., 2002; Schweimer & Hauber, 2005; Walton et al., 2002), human lesion studies (Bechara et al., 1994; Bechara et al., 1999; Bechara et al., 1998; Tranel et al., 2002), studies of pathologic human conditions (Bechara & Damasio, 2002; Cavedini et al., 2002; Hoffman et al., 2006; Monterosso et al., 2007) and functional brain imaging studies (Breiter et al., 2001; Greene et al., 2001; McClure et al., 2004; Northoff et al., 2006; Sanfey et al., 2003) of decision-making have focused primarily on the role of the prefrontal cortex (PFC). Imaging studies in healthy adults and clinical reports of poor decision-making in individuals with frontal lobe abnormalities (Bechara et al., 1994; Fellows, 2004) implicate the PFC in working memory, goal-maintenance, insight, judgment of fact, and reasoning (Miller & Cohen, 2001; Krawczyk, 2002; Goldman-Rakic, 1992; Fuster, 1973). The PFC, along with the striatum, is particularly responsive to changes in reward, especially

accumulation of reward (Floresco & Ghods-Sharifi, 2006) and reward prediction (as reviewed in Schultz, 2006). In addition, the PFC activates in response to the emotional salience of rewards (Rolls, 2000), changes in reward size (Ernst et al., 2004) and the receipt of rewarding social stimuli (Fehr & Camerer, 2007). In the following experiments, I will also focus on the role of the DLPFC.

-----Insert Figure 1 here-----

The DLPFC is essential in executive tasks that involve the manipulation and integration of cognitive information (Krawczyk, 2002). DLPFC neurons encode unique signals necessary to optimize a decision-making strategy in primates (Barraclough et al., 2004). DLPFC neuronal activity is associated with the calculation of reward value when comparing two alternatives to guide choice behavior (Barraclough et al., 2004) and encode information about previous choices, such as whether or not reward was received. These data indicate that the DLPFC is also important for memory signals associated with decisions (Seo et al., 2007). In humans, DLPFC activity is associated with complex decisions that involve discounting (McClure et al., 2004), fairness (Sanfey et al., 2003; Knoch et al., 2006), risk (Ernst et al., 2003), and social interactions (i.e., Heekeren et al., 2003; Sanfey et al., 2003). For example, the DLPFC is more active when participants accept low, unfair offers in the Ultimatum Game (Sanfey et al., 2003). More DLPFC activity in this case may represent a cognitive control mechanism that allows one to overcome the impulse to reject unfair offers (Sanfey et al., 2003; but see Knoch et al., 2006). Taken together, these findings indicate that the DLPFC is involved in cognitive operations that optimize decision-making.

The anterior insular cortex is associated with visceral representation and emotional experiences, which aid in decision-making, particularly when decisions involve uncertainty (Singer et al., 2009). Specifically, the anterior insula activates to changes in bodily states, such as touch, taste, craving

and pain as measured in human neuroimaging studies (Craig, 2003; Craig, 2009; Critchley et al., 2002; Critchley, 2005; Naqvi et al., 2006). In addition, activation of the anterior insular cortex is found for a number of negative emotional states including anger and disgust (Singer et al., 2009; Calder et al., 2007; Derbyshire et al., 1997; Fellows, 2004), and when one empathizes with others in these emotional states (Jabbi et al., 2008; Saarela et al., 2007; Singer et al., 2004b). For example, bilateral anterior insula is engaged when one experiences a painful stimulus, such as an electrical shock, and when one observes another person being shocked in the same manner (Singer et al., 2004b; Singer et al., 2009). The anterior insula is implicated in associating emotional experience with choices that involve risk, uncertainty (Huettel, 2006; Kuhnen & Knutson, 2005; Paulus et al., 2003; Preuschoff et al., 2008) and social interaction (Sanfey et al., 2003; Chang & Sanfey, 2009). For instance, low or unfair offers in the Ultimatum Game result in greater activation of the anterior insula and other cortical brain regions as compared to fair offers (Sanfey et al., 2003). Furthermore, anterior insula activity is associated with the rejection of unfair offers in this game (Sanfey et al., 2003). This indicates that the anterior insula is sensitive to aversive decision outcomes and may guide choice in these situations. Thus, the anterior insula may integrate bodily and affective information into the cognitive aspects of decision-making and help guide choice behavior, particularly in social situations.

The DLPFC and anterior insula have vast connections to ‘subcortical’ structures (for review see Fellows, 2004) implicated in decision-making. The ventral striatum and nucleus accumbens are involved in reward processing and expectancy of outcomes. Single-unit recording studies of nonhuman primates show a positive relationship between activity of midbrain dopamine neurons and reward probability or expected reward (Fiorillo et al., 2003; Tobler et al., 2005). Human functional magnetic resonance imaging (fMRI) studies show that

these structures activate to primary rewards, such as gustatory stimuli (Berns et al., 2001; O'Doherty et al., 2002) and secondary rewards, such as money, particularly during decision-making tasks (Breiter et al., 2001; Elliott et al., 2000; Elliott et al., 2003; Knutson et al., 2000; Knutson et al., 2001; Knutson et al., 2003). The amygdala, most commonly associated with emotion processing, also plays an important role in decision-making (as reviewed in Seymour & Dolan, 2008). Lesions of the amygdala cause a deficit in the appreciation of affective stimuli and memory for affective information in both animal models (Gale et al., 2004; Gale et al., 2004) and humans (Adolphs & Tranel, 2004; Adolphs & Tranel, 1999; Adolphs et al., 1999; Adolphs & Tranel, 2004). Bilateral inactivation of the basolateral amygdala impairs effort-based decision-making in rats (Floresco & Ghods-Sharifi, 2006). Rats that were given a choice between working to obtain high (4 food pellets) or lower (2 food pellets) value rewards had a strong preference for working for the high reward option. However, after bilateral inactivation of the amygdala, rats no longer showed this preference (Floresco & Ghods-Sharifi, 2006). This suggests that the amygdala modulates rats' motivation to seek particular rewards. In human studies, patients with bilateral amygdala lesions make more disadvantageous decisions in the Iowa Gambling Task as compared to controls (Bechara et al., 1999). In addition, they fail to show anticipatory skin-conductance responses before making poor choices (Bechara et al., 1999). Neuroimaging studies show that amygdala activity is associated with how decision options are framed even if the outcome is the same (De Martino et al., 2006). For example, the amygdala responds more when a participant is told that he/she might *lose* \$80 out of a possible \$100 than when they are told that they might *gain* \$20 out of a possible \$100 (De et al., 2006). The amygdala also responds to complex social information such as trust and moral status

(Adolphs et al., 1997; Adolphs & Spezio, 2006; Calder & Young, 2005; Moll et al., 2008; Singer et al., 2004a; Winston et al., 2002), which may influence decisions in social contexts. For example, the more untrustworthy a face is rated, the more the amygdala responds (Winston et al., 2002). Thus, the amygdala's role appears to be to integrate affective information about the decision context with the features of a given decision. In chapter 3 I focus on the role of the amygdala in social economic decision-making.

Measuring brain activity

Human brain activity during decision-making is measured using fMRI. Functional MRI safely and noninvasively measures the blood oxygenation level dependent (BOLD) changes induced by neural activity during mental activity. This method detects brain regions whose BOLD signal fluctuations correlate across time with task demands (Buxton, 2002; Huettel et al., 2004). Others have used it to map cognitive processes, such as working and long-term memory (Wagner et al., 1998; Greicius et al., 2003; Cohen et al., 1993), and disease (for review see Hennig et al., 2003) and age-related (Cabeza et al., 2004; Gunning-Dixon et al., 2003; Lidaka et al., 2002) changes in brain activity. This technique has elucidated a number of cortical and sub-cortical brain regions involved in making decisions (for review see Loewenstein et al., 2008). In Chapter 3, I will compare the BOLD activity of the DLPFC, anterior insula and amygdala in the young and old during a social economic decision-making task.

Aging and decision-making

Older adults face demanding decisions, including choices about retirement, savings, health care and end-of-life care, at a time when their cognitive abilities are declining (Baltes & Baltes, 1990; Baltes et al., 1999). Attention (for review see Verhaeghen & Cerella, 2002), memory (for review see Zacks et

al., 2000; Buckner, 2004) and executive function (Salthouse et al., 2003) are diminished in aging and may contribute to changes in decision-making across the lifespan (Brand et al., 2008; Zamarian et al., 2008). However, it is unclear how neurocognitive functioning interacts with optimal decision-making in older adults. As people age their ability to recover from or compensate for poor decisions diminishes (Finucane et al., 2002). For instance, older adults forget decisions more rapidly, deliberate for less time when making decisions, seek out less information to make an informed decision and are more decision avoidant (as reviewed in Kennedy & Mather, 2007). Older adults shift less frequently to advantageous options in the Iowa Gambling Task (Denburg et al., 2007; Denburg et al., 2009; Zamarian et al., 2008; but see Denburg et al., 2005), which may result from deficiencies in working-memory (Bechara & Martin, 2004) or other executive functions, such as feedback processing (Brand et al., 2007). Furthermore, older adults adopt poorer strategies and alternate between risky and conservative decision strategies more often than younger subjects in the Game of Dice Task (Brand & Markowitsch, 2009). Thus, decision-making appears affected by aging, particularly if the decision situation requires complex cognitive processing (Brand & Markowitsch, 2009). Yet, older adults remain able to make many high-quality decisions in a variety of other situations. Many older adults show similar levels of risk aversion, perceive similar amounts of risk in the Probability-Associated Gambling Task (PAG; Sinz et al., 2008; Zamarian et al., 2008), and discount delayed rewards similarly to their younger counterparts (Green et al., 1994b), especially when matched for socioeconomic status (Green et al., 1996). Taken together, these data suggest that age-related changes in decision-making may be sensitive to the decision situation and that factors other than cognitive ability also play a role in decision-making. In Chapter 2, I compare decision-making in older adults in non-social and social decision situations.

Age-related changes in emotional experiences (Carstensen et al., 1999; Mather et al., 2004; Mather & Carstensen, 2003; Leigland et al., 2004; Levenson et al., 1994) and emotional regulation (Lawton et al., 1992; Mroczek & Kolarz, 1998) play a significant role in guiding decisions. For example, older adults experience less negative affect (Charles et al., 2003; Mather & Carstensen, 2003). The perception and memory for emotional information also changes with aging (Charles et al., 2003; Neiss et al., 2007; Lawton et al., 1992; Mroczek & Kolarz, 1998) and may be a source of age effects on decision-making. Most apparent in the old is enhanced memory for material with a positive valence, and poorer recollection of negatively valenced material, be it words (Leigland et al., 2004), faces (Mather & Carstensen, 2003) or pictures (Charles et al., 2003), as compared to the young. Working memory for the emotional intensity of scenes is enhanced for positive versus negative scenes in the elderly, but the opposite is true for younger people (Mikels et al., 2005). Older adults attend less to negative faces (Mather & Carstensen, 2003) and rate negative pictures as less arousing than younger adults (Mather et al., 2004). Well-being studies suggest that old age brings greater emotional control and less negative affect, and this results in a positive outlook (Lawton et al., 1992; Neiss et al., 2007). Carstensen's socioemotional selectivity theory posits that awareness of endings promotes emotional goals, greater emotional control and positive affect (Carstensen, 2006; Carstensen, 1995; Carstensen et al., 1999). These studies suggest that emotional goals change across the lifespan due to a change in social interactions and social relationships (Carstensen, 2006).

Age-related changes in social interactions are important, considering many everyday decisions occur in social situations (Sanfey, 2007) and recent social trends emphasize continued independence throughout old age. This creates a need for maintaining sound decision-making capabilities throughout the lifespan (Finucane et al., 2002). However, there are few previous studies that directly

assess the influence of social interactions on decisions made by older adults. In Chapters 2 and 3, I investigate age-related changes in social decision-making and the impact that age-related changes in emotion may have on economic decision-making.

Aging of the Decision-Making Brain Systems:

Aging results in changes of the prefrontal and subcortical regions of the brain associated with decision-making. For instance, the old show more bilateral PFC activation (Lee et al., 2008) and more anterior insular cortex activation (Lee et al., 2008; Samanez-Larkin et al., 2007) during risky decisions as compared to the young (Lee et al., 2008). Amplification of prefrontal cortical activity may reflect a change in cognitive strategy (Cabeza et al., 2002; Mata et al., 2007; Pachur et al., 2009) or cognitive control (Braver & Barch, 2002) that would influence complex cognitive processing, including decision-making. In addition, older adults show dysregulation in subcortical structures that underlie economic decision-making. The old show less activation of ventral striatum (Samanez-Larkin et al., 2007; Schott et al., 2007; Cox et al., 2008) during reward-based decision-making tasks and less nucleus accumbens (Samanez-Larkin et al., 2010) activity during economic decisions as compared to the young. For example, the old had less striatal activity when presented with cues that reliably predicted monetary rewards, which led to less financial gain by the old as compared to the young (Schott et al., 2007). These data suggest that the old have difficulty in estimating the reward value and this leads to non-optimal outcomes.

Age-related changes in decision-making are related to age-associated changes in brain pathophysiology. The old lose brain grey matter in the prefrontal cortex (Allen et al., 2005; Grieve et al., 2005; Salat et al., 2001; Salat et al., 1999), insular cortex (Resnick et al., 2003; Allen et al., 2005; Good et al., 2001; Tisserand et al., 2004) and amygdala (Allen et al., 2005; Grieve et al., 2005; Salat et al.,

2001). These three regions are implicated in the production of emotional states (Phillips et al., 2001; Rolls, 2006). Age-related changes in emotion processing typically manifest as less amygdala and more prefrontal cortex activity (Roalf et al., in press; Gunning-Dixon et al., 2003; Lidaka et al., 2002). The amygdala has greater activity for positive as compared to negative pictures in older adults, whereas the same stimuli induce equivalent amygdala responses in the young (Mather et al., 2004). Older adults activate frontal regions, but not the amygdala, when exposed to emotional faces, in contrast to young adults who activate the amygdala and temporal-limbic regions, but have little activation of frontal regions for face stimuli (Gunning-Dixon et al., 2003). The amygdala and hippocampus have higher activity to angry faces in the young than the old, whereas in the old, higher activity to anger was found in the insula and prefrontal cortex (Fischer et al., 2005). The amygdala activates in both young and old participants while they matched emotions on angry and fearful faces (positive emotions were not examined; Tessitore et al., 2005). However, younger subjects had relatively more activity in the right amygdala and the fusiform "face region" and the elderly had relatively greater response in prefrontal regions (Tessitore et al., 2005). Older adults have more insula activity while viewing negative emotional stimuli, particularly disgusting stimuli, as compared to the young (Fischer et al., 2005) and similar higher activity in the insula is found during a risky decision-making task (Lee et al., 2008). The amplified prefrontal activity in aging has been considered "compensatory" activity and is related to better memory (i.e., Cabeza et al., 2002), but that relationship is less clear with regard to emotion processing (i.e., Roalf et al., in press). Neuroimaging studies in young adults (Hariri et al., 2003; Johnstone et al., 2007) and electrophysiology studies in rodents and felines (Quirk et al., 2003) show an inverse relationship between activity in the amygdala and regions of the PFC. While these two brain structures share some level of functional correlation, a detailed explanation of their

functional relationship in emotion processing, particularly in aging, remains obscure, although inhibition of the amygdala by the PFC does occur in aging and is related to cortisol secretion (Urry et al., 2006). This relationship may be critical during emotion and emotion regulation which may have a significant influence on decision-making in older adults. In chapter 3, I use event-related functional magnetic resonance imaging in young and old adults to probe age-related changes in the social decision-making neural network.

Summary

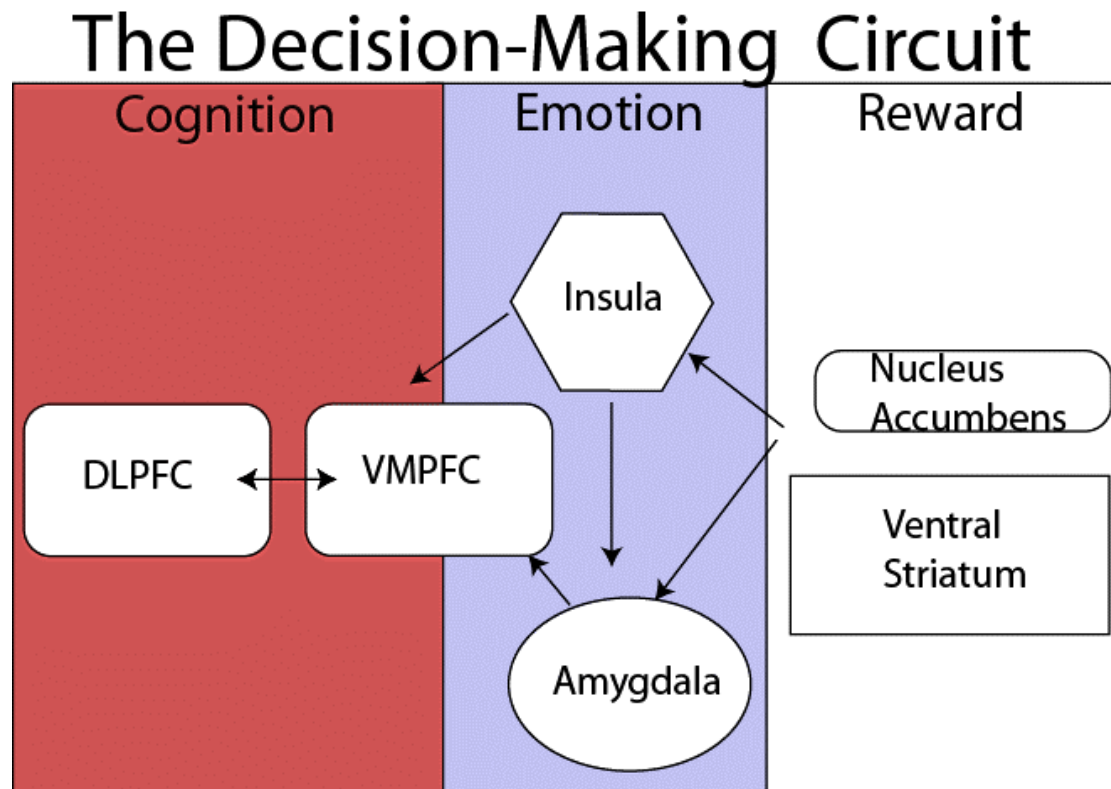
Older adults face complex and life-changing decisions simultaneously with declining neural resources. They base decisions on a lifetime of learning and simultaneously have changes in emotion that may adversely affect decision-making. Understanding the cognitive and emotional factors that influence decision-making among older adults will become especially useful as increasing numbers of Americans reach retirement age. The studies described in this dissertation aim to determine whether the behavioral processes and neural basis of decision-making are altered during the latter stages of life. In the following chapters I assess the effects of aging on non-social and social decision-making and investigate the neural networks supporting social decision-making. *Overall, I suggest that age-related changes in emotion regulation affect decision-making and the brain regions critical for decision-making processes. I believe that the old use an equity rule that is based on changes in emotion processing. This change in decision-making behavior is mediated by an age-related shift towards emotional (i.e., outcome equality) rather than objective goals (i.e., reward maximization).*

Figure Caption

Figure 1:

Simplified decision-making network. Decision-making neural network includes regions associated with reward, emotion and cognitive processing. In general, the nucleus accumbens and ventral striatum are important for reward processing. The amygdala, anterior insula and the ventromedial prefrontal cortex are involved in emotion (i.e., valence, arousal, mood). The VMPFC and DLPFC are critical regions for cognitive functions including executive functions and goal-oriented choice.

Figure 1



DLPFC, Dorsolateral Prefrontal Cortex
VMPFC, Ventromedial Prefrontal Cortex

Chapter 2:

Social equity influences economic decisions in healthy older adults

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Abstract

Little is known about the influence of social interaction on decision-making in the elderly. This study investigated the role of aging in social and non-social economic decision-making. Here we examined self-report measures of risk behavior, and social and non-social economic decision-making in 29 young (21-45 years of age) and 30 older (65-85 years of age) participants. Self-report inventories included the Barratt Impulsiveness Scale (BIS –version 11) Sensation Seeking Scale (SSS) and the Domain Specific Rating Scale (DOPSERT). Social decision-making was assessed using the Ultimatum Game and the Dictator Game while delay discounting decisions were considered non-social decisions. Older adults reported that they engaged in impulsive or sensation seeking behavior less frequently and were less willing to take social risks as compared to the young. Older adults made more equitable divisions of money in the Dictator Game and were more likely to reject unfair divisions of money during the Ultimatum Game leading to lower experimental payoffs as compared to the young. However, young and old adults showed similar patterns of economic decision-making in delay discounting where there was no social component. Thus, these studies suggest the old place emphasis on fairness or equity and this especially affects decisions with a social context.

Keywords: aging, decision-making, emotion, temporal discounting, Ultimatum game

General Introduction

Decision-making is a multifaceted behavior that integrates cognitive and emotional cues about potential rewards. Complex decision-making involves deliberative processes such as determining utility, value and risk, and affective processes such as the assessment of fairness, trust, and the maintenance of social standing (Montague et al., 2006; Berg et al., 1995; Weigelt & Camerer, 1988; Sanfey et al., 2003). Standard economic theories suggest that decisions are made using cognitive, goal-oriented strategies in which the value of all possible outcomes is determined and then a choice is made (Rustichini, 2009). Yet, recent economic theories of social preference show that decision-making requires a balance of goal-oriented choices that maximize one's own reward balanced with the emotional motives of social interactions.

Age-Related Changes in Cognition and Emotion on Decision-Making

Age-related changes in cognition and emotion are well established, however, little is known about their influence on decision-making. Reductions in cognitive flexibility and memory in older adults (Bechara et al., 1998; Bayen et al., 2000) may change the rules or strategies used during decision-making (Mata et al., 2007). In addition, older adults have a positive emotional bias (Charles et al., 2003; Lawton et al., 1992; Leigland et al., 2004; Levenson et al., 1994; Mroczek & Kolarz, 1998) which is the result of altered social-emotional goals (Carstensen et al., 1999). This bias in the old may result in altered outcomes during decisions that involve social interactions. We sought to understand age-related differences in decision-making in the presence and absence of a social component.

The majority of research on decision-making in the old has focused on the role of cognitive dysfunction. For example, older adults are more likely to rely on recent information during financial

decision-making due to memory deficits, as compared with younger subjects (Wood et al., 2005). Older adults are less consistent, use less information (Johnson, 1990), view information longer (Riggle & Johnson, 1996; Johnson & Drungle, 2000; Kovalchik et al., 2005), have more difficulty understanding decision options (Finucane et al., 2005) and show rapid forgetting of the value of options (Wood et al., 2005) when making a decision as compared to the young. These findings are consistent with typical age-related cognitive declines in memory and attention (e.g., Lindenberger & Baltes, 1997; Craik et al., 1990).

While intact cognitive function is critical to effective decision-making in the old, recent research indicates that socio-emotional motivations may be just as, if not more, important (Lockenhoff & Carstensen, 2007; Lang & Carstensen, 2002). Age-related changes in emotion alter the importance of social goals. Older adults experience less negative affect, attend less to negative stimuli, show disproportionately better memory for positive stimuli than for negative or neutral stimuli, and report superior emotional control as compared to younger adults (Charles et al., 2003; Leigland et al., 2004; Mather & Carstensen, 2003; Mather et al., 2004). Socioemotional selectivity theory, one explanation of the emotional changes in aging, proposes that the priority of social goals changes due to the limited time perspective in the old (Carstensen et al., 1999), resulting in greater regulation of emotion (Carstensen, 2006; Carstensen & Lockenhoff, 2003). Despite the fact that social interactions are more demanding to maintain late in life (Rohr & Lang, 2009), older adults show stronger preferences for social partners who are well-known and meaningful to them as compared to the young (Fredrickson & Carstensen, 1990; Fung et al., 2001a; Fung et al., 2001b). Taken together, this evidence suggests that the social-emotional interactions during a decision may differentially affect younger and older individuals.

Economic Theories of Decision-Making

While some traditional economic theories propose that rational decision-making is the result of pure cognitive assessments of the alternatives and of the consequences of a decision (Nash, 1950), most economic models that deal with social interactions do not assume totally selfish preferences (Becker, 1981). Standard economic theories assume that people maximize their own interests when interacting with other individuals (Santos & Chen, 2009). Newer theories based on neuroeconomics and social preference propose that the interaction of cognitive and emotional components better describes real-world decisions (Camerer, 2003; Fehr & Camerer, 2007; Loewenstein et al., 2008). For example, one idea put forth by Loewenstein & O'Donoghue (2004) suggests that choice behavior results from the interaction between an 'affective' and 'deliberative' system. This theory assumes that the affective system is in control of behavior and that the deliberative system modifies choice behavior through effortful cognitive control. This and other theories indicate that decision-makers consider both cognitive and emotional factors (Sanfey et al., 2003; Camerer, 2003). We would expect aging to affect decisions with an emotional component as older adults have alterations in both cognitive and emotional processing.

Decision-making assessments

Behavioral research utilizes an assortment of methods that simulate real-life scenarios to test decision-making theories. Self-report questionnaires assess traits such as impulsivity, arousal and risk perception during hypothetical decision-making scenarios. For example, impulsivity is measured using the Barratt Impulsiveness Scale in which participants indicate how likely they are to engage in a particular behavior (Barratt, 1959; Patton et al., 1995). Another self-report inventory, the Domain Specific Risk Taking (DOSPERT) Scale measures risk-taking and perceived-risk attitudes

(i.e., risk-perception) across five commonly encountered domains (Weber et al., 2002). These measures indicate that decisions differ based upon the situation. For example, financial decisions may be viewed as having more risk than social decisions. This scale has been used in the young, but not in older adults. These questionnaires provide insight into behavioral traits and tendencies that may lead to good or bad decision-making, but they do not necessarily correspond to direct measures of decision making (Oxoby & McLeish, 2006). Impulsivity and sensation seeking questionnaires in the current study have been used in previous studies with older adults. We include these measures in order to draw comparisons of behavioral traits in our sample to findings from past studies.

Experimental laboratory studies of decision-making measure choice behavior for differing options and in a variety of situations. For example, gambling tasks investigate an individual's ability to make advantageous monetary choices in the face of uncertainty (Bechara et al., 1997). Delay discounting tasks measure an individual's preference when weighing rewards that are modified by a potential delay until it is received (e.g. Rachlin et al., 1991; Richards et al., 1999). Effective decision-making in such tasks requires cognitive evaluation of the economic alternatives and are often motivated by self-interest. These decisions are made in social isolation, as the outcomes rarely affect anyone other than the decision-maker (Sanfey, 2009). We will refer to these types of decisions as 'non-social' decisions.

Economic decisions are also influenced by social interactions. Social economic decisions are studied using Game Theory, a collection of models that help to predict the effect of social interactions on decision-making (von Neumann & Morgenstern, 1947). In these games, individuals interact with another person. For example, one person (proposer) may offer another (responder) a

share of \$10, and the responder then decides whether to accept or reject the proposer's offer. Examples of social economic decision-making include the Ultimatum Game (Guth et al., 1982; Thaler, 1988; Bolton & Zwick, 1995; Sanfey et al., 2003; van 't Wout M. et al., 2006; Koenigs & Tranel, 2007) and Dictator Game (Forsythe et al., 1994; Bolton et al., 1998) both of which are also used in the experiments reported here. The results of these games in younger participants show that decisions about monetary reward are affected by social factors and not purely motivated by financial self-interest (Sanfey et al., 2003). For example, younger adults are willing to forgo a small financial reward (i.e., \$1) if they feel they are being treated unfairly by another person (Eckel & Grossman, 1996; Sanfey, 2007). Like standard economic tasks, these games provide a measure of the value that participants assign to alternatives but also provide information about the effects of interacting with another person during a decision (Rilling et al., 2008a). The games that test these models have not previously been used in older adults.

Age-related changes in decision-making

Aging results in changes in decision-making (Deakin et al., 2004). Older adults report less impulsivity (Spinella, 2007; Patton et al., 1995; Stanford et al., 2009) and less sensation seeking (Zuckerman et al., 1978; Roth et al., 2005) as compared to the young. Older adults also show different decision-making outcomes in laboratory measures (Green et al., 1994; Deakin et al., 2004). For instance, some older adults consistently choose less advantageously in terms of expected payoffs than the young on the Iowa Gambling Task (IGT; Bechara et al., 1997; Fein et al., 2007; Zamarian et al., 2008; Denburg et al., 2005). This may be because they fail to recognize the most favorable options, which may indicate age-related decline in executive functioning, or that they employ different decision strategies than the young (Denburg et al., 2005; Zamarian et al.,

2008). Furthermore, good performance on the IGT requires intact learning and memory (Bechara et al., 1997), thus it is also possible that age-related changes in learning or memory result in poorer performance in the IGT. However, older adults do not always perform poorly on the IGT (see Kovalchik et al., 2005; Brand et al., 2007; Lamar & Resnick, 2004; MacPherson et al., 2002; Wood et al., 2005). Older adults also discount the amount of a delayed monetary reward less than the young in a delay discounting task; that is, the old are more willing to wait for rewards (Green et al., 1994), but see (Harrison et al., 2002; Read & Read, 2004). While cognitive decline may cause the old to have difficulty comparing current reward amount to delayed rewards, the direction of this effect on choices is not obvious. In addition, the difference in discounting behavior in older adults is affected by socioeconomic status, as older adults with high income show less discounting than older adults with low income (Green et al., 1996). It is important to acknowledge the age-ranges of these studies vary with respect to what is considered 'old'. For example, some studies report data from individuals as old as 89 years of age (Read & Read, 2004), while others (i.e., Green et al., 1996; Harrison et al., 2002; Kovalchik et al., 2005), including our sample, use on average individuals who are not as old (i.e., mean age approximately 70). To our knowledge, there are no previous studies of social decision-making in older adults.

How do age-related changes in cognition and emotion affect decision-making in different contexts? To answer this question we tested decision-making in younger and older adults using decision-making questionnaires, and social and non-social economic decision-making tasks. We used standard self-report measures of decision-making that have previously been used in the literature in order to compare our sample to previous findings. Furthermore, we complement this

data with additional questionnaire and decision-making tasks where no data is available in the elderly. We hypothesize the following:

1) Self-report measures will indicate that the old are more risk-averse than the young as shown in previous studies; 2) If social-emotional changes affect decision-making, older adults will make less optimal social decisions (i.e. earn less money) as compared to younger adults; 3) If age-related cognitive decline affects decision-making, older adults will make less optimal decisions during both social and non-social decisions as compared to the young. These studies will contribute to the understanding of the role of age-related changes in cognition and emotion on decision-making in older adults.

General Methods

Participants

Participants were 30 healthy older adults (50% male) and 29 healthy younger adults (48% male) recruited from an urban population (see Table 1). Health histories were obtained via phone interview. Inclusion criteria required older individuals be 65-85 years of age and younger individuals be 21-45 years of age. These age brackets permitted recruitment of healthy people that significantly differed in age but had experienced relatively comparable life styles including education and employment. All participants understood English and had adequate hearing and vision (with correction if necessary) to view computer and paper-pencil tasks. Older and younger participants did not differ on the vocabulary sub-test of the Wechsler Adult Intelligence Scale-Revised (Table 1). This sub-test provides a standardized approximation of functional intelligence and is highly correlated with IQ (Wechsler, 1981). It controls for cohort-related differences in education environments. Estimates of current income were not

normally distributed. The old reported significantly greater income as compared to the young (Mann-Whitney U, $Z = -2.91$, $p = .004$), thus analyses for all decision tasks were adjusted by using income as a covariate.

-----Insert Table 1 here-----

Participants were excluded if they had a self-reported history of neurological problems (e.g., stroke, seizure, or head trauma), significant medical problems (e.g., uncontrolled hypertension), current or previous psychiatric conditions (e.g., schizophrenia), or current use of medications likely to affect mood or cognition such as anti-anxiety agents. The Mini-Mental Status Examination (MMSE; Folstein et al., 1975) and Geriatric Depression Scale (GDS; Sheikh et al., 1991) were used as screening measures to exclude older participants with possible dementia ($MMSE < 26$) or depression ($GDS > 10$). However, no older participants had abnormal MMSE or GDS scores. This study was approved by the OHSU IRB and all participants provided written informed consent.

The number of participants that completed the decision-making measures in each experiment varied slightly, hence the number of participants is noted for each experiment. These subgroups of older and younger participants were matched for the same variables as the entire sample described above. Effect sizes for results of all decision questionnaires and tasks are reported in Supplemental Table 1.

Payment Procedure

Participants were paid \$10 in cash for participation, however in order to make the economic and risk nature of the tasks realistic, participants were informed that additional compensation could be earned based on their performance. Participants were reminded they

were playing for actual money before beginning each task and were informed of their total earnings at the completion of all decision-making tasks. The additional compensation was a one-time payment based on the earnings from a randomly drawn trial from the test session. Others have shown that immediate, in hand, rewards are over-weighted due to a certainty effect (Hertwig & Ortmann, 2001; Kahneman & Tversky, 1979). Therefore, this additional payment was mailed to participants after the completion of the study visit so as not to influence performance. The order of task performance was randomized across participants.

Experiment 1: Decision-making scales

We used self-report questionnaires of impulsivity, sensation seeking and risk-taking to examine age-related changes in factors that influence decision-making. Given that the Barratt Impulsiveness Scale and the Sensation Seeking Scale have previously been used in older adults we can use these measures to confirm that our older and younger groups report similar levels of impulsiveness and sensation seeking as in previous studies. To our knowledge the DOSPERT has not been used to compare younger and older individuals self-reported risk taking and will thus add to the literature in this area. These measures were selected as they are well validated and commonly used to assess behavioral and personality states/traits that may relate to real-world decision-making. Thirty older and 28 younger participants completed the decision-making questionnaires.

Barratt Impulsiveness Scale

The Barratt Impulsiveness Scale, Version 11, is a reliable self-report measure in which a participant rates 30 items on a 4-point scale from rarely/never to almost always/always (Patton et al., 1995). Higher scores indicate higher levels of impulsivity. The scale consists of three

higher-order factor-based dimensions: attentional impulsivity (i.e., rapid shifts in attention or impatience with complexity), motor impulsivity (i.e., acting in an immediate, spontaneous manner), and non-planning impulsivity (i.e., absence of considering long-term consequences). The total and subscale scores were used as outcome measures. This scale has been used in young and older populations and shows that the old engage less in impulsive behavior (Spinella 2007; Patton et al., 1995; Stanford et al., 2009).

Sensation Seeking Scale

The Sensation Seeking Scale (SSS) Form V was used to measure the tendency to seek out intense sensory experiences (Zuckerman et al., 1964). Internal consistency, convergent validity, and the reliability of the SSS and the subscales have been previously established (Zuckerman et al., 1978). The total score, which is composed of the scores from subscales that measure experience seeking, thrill seeking, disinhibition, and boredom susceptibility was used as the outcome measure. Higher scores indicate greater tendency to take risks in order to seek out novel, stimulating experiences. Previous studies indicate that older adults have reduced sensation seeking behavior (Zuckerman et al., 1978; Roth et al., 2005) and less need for stimulation (Roth et al., 2007).

Domain Specific Rating Scale (DOSPERT)

The Domain-Specific Risk-Taking (DOSPERT) scale was used to assess self-reported risk-taking and perceived risk of an activity. The scale has been used and validated, and its factor structure replicated in a wide range of settings and populations (Blais & Weber, 2006), however to our knowledge has not been used to directly compare risk-taking in younger and older adults. In addition, prior studies using these measures have not compared responses to

laboratory measures of decision-making. Use of the scale will provide new information about risk-taking and risk-perception across multiple domains. It contains five common decision domains, 1) ethical, 2) financial, 3) health/safety, 4) social, and 5) recreational (Weber et al., 2002). The Total Score for reported risk-taking and perceived riskiness were used as the main outcome measures, followed by exploratory analyses on the domain sub-scale scores.

Data Analysis

Separate independent sample t-tests were used to test age effects on total scores in Barratt Impulsiveness and Sensation Seeking Scales. Exploratory between-group t-tests were used to investigate subscale scores. Repeated-measures analysis of covariance (ANCOVA) was used to examine group differences for risk-taking and risk-perception for the different domains on the DOSPERT scale (Weber et al., 2002). Current income was used as a covariate. For all three experiments, homogeneity of variance was confirmed using Levene's test and values below $p=0.10$ were considered significant violations. Corrected degrees of freedom are shown to the nearest whole integer. The two-tailed significance threshold was $\alpha = 0.05$ and Bonferroni corrections were applied to correct for multiple comparisons in the DOSPERT (corrected $\alpha = .01$). Results in the Barratt Impulsiveness and Sensation Seeking Scales remained the same when the data was adjusted for income level. Effect sizes for each questionnaire are reported in Supplemental Table 1.

Results

Barratt Impulsiveness and Sensation Seeking Scales

Younger participants reported higher levels of impulsive behavior ($t(56)=2.16$, $p=.04$; Table 2a) as compared to the old. The young reported greater motor planning

[$t(56)=2.12, p=.04$] and marginally greater non-motor planning ($p=.09$) impulsiveness, but equivalent attentional impulsivity as compared to the old. The young reported higher sensation seeking total scores ([$t(56)=4.68, p<.01$]; Table 2b) and had higher scores on all subscales (all p 's $< .05$) as compared to the old.

Domain Specific Rating Scale (DOSPERT)

Results from the DOSPERT are presented in Figure 1. The young reported more risk-taking behavior than the old [$F(1,56)=22.08, p<.001$]. Risk-taking behavior differed across domain [$F(3,182)=68.43, p<.001$]. There was an interaction between age group and decision domain [$F(3,182)=9.39, p<.001$]. The young reported greater risk-taking in Health Safety [$t(56)=4.42, p<.01$], Recreation [$t(56)=5.12, p<.01$] and marginally more Social ($p<.02$, uncorrected) and Ethical ($p=.06$, uncorrected), but not Financial ($p=.22$) risk-taking as compared to the old (Figure 1A). Within group ANOVAs revealed that both the young ([$F(4,108) = 36.59, p<.01$] and old [$F(3,88)=41.32, p<.01$] reported significant differences in risk-taking behavior across decision domains. The young reported the greatest risk-taking during Social and Recreational decisions, the least during Ethical decisions (Ethical $<$ Financial, Health Safety $<$ Recreation, Social; all $ps<.01$). The old also reported the greatest risk-taking for Social decisions, the least risk-taking for Ethical decisions, but similar levels of risk-taking for all other domains (Ethical $<$ Financial, Health Safety, Recreation $<$ Social; $p<.01$).

-----Insert Figure 1 here-----

The old perceive more risk in activities than the young [$F(1,56)=29.08, p<.01$]. Risk perception also differed across domains [$F(4,197)=143.31, p<.01$]. There was an interaction between age group and domain [$F(4,197)=7.92, p<.01$]. The old showed more risk-perception

in Financial [$t(40)=3.48, p<.01$], Health Safety [$t(56)=5.94, p<.001$], Recreation [$t(56)=5.26, p<.01$], and Ethical [$t(56)=2.84, p<.01$] decisions but not for Social decisions ($p=.86$) than the young (Figure 1B). The young ($[F(3,77) = 40.32, p<.01]$) and old ($[F(4,116) = 129.52, p<.01]$) showed a significant difference in risk-perception across decision domains. The young showed the same pattern as the main effect for domain (Social < Recreation < Health Safety, Financial, Ethical); $ps<.01$). The old showed lowest risk perception for Social decisions as compared to all other domains, and Financial and Health Safety decisions were perceived to have greater risk than Ethical and Recreational decisions (Social < Recreation, Ethical < Financial, Health Safety; $ps<.01$).

Discussion

This is the first study to show that age-related changes in self-reported risk behavior are domain dependent. The old engaged in impulsive or sensation seeking behavior less than the young, as reported in previous studies. They also reported taking fewer risks and perceived activities as more risky than the young. However, differences in risk-taking and risk-perception were domain dependent. The young reported more risk-taking behavior than the old in Health/Safety and Recreation activities but not during Social, Ethical or Financial decisions. On the other hand, the old perceived more risk than the young in all decision domains except for Social decisions.

Taken together, these findings confirm prior reports that aging lowers impulsiveness, sensation seeking and increases risk aversion [(Zuckerman et al., 1978; Roth et al., 2005) but see (Ball et al., 1984; Spinella, 2007)]. Lower Barratt Impulsiveness scores indicate that the old are less inclined to engage in behaviors that involve risk. Lower sensation seeking in the old indicates a decline in the need for physiological arousal, novel experience, and/or less

willingness to take risks to obtain such arousal as compared to the young (Bardo et al., 1996; Zuckerman, 1979; Zuckerman, 1994). These data indicate that younger and older participants in this study self-report similarly to previous decision-making questionnaire studies.

The DOSPERT, which has not been previously used to compare younger and older adults, indicates more risk perception and less risk-taking in the old as compared to the young. First, decisions about Health/Safety and Recreation indicate a risk-aversion pattern. The old showed increased risk perception and correspondingly less risk-taking for these decisions as compared to the young. This is not surprising given that older adults are more likely to suffer from poor health and are less likely to engage in physical activity (King et al., 1998).

Interestingly, they perceived more risk in Financial and Ethical decisions than the young, but reported similar risk-taking behavior as the young. Thus, risk-taking in these domains in the old is not being fully guided by perceived risk, perhaps because of their generally higher income or they may simply have more experience with these types of decisions as compared to the young. It may also reflect the saliency of these domains in aging. For instance, both younger and older adults pay more attention to decision when they involve complex financial choices (Hershey & Wilson, 1997), and thus may be keenly aware of potential risks in financial domains. Finally, social decisions are the only domain in which the old reported equivalent risk-perception and marginally less risk-taking behavior than the young. Older maybe less likely to take risks during social decisions as compared to the young due to age-related increases in the importance of close social relationships (Lang & Carstensen, 2002). It is possible that due to a change in life goals the old place more of an emphasis on meaningful social interactions than the young and that they are less willing to disrupt those social bonds (Lang & Carstensen, 2002). This age-

related difference in reported risk-taking should be followed up experimentally with direct investigations of social risk taking. Taken together, these data indicate that the current sample of older adults is comparable to previous reports of impulsive and sensation seeking tendency and suggest that aging differentially affects social decision-making.

However, the interpretation of these data should proceed with caution. First, it is unclear whether these are measures of the current state of an individual or a persistent trait. Thus, it is possible that these measures may fluctuate for any given individual, particularly over time. Longitudinal studies of these measures are necessary to elucidate this issue. Furthermore, it is unclear how appropriate these questionnaires are for older adults. Typically, these measures are validated on large groups of young to middle age adults. Thus, it is possible that some of the questions may contain irrelevant content or be worded in a manner that is inappropriate for those 65 years of age or older. Thus, validation studies of these measures in older cohorts are warranted.

Experiment 2: Social Economic Decision-Making

This study examines the effects of aging on decision fairness using the Ultimatum (Guth et al., 1982; Thaler, 1988; Bolton & Zwick, 1995) and Dictator games (Hoffman et al., 1994; Forsythe et al., 1994; Bolton et al., 1998). In the Ultimatum game, one player (proposer) offers a split of a sum of money. The other player (responder) decides whether to accept or reject the offer. Accepted offers are divided according to the proposal; rejected offers result in no money for either person. Economic models predict that if people are purely motivated by financial self-interest then responders should accept any non-zero offer, and knowing this, proposers should offer the smallest amount possible (Forsythe et al., 1994). However, these outcomes

are rarely seen in practice. Many responders reject offers of 30% or less, almost all reject 10% and proposers typically offer a 40-50% split (Rilling et al., 2008b). This common rejection of “unfair” offers by responders in the Ultimatum game indicates that people will forgo financial gain, or pay to punish unfairness (Camerer & Thaler, 1995; Thaler, 1988). This action by responders corresponds with the idea of fairness equilibrium (Rabin, 1993), which indicates that people are motivated by the fairness that others show. If responders think that low offers are unfair, they will retaliate by rejecting such offers, punishing a proposer for his/her actions (Rabin, 1993).

Given the possibility of rejection, even a selfish proposer has some incentive to make a large offer in the Ultimatum game. The Dictator game gives a purer measure of giving behavior or altruism (Bolton et al., 1998). In this game one player (dictator) decides how to distribute a sum of money between him/herself and another anonymous person. The second player cannot punish the proposer. Economic models predict that if people are purely motivated by financial self-interest then they should maximize their earnings by keeping most, if not all, of the money for themselves. However, this is rarely seen. For example, young adults give away more money than expected, with the modal amount being about 30 percent of the total (Bolton et al., 1998). Thus, this game has been cited as a negation of the rationally self-interested individual model of economic choice (Henrich et al., 2005). It also indicates that people do not want to be seen as greedy by others (Bolton et al., 1998). Hypotheses are that people are guided by “other-regarding” interests (Forsythe et al., 1994) or that they have an aversion to making an unfair decision. Thus, people have concerns about monetary gain as it relates to behaving in a socially appropriate manner (Cason & Mui, 1998). It is not known how age affects decision-making in

either the Ultimatum or Dictator games of social economic decision-making. Based on changes in social-emotional processing (i.e., positivity bias) we hypothesize that older adults would be more willing to accept low, unfair offers in the UG as compared to the young as they would be less responsive to unfair (i.e., negative) offers. In the DG, we hypothesize that older adults would be more likely to share the sum evenly as compared to the young as a means to maintain positive social-emotional feelings.

Participants:

Thirty elderly and 29 younger participants acted in the role of responder.

Procedure:

Ultimatum Game

We used a version similar to that employed by Sanfey et al., (2003). The game is played between a proposer, played by the computer, and a Responder, played by the participant. In this game, the proposer (computer) proposes a split of a sum of money that is either accepted or rejected by another, the responder. If the proposal is rejected, neither player gets any money. Participants played the game with 50 novel computer-generated proposers, who were depicted by a photograph and proposer's name on the screen (Minear & Park, 2004). Participants were told that responses with one proposer would not affect subsequent interactions (Figure 2). All participants saw the same set of offers. Ten dollars was proportionally divided on every trial (e.g., "Joe 1 keeps \$8" and "You receive \$2"). The offers varied: 20% of offers were split evenly (\$5:\$5), 60% of offers were moderately unequal splits (\$6:\$4, \$7:\$3), and 20% of offers were extremely unequal splits (\$8:\$2, \$9:\$1). Five practice trials exposed participants to one of each offer type and ensured the participants understood the task.

-----Insert Figure 2 here-----

Dictator Game

The version of the Dictator Game used was similar to previous studies (Bolton et al., 1998). The Dictator Game is played between a proposer and a responder. The proposer decides how much of a \$10 endowment to keep for themselves and how much to give the unknown responder. Participants played the role of proposer and saw all possible whole-dollar combinations by which \$10 could be divided and made their selection on a computer. Participants were tested alone and were told that their decision would affect another participant already enrolled in the study. Participants were labeled as “generous” (keeping less than half of \$10), “fair” (keeping \$5 and giving away \$5) or “greedy” (keeping more than half of \$10). Dictator game data was not collected from three elderly due to computer error.

Data Analysis:

A 2 X 5 (Group X Offer) mixed model repeated-measures analysis of variance was used to examine group differences in the acceptance rates of offers during the Ultimatum game. Bonferroni corrections were applied to correct for multiple comparisons in the UG (corrected alpha = .01). Chi-square analyses were used to determine the number of participants in each age-group offering equal (\$5:\$5) or unequal shares of the \$10 endowment in the Dictator game. In addition, between-group t-tests were used to compare the average offer amount. Correspondence between Ultimatum and Dictator game responses was analyzed using a contingency table. “Unfair acceptors” were those with average acceptance rates above 50% for the most unfair offers (\$2:\$8 and \$1:\$9) while “Unfair rejecters” were those with average acceptance rates equal to or below 50% for these unfair offers. It was then determined how

many “Unfair acceptors” or “Unfair rejecters” were classified as “greedy”, “fair”, or “generous” during the Dictator game. Fisher’s exact test was used to analyze this data. All results remained the same when the Ultimatum and Dictator game data were adjusted for income level. Effect sizes for the UG are reported in Supplemental Table 1.

Results

Ultimatum Game

The young accepted more offers than the old [$F(1,57)=6.15$, $p=.01$, Figure 3A]. Acceptance rates were affected by offer amount [$F(2,140)=49.12$, $p<.01$]. Acceptance of offers declined based on their divergence from equality ($\$5:\5 and $\$4:\$6 > \$3:\$7 > \$2:\$8 > \$1:\9 ; all $p's<.05$). The interaction between the offer amount and age was not significant ($p=.15$), however, in an exploratory analysis of only unfair offers, the old rejected offers that slightly deviated from equity more so than the young, [$\$4:\6 ($p=.06$) ; $\$3:\7 $p<.01$] but with increased divergence from equity, age differences weakened [$\$2:\8 ($p=.13$), and $\$1:\9 ($p=.08$;Figure 3A)] suggesting that both old and young reject obvious inequities. In addition, there were no age-group differences in median reaction time for each offer type. In all, ten younger and seven older participants accepted all UG game offers. Removal of these participants from the analysis did not change the pattern of results.

-----Insert Figure 3 here-----

Dictator Game

Younger ($M\pm SD$, 4.00 ± 2.51) and older (4.23 ± 1.70) adults made similar average offers. The young were just as likely to distribute funds equally (“fair”) as unequally (“generous” or “greedy”). The old were more likely to distribute funds equally than unequally ($\chi^2(2)=31.67$, $p<.001$; Figure 3B). Two

young participants were “generous”, as they gave more to another than keeping for themselves (e.g., \$0 for me, \$10 for you), but no old participants behaved in this manner. The difference between old and young remained significant when “generous” responders were removed from the analysis.

Correspondence between Ultimatum and Dictator Games

There was no correlation between Ultimatum and Dictator game responses for either the young ($p=.34$) or older participants ($p=.15$). However, as the results above show, the young do accept smaller offers in the Ultimatum game, and they make smaller offers in the Dictator game.

Discussion

To our knowledge this is the first study to show that young and old differ during social economic decision-making games. Younger and older adults decrease acceptance rates as offers become more unfair, but overall the old accept fewer offers than the young. Differences in acceptance rates are particularly noticeable at offers that slightly deviated in equity (e.g., \$4:\$6 & \$3:\$7). The old rejected offers with even slight inequities. The young have a 50% acceptance rate for the most unfair offer (\$1:\$9), which is comparable to many previous Ultimatum game experiments (see Camerer, 2003), however, the average acceptance rate for older adults is substantially lower (29%), although not statistically different than the young. When the roles are reversed and participants are asked to divide a sum of money in the Dictator game, older adults are more likely than the young to evenly split the money. These results imply that the old attempt to maintain fairness during social interactions, whereas the young are less guided by fairness rules. However, it does not appear that an individual’s view of fairness when accepting offers is related to their generosity when giving money away as the correspondence analysis was not significant. Overall, these differences may be due to age-related changes in the affective or deliberative systems required for effective decision-making.

Age-related changes in emotion processing may result in greater rates of rejection of unequal monetary offers. This may occur due to an increase in inequality aversion in the old. Inequality aversion asserts that people find unequal outcomes aversive and people employ a fairness rule that rewards or sanctions fair or unfair behavior, respectively (Bolton & Ockenfels, 2000; Fehr & Schmidt, 1999). Thus, if a proposer decreases a responder's reward to his/her own benefit, the responder will reject this offer due to an aversion to unfairness, even if it results in less reward for the responder. We see this pattern of responding in our study as both young and old participants rejected more offers as the inequity became greater. However, the old appeared to be more sensitive to inequity as they rejected more unfair offers and offers with minor deviations in fairness more than the young. Furthermore, older adults are less likely to make Dictator game offers that are unequal as compared to the young. This interpretation of the data suggests that older adults have an increased negative emotional response to social decisions that result in inequity. This corresponds to a recent fMRI study which indicates that the old, as compared to the young, make fewer risky choices while showing greater activity of the insular cortex, a region that responds to aversive stimuli (Lee et al., 2008, but see Samanez-Larkin et al., 2007). This explanation, however, is in contrast to typical age-related emotion processing changes. In general, the old have a positivity bias (Carstensen et al., 2000) where they focus less on the negative and more on the positive (Charles et al., 2003; Leigland et al., 2004; Mather & Carstensen, 2003; Mather et al., 2004). If age-related changes in emotions affect social decisions in a similar manner, we would expect older adults to view unfair outcomes less negatively than the young, but they do not. Rather, this suggests that traditional age-related changes in emotion processing do not influence social decisions, but a heightened aversive response to inequity better explains choices made by the old.

Alternatively, rejection of unequal monetary offers and forgoing monetary rewards in the old may be the result of over-reliance on decision rules during decision-making. In our study, older adults appear to make decisions in both the Ultimatum and Dictator game that were focused on the equity of an offer. It is possible that the old tend to use the simplest and most salient strategy, which is to employ a fairness rule, and may be based on aversive emotional responses. The old fail to adopt a strategy that maximizes their potential monetary return, and this is similar to behavior seen in other decision-making studies (Denburg et al., 2005; Zamarian et al., 2008). The use of decision rules, or heuristics, reduces the cognitive burden of evaluating choices by focusing the decision-maker on the most promising strategies (Kahneman & Tversky, 1979). In general, older adults are more likely to use heuristics (Johnson, 1990), use different heuristics (Peters et al., 2007) and select simpler decision strategies (Mata et al., 2007) as compared to younger adults. In fact, studies of decision strategy in older adults suggests that the old prefer to use simple strategies or knowledge from previous experiences both of which require less integration of information when making decisions (Mata, 2007; Johnson, 1990). Thus, it is possible that emotional (i.e., aversive) information is more salient to older adults than younger adults when making social decisions, which leads them to use a different decision rule than the young. Thus, age may change the implementation of decision rules/heuristics, at least with respect to fairness in social decisions.

Experiment 3: Non-social Economic Decision-Making: Delay Discounting

Decision-making often involves comparing outcomes that differ along several dimensions such as choice patterns between smaller, more immediate gains and larger, delayed gains (Rachlin et al., 2000; Richards et al., 1999). A common procedure involves estimating the subjective value of a larger, delayed monetary reward by identifying the amount at which

individuals are indifferent between a smaller, immediate amount of money and a larger amount money that is received only after a delay (Mitchell & Wilson, 2010). This procedure, known as delay-discounting, requires an individual to make choices for only him/herself without interaction with other participants. Thus, here we consider it to be a non-social decision task.

Participants:

Twenty-five older and 29 younger participants completed this experiment.

Procedure:

The version of the Delay Discounting Task was similar to prior studies (Hoffman et al., 2006; Mitchell, 1999; Mitchell & Wilson, 2010). The task involved choices between \$10 at some future date, or some smaller amount of money without the substantial delay (for example question see Figure 4). Questions were presented in random order on a computer. Participants indicated their preference with a mouse button press. Participants were presented with questions one at a time on a computer screen and indicated which of two items they preferred: delayed or nearly-immediate money. The delayed money was \$10.00 available after one of six delays (1, 7, 30, 90, 180 or 365 days). The “nearly-immediate” money (\$0.00, \$2.50, \$5.00..... \$10.50) was available the next day, and each subject saw all permutations in random order. We used real rewards with real delays (Chabris et al., 2007; Chabris et al., 2007). We did not use a truly immediate option, as other studies have shown that immediate, in hand, rewards are over-weighted due to a certainty effect (Hertwig & Ortmann, 2001; Kahneman & Tversky, 1979) and there is some evidence that immediately available rewards preferentially engage emotional processing (McClure et al., 2004; McClure et al., 2007). At the conclusion of

the experimental test session one trial was randomly selected and that outcome was realized. For example, if the participant randomly chose a trial on which he/she selected to receive \$2.50 in 1 day, the money was mailed the following day, if the participant chose to receive \$10 in 365 days, the money was mailed to them one year after the test day.

The indifference point was calculated for each participant and each delay (e.g., Rachlin et al., 1991). The indifference point is the value at which preference switches between the nearly immediate and delayed rewards. This point was operationally defined as being midway between the smallest value of the nearly immediate alternative accepted and the largest value that was rejected (see Mitchell, 1999). A hyperbolic equation was fitted to each participant's indifference point using the Solver subroutine in Microsoft Excel 2007:

$$\text{Equation 1: } V = M / (1 + kD)$$

where V represents the value of the delayed item indexed by the indifference point, M represents the amount of money available from the delayed alternative item (e.g., \$10.00), D represents the length of the delay, and k is a fitted parameter indexing the rate of discounting with lower indifference points indicating less tolerance for delayed monetary rewards (more preference for the immediate reward; Ainslie, 1992; Mazur & Coe, 1987; Rachlin et al., 1991; Raineri & Rachlin, 1993; Mitchell, 1999).

Goodness of fit (R^2) for the hyperbolic function and area-under the curve (AUC) was also determined.

-----Insert Figure 4 here-----

Data Analysis

Group differences in the indifference points were analyzed with a mixed-model ANOVA with delay as a within-subjects factor and age-group as a between subjects factor. In addition, t-tests were used to compare age-effects on log transformed k -values, the goodness of fit for

the hyperbolic delayed function and AUC. Post-hoc t-tests were used to compare age-effects at each delay interval. All results remain the same when the data was adjusted for income level.

Results

Age did not affect delay discounting (Figure 5) as measured by the indifference points ($p = 0.23$), nor did age affect k values ($p = 0.40$). Overall, indifference points decreased as delay interval increased [$F(5,265) = 101.66, p < 0.001$]. There was not a significant interaction between delay and age group ($p = 0.12$). Exploratory between-group comparisons indicated that older participants were less willing to wait for a monetary reward at the longest delay interval (365 days) as compared to the young [$t(52) = 2.05, p < .05$, uncorrected], but not at any other delay interval. These data remained the same when individuals (3 young and 1 old) that exhibited nonsystematic discounting were removed (i.e., an indifference point larger than the indifference point for the next smallest delay by more than 20% or a ‘non-discounter’; Johnson & Bickel, 2008; Mitchell & Wilson, 2010). The hyperbolic discount function fit (R^2 values) the indifference point curves similarly for the young and old ($p_s > 0.12$). Finally, we calculated AUC as a function-free measure of discounting (Myerson et al., 2001). There was no age group difference in AUC measures (k -values, AUC and R^2 data are shown in Supplemental Table 2).

-----Insert Figure 5 here-----

Discussion

Temporal discounting of real rewards in the young and old was similar. The young and old did not differ in indifference points or discounting rate. Exploratory analysis showed that the old discounted the reward value more than the young when the reward was substantially delayed (365 days). A hyperbolic discounting function fit the indifference points well for both

groups. A function-free measure of discounting also showed no difference between the young and old. Thus, it appears that the ability to weigh the value of economic alternatives on the basis of reward and delay is not affected by aging.

Our data confirm the view that discounting behavior is similar in younger and older adults and implies that the cognitive processes used to make delay-discounting choices are intact in older adults (Green et al., 1996). Younger and older adults prefer outcomes that occur sooner, rather than later. However, if the amount available sooner is substantially small or if the delay to the large reward is long both young and old adults adjust their choices. Recent neuroimaging studies of younger subjects suggest that long-run patience for a reward during delay discounting is mediated by the lateral prefrontal cortex and associated structures, which support higher cognitive functioning (McClure et al., 2004). These brain regions evaluate the properties of abstract rewards, including the amount of time until a reward is available (McClure et al., 2004). There is evidence that the lateral prefrontal cortex is more active in the old than the young during cognitively demanding tasks including decision-making (Grady et al., 1994; Cabeza et al., 1997; Rypma & D'Esposito, 2000; Persson et al., 2004). If this is the case during delay discounting, an increase in activity may reflect nonspecific recruitment in older adults based on the difficulty of the task (Logan et al., 2002) or it may reflect a compensatory mechanism (Cabeza et al., 2002; Grady et al., 2005) leading to similar outcomes as the young. However, the underlying mechanism for this behavior has not been thoroughly investigated in older adults and neuroimaging studies of delay discounting are necessary to elucidate potential mechanisms.

These results are in contrast to previous studies in which the old discounted more than the young (Green et al., 1994; Read & Read, 2004). The old discount more when asked to hypothetically compare fewer but immediate vacation/sick days to more but delayed vacation/sick days (Read & Read, 2004). A similar result was found for real monetary choices (Harrison et al., 2002). Thus, it is possible that age does result in changes in discounting particularly if what is being discounted is a substantial amount of money (i.e., hypothetical \$10,000) or something that has other incentive value (i.e., vacation). Again, changes in social-emotional well-being may affect older adults willing to wait for items/events that have strong emotional components (i.e., vacation to spend time with friends/family). It is important to note that the methods of these previous studies differ in subtle ways from ours. For example, some studies used hypothetical outcomes (Green et al., 1994; Read & Read, 2004) as opposed to our real outcomes, and this can result in different choice patterns (Edwards, 1953; Slovic, 1969, but see Reynolds, 2006). The age ranges of the study populations also differ, ours being older than prior studies, which may lead to the different findings. Finally, we adjusted for income when comparing discounting rates in the two age groups and like other studies (Green et al., 1996), which may better explain differences found between younger and older adults in other studies (i.e., Green et al., 1994). In summary, our results suggest that, in general, age does not alter the assessment of the value of economic alternatives on the basis of costs (e.g., delay) and benefits (e.g., money), at least when there are no social consequences of the decisions.

Across Task Correlations:

Pearson correlations across questionnaire and decision tasks for all participants are presented in Supplemental Table 3. All correlation coefficients reported are uncorrected. In

general, the questionnaire measures were correlated with each other. In addition, higher average acceptance rates in the UG were correlated with higher SSS and higher total DOSPERT risk taking scores. Delay discounting (k-values) did not correlate with questionnaire measures or performance on the UG. Pearson correlations were used to compare performance across decision tasks for younger and older adults, separately. Barratt impulsiveness, Sensation Seeking, and DOSPERT scores did not correlate with any other measures within young or older adults. Performance on social and non-social decision-making tasks did not correlate with each other for younger or older adults.

General Discussion

This study used behavioral measures to examine the effects of aging on decision-making. The study yielded three main findings. First, self-report measures confirm that older adults report being more risk-averse as they engage in impulsive or sensation seeking behavior and are less and are less willing to take social risks as compared to the young. These data provide evidence that the sample of older adults in the current study is comparable to previous studies of decision-making. However, these self-report measures do not correspond well with performance on decision-making tasks, indicating that self-report and laboratory evaluation of decision-making measures separate constructs. Second, this is the first study to show that older adults weigh decision fairness more than financial gain during social decisions. The old reject more unfair monetary offers and retain less money as compared to the young. Finally, young and old adults show similar patterns of decision-making during non-social economic decisions, indicating that they weigh financial rewards similarly to the young, at least when they

do not contain social interaction. Taken together, these findings suggest the old focus more on social equity while the young focus on reward outcomes during economic decisions.

These data confirm previous findings that the old have higher risk-aversion and similar decision-making during delay discounting as compared to the young, and adds new insights about importance of social interactions on decision-making. It is not that age universally affects decision-making, but that the context in which decisions are made fundamentally changes the nature of those decisions. The similarity of non-social decision-making between young and old in combination with the difference in social decision-making suggests that one important effect on decision making in aging is social context. We suggest that age-related changes in cognitive evaluation of social decisions alter the use of decision rules, which affects the perception of fairness during social decisions.

Why does aging affect social economic decisions more than non-social decisions? Non-social (i.e., McClure et al., 2004; McClure et al., 2007; Knutson & Bossaerts, 2007) and social economic decisions (Sanfey et al., 2003; Loewenstein & Small, 2007) both require integration of cognitive and emotional information when making a choice. However, the context in which these decisions are made differs. Non-social decisions are often made in isolation as the outcomes mostly affect the decision-maker. However, social economic decisions require sophisticated perception and reasoning about motivations of other players (Rilling et al., 2002) while integrating that information with the cognitive evaluation of options and possible outcomes. Less self-reported social risk-taking in older adults indicates that they may have more trouble deciphering social cues or that social interactions are more flexible as compared to the young. This may lead the old to fall back on experiential knowledge-based strategies,

such as employing a 50/50 equity rule, instead of evaluating and integrating social and cognitive information about potential rewards when making a decision.

The interpretations of these results are tempered by a few limitations. First, we do not know how lifetime experience affects decision-making and social interaction. Older participants likely have more experience with particular decisions or social interactions. This may affect decision strategy used by the older adults. Future studies in older adults may consider a debriefing in which participants are asked about their particular strategy as well as asking older adults what strategy would result in the maximization of reward. We do not know how aging affects social expectations (Sanfey, 2009), social norms or motivation toward small amounts of money (Brown & Ridderinkhoff, 2009). However, we tried to control motivation by 1) reminding participants that they were playing for actual money before each task; 2) only paying subjects a small show-up payment; and 3) informing participants that additional compensation could be earned based on their performance. In addition, the old value money similarly to the young as evidenced by equivalent discounting performance. Thus, it is unlikely that motivational issues cause the age-related findings in the social economic decision tasks. Future studies might investigate whether the young and old have similar expectations during social decision-making and whether manipulation of expectation affects social decisions similarly (See Chapter 4). Manipulation checks to verify that participants believed the decisions made on the computer were impactful upon real people would also aid the current interpretations. The lack of correlation between questionnaire and decision-making tasks, and within decision-making tasks, suggests that these tasks assess unrelated features of decision-making. These findings are not unique and suggest that these measures may not evaluate the same specific behavioral trait, but rather unique components of decision-making behavior (McLeish & Oxoby, 2007; Scheres & Sanfey, 2006; Eckel & Grossman, 1996).

In addition, the lack of correspondence between responses in the Ultimatum and Dictator games suggests the implementation of fairness rules depends upon the decision situation. This is not surprising as previous studies have shown little or no correspondence between these two games (Scheres & Sanfey, 2006) and that context in which the game is played is central to performance (Eckel & Grossman, 1996). Finally, the authors acknowledge that the effects observed in the current study are modest due to the limited sample size and relatively small effect sizes.

Further studies at the intersection of emotion and cognition during decision-making in the old are needed to fully understand decision-making in aging. For example, studies that directly manipulate affect (i.e., mood induction) or increase cognitive burden during social decisions would add valuable insight. Follow-up studies that employ neuroimaging may reveal the neural basis of age-related changes in emotion or cognition particularly for social decisions. Finally, there are other decision models, such as reciprocal fairness, that may also help explain our findings and should be further explored in future studies.

In conclusion, this study found dissociation between social and non-social economic decision-making in aging. The unique aspect of this study is that we show that age modulates social decisions, but not non-social economic decisions. This may be due to the greater sensitivity to deviations of equity in the old during social interactions and we suggest this is due to changes in the cognitive implementation of decision rules during social decisions, not age-related changes in emotion-processing. It is important that we understand the factors that influence decision-making, as older adults make a myriad of critical decisions such as choosing health-care options for themselves and loved ones. A greater understanding is needed to devise strategies and possible interventions that improve decision-making in older populations.

Disclosure statement: The authors certify that they have no actual or potential conflicts of interest including any financial, personal or other relationships with other people or organizations within three years of beginning the work submitted that could inappropriately influence our work. This experiment was approved for ethical treatment of human participants by the Institutional Review Board at Oregon Health & Science University and all participants provided written consent.

Table 1. Mean (SD) for Various Participant Characteristics

	N	Gender (M/F)	Age (years)	Education (years)	MMSE	WAIS-R Scaled	Income (% greater than \$40K)
Young	29	15/14	30.14** (5.53)	15.00 (2.80)	—	11.86 (2.64)	10%**
Old	30	15/15	71.30 (4.36)	15.00 (3.60)	28.97 (1.03)	12.53 (2.66)	43%

MMSE = Mini Mental Status Exam;

WAIS-R = Weschler Adult Intelligent Scale-Vocabulary Sub-Test

**p<.01 between groups t-test

Table 2a. Mean (SD) total and subscale scores for Barratt Impulsiveness Scale.

	Barratt Impulsiveness Scale (Total Score)	Attentional	Motor Planning	Non-Motor-Planning
Young	64.42* (9.93)	15.82 (4.06)	24.11* (3.84)	24.50# (3.93)
Old	59.30 (8.11)	14.40 (3.19)	21.97 (3.85)	22.93 (2.84)

*p<.05 between groups t-test

#p<.10 between groups t-test

Table 2b. Mean (SD) total and subscale scores for Sensation Seeking Scale

	Sensation Seeking Scale (Total Score)	Disinhibition	Thrill/Adventure	Experience	Boredom Susceptibility
Young	23.14* (7.06)	5.39* (2.81)	7.29* (2.73)	7.39* (1.99)	3.07* (1.80)
Old	14.10 (7.61)	2.77 (2.60)	4.50 (2.81)	4.83 (2.37)	2.00 (2.02)

*p<.05 between groups t-test

Supplemental Table 1: Effect sizes for decision-making questionnaires and tasks

Measure	Young	Old	Cohen's <i>d</i>	Effect Size <i>r</i>
BIS	64.42 (9.93)	59.30 (8.11)	0.56	0.27
SSS	23.14 (7.06)	14.10 (7.61)	1.23	0.52
DOSPERT-Risk Taking	21.57 (9.07)	15.96 (8.49)	0.64	0.30
DOSPERT –Risk Perception	23.02 (8.55)	28.64 (9.65)	0.61	0.29
Ultimatum Game (% accept)	76.37 (24.33)	57.73 (33.18)	0.64	0.31
Delay discounting (k-values)	0.013 (.027)	0.020 (.035)	0.22	0.11

Supplemental Table 2. Delay discounting: Mean (SD) indifference points and discounting parameters (k-value).

	1 day	7 days	30 days	90 days	180 days	365 days	k-value	R ²	AUC
Young	9.98 (0.09)	8.70 (1.32)	7.51 (2.42)	6.56 (2.88)	6.07 (3.04)	5.22 (2.94)	.013 (.027)	0.76 (0.25)	0.63 (0.27)
Old	10.03 (0.15)	8.46 (1.55)	7.22 (2.59)	5.70 (2.99)	4.89 (3.41)	3.74 [#] (3.02)	.020 (.035)	0.87 (0.16)	0.53 (0.29)

AUC= Area under the curve

p<.10

Supplemental Table 3: Across task correlations for all participants (N=58)

	Discounting (k-values)	BIS	SSS	DOSPERT Risk Taking	DOSPERT Risk Perception	Ultimatum Game
Delay discounting (k-values)	---					
BIS	-.005	---				
SSS	-.079	.360*	---			
DOSPERT-Risk Taking	.006	.543*	.675*	---		
DOSPERT – Risk Perception	.208	-.242	-.469*	-.615*	---	
Ultimatum Game (% accept)	.153	.183	.314*	.349*	-.241	---

*p<.05, uncorrected

Figure 1: Mean (\pm SD) self-report scores for the DOSPERT. Older adults report less risk-taking and more risk perception in specific decision domains.

Figure 1

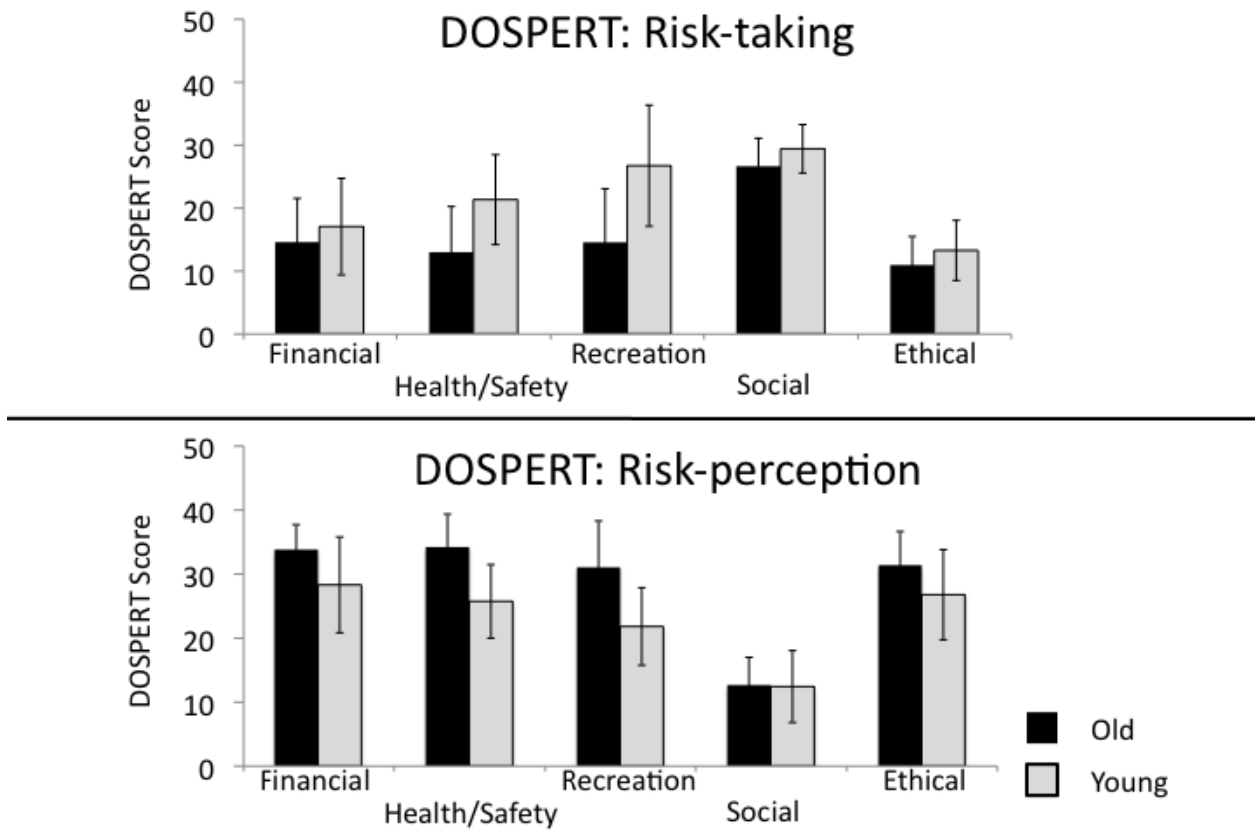


Figure 2: Example trial in the Ultimatum game.

Figure 3a: Average acceptance rates in the Ultimatum game (Mean \pm CI). The old accept fewer unfair offers as compared to the young.

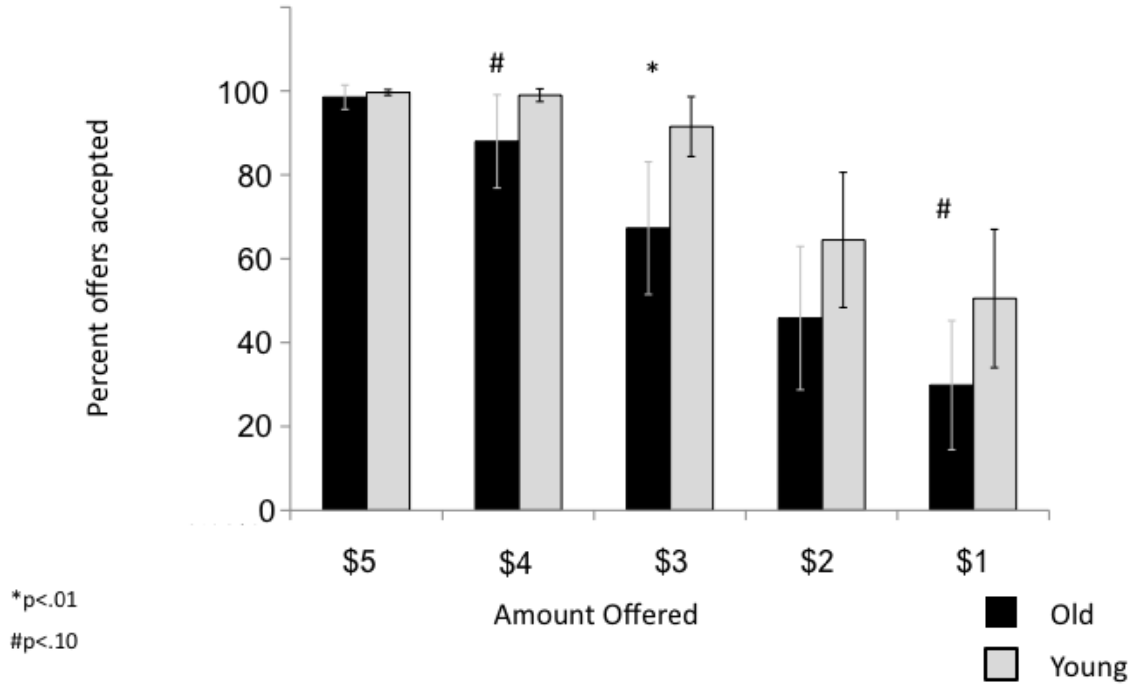


Figure 3b: Responses in the Dictator Game. Older adults are more likely to evenly split a sum of money as compared to the young. The numbers indicate how many participants fell into each category.

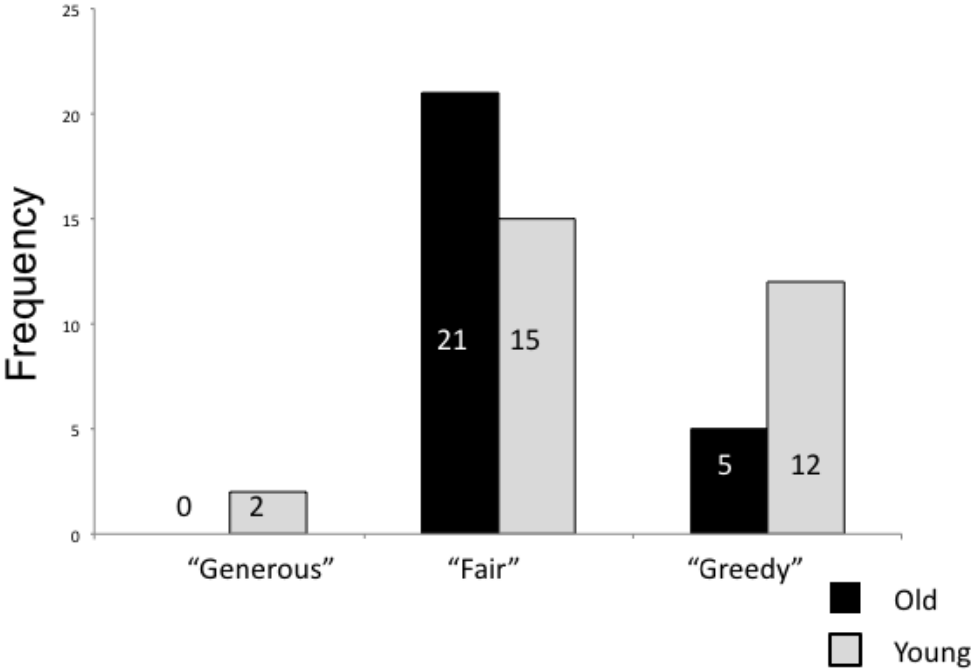
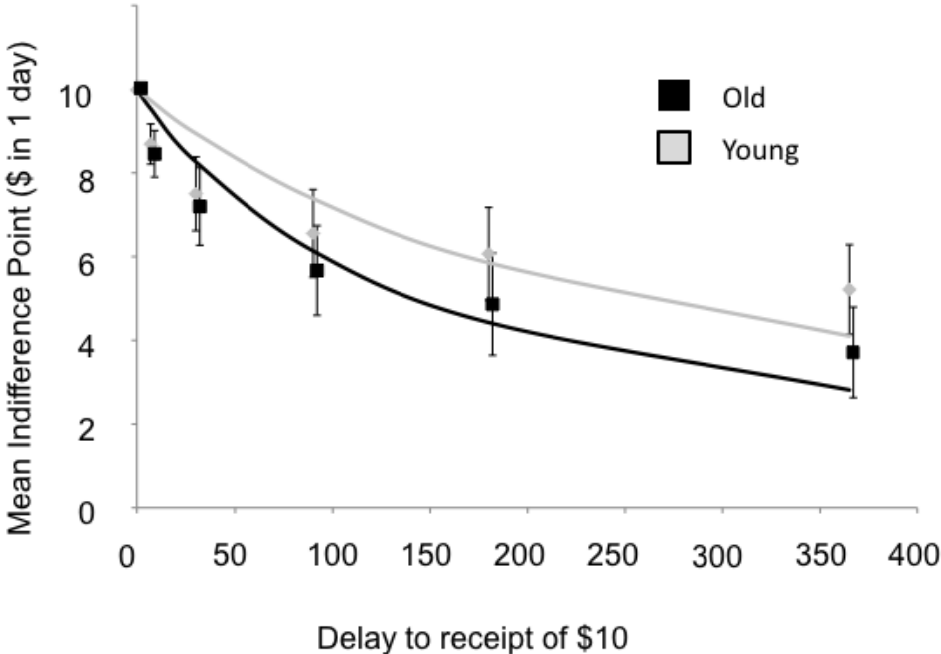


Figure 4: Example of stimuli in the delay discounting task.

Question 1:
At this moment which would you prefer?

\$10 in 90 days	\$7 in 1 day
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Figure 5: Mean indifference ($\pm 95\%$ CI) points for delay discounting. Young and old did not differ in delay discounting.



Chapter 3:

A fair shake: the role of the insula and prefrontal cortex in social economic decision-making in older adults

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Abstract:

Older adults prefer outcomes that are equitable more than younger adults. This behavior may be related to age-associated changes in cognitive or emotion processing. However, little is known about the neural mechanisms that underlie this behavior. Brain regions involved in decision-making include cognitive and emotion-processing regions such as the amygdala, anterior insula and DLPFC, all of which show significant age-related functional changes. Thus, we examined age-related functional changes during decisions about fairness using functional magnetic resonance imaging (fMRI). We examined activity of the amygdala, anterior insula and dorsolateral prefrontal cortex (DLPFC) in 13 young and 14 old participants while they made decisions regarding generous, fair and unfair monetary offers from both human and computer proposers in the Ultimatum Game. Older adults rejected more generous and unfair, offers than the young. The old had more activation of the anterior insula and DLPFC for generous and unfair offers, but not fair offers as compared to the young. Both young and old participants had greater activation of the amygdala to offers made by human as compared to computer proposers. These data indicate that older adults strive for equity in decision outcomes, even to the point of refusing overly generous offers. This behavior is mediated by more activation in brain regions that are responsible for the integration and regulation of emotion during decision-making.

Introduction:

Everyday decisions occur in complex social situations and thus require an individual to determine the best outcome while incorporating information about the social context. Older adults, in particular, face complex and life-changing decisions simultaneously with declining neural resources. Furthermore, socio-emotional features of aging may complicate decision-making processes in older adults (Samanez-Larkin et al., 2007; Lee et al., 2008; Roalf et al., under review). For example, we recently showed that older adults were less likely to accept unfair monetary offers, as compared to the young, in a social economic decision-making task, but they do not differ from the young on economic tasks where there is no social context (Roalf et al., under review). Older adults have stronger preferences for social partners who are known well and meaningful to them as compared to the young (Fredrickson & Carstensen, 1990; Fung et al., 2001a; Fung et al., 2001b) and this occurs even though social interactions are more demanding to maintain later in life (Rohr & Lang, 2009). These age-related changes are associated with an increase in the importance of social-emotional goals (Carstensen, 2006). Older adults are more conservative decision-makers (Deakin et al., 2004; Pachur et al., 2009; Finucane et al., 2005; Mata, 2007). In addition, they forget decisions more rapidly, deliberate for less time when making decisions, seek out less information to make an informed decision and are more decision avoidant (as reviewed (Kennedy & Mather, 2007). Thus, change in social goals coupled with known cognitive and emotional changes in aging (Carstensen, 2006; Carstensen & Lockenhoff, 2003) may alter the quality of social decisions.

Theories from the field of economics predict how individuals will make complex social decisions. For example, Game Theory is a set of models that explain how people interact with each other when making decisions (von Neumann & Morgenstern, 1947). Strategic bargaining behavior,

one component of Game Theory, is typically assessed using a social decision-making task called the Ultimatum Game (UG; Sanfey, 2007; Sanfey et al., 2003; Knoch et al., 2006; Pillutla & Murnighan, 1996; Chang & Sanfey, 2009). It measures views about fairness by having two individuals determine how to divide a sum of money (Guth et al., 1982). One player (proposer) offers a split of a sum of money while the other player (responder) decides whether to accept or reject the offer. Accepted offers are divided accordingly; rejected offers result in no money for either person. This simple social decision-making game requires sophisticated reasoning about the motivations of others (Sanfey, 2007).

The primary influence on decision-making during the UG is the perceived fairness of an offer and not financial self-interest (Guth et al., 1982; Sanfey, 2009; Sanfey et al., 2003; Pillutla & Murnighan, 1996; Xiao & Houser, 2005; Nowak et al., 2000). Rejection of the most unfair (i.e., \$9:\$1) offers in the UG indicates that people will forgo financial gain either to maintain a level of fairness or alternatively, to punish proposers for unfair offers (Camerer & Thaler, 1995; Thaler, 1988). This is contrary to many economic models that propose individuals should make decisions in a self-interested, goal-oriented manner. If this were the case, no offers in the UG should ever be rejected, however this is rarely seen in practice. For example, young adults accept all offers that are divided equally (50/50 split), but reject more offers as the level of fairness decreases (i.e., 90/10 split) despite the knowledge that rejecting an offer results in forgoing a monetary reward (Sanfey et al., 2003). The old are even more likely than the young to reject unequal offers and forgo monetary rewards in the UG (Roalf et al., under review). They even reject mildly unfair offers. It is possible that age-related alterations in emotion causes increased sensitivity to fairness.

Several brain regions provide the neural substrate for economic decisions in a social context. The amygdala is important for evaluating emotional information (Davis & Whalen, 2001; Murphy et al., 2003; Whalen et al., 1998; Adams, Jr. et al., 2003; Whalen et al., 2001; Calder et al., 2001; Gunning-Dixon et al., 2003; Gur et al., 1994; Hariri et al., 2002; Phan et al., 2003; Whalen et al., 2004; Wright et al., 2006), emotional memory (Cahill et al., 1995; Canli et al., 2000; Hamann et al., 1999; Phelps et al., 1997) and is responsive to facial appearance during social interactions (Winston et al., 2002). For example, more amygdala activity is associated with faces that are judged to be untrustworthy (Winston et al., 2002). Furthermore, the amygdala responds to facial expressions that suggest information about moral status and suspicion (Adolphs & Spezio, 2006; Calder & Young, 2005; Moll et al., 2008; Singer et al., 2004). The anterior insula, which activates during disgusting and painful stimuli (Calder et al., 2001; Damasio et al., 2000; Phillips et al., 1997), is important for labeling social interactions as unpleasant (Singer et al., 2009; Sanfey, 2007) and has greater activation to unfair vs. fair UG offers in young adults (Sanfey et al., 2003; Chang & Sanfey, 2009). There is a positive relationship between the magnitude of anterior insula activity and rejection rate of unfair UG offers (Sanfey et al., 2003) and the labeling of faces that are considered untrustworthy (Winston et al., 2002). Activation of the insula is therefore linked to the emotional resentment caused by unfair offers (Fehr & Camerer, 2007). Regions of the PFC are implicated in balancing social-emotional motives such as the maintenance of social reputation, and goal-oriented motives such as economic self-interest (Fehr & Camerer, 2007; van den Bos & Guroglu, 2009). The dorsolateral prefrontal cortex (DLPFC; peak voxel Talairach coordinates $X = -34$, $Y = 45$, $Z = 16$) activates to unfair offers in the UG in young adults (Sanfey et al., 2003). In fact, when DLPFC activity is greater than anterior insula activity, unfair offers tend to be accepted in the UG. Offers that are rejected show

the opposite relationship, with lower DLPFC and higher anterior insula activity (Sanfey et al., 2003).

Thus, this region may be involved in determining which offers should be accepted or rejected.

Activation of more posterior regions of the DLPFC (peak voxel Talairach coordinates $X = -46$, $Y = 14$, $Z = 24$) are associated with the initiation and maintenance of cognitive control and goal-oriented behavior (Hare et al., 2009). These studies suggest that both affective and deliberative regions of the brain are critical in the evaluation of social decisions.

Older adults have functional changes in brain regions responsible for emotion (Roalf et al., in press; Mather & Knight, 2005; Mather et al., 2004; Mather & Carstensen, 2003; Mroczek & Kolarz, 1998; Gunning-Dixon et al., 2003; Iidaka et al., 2002; Tessitore et al., 2005; Williams et al., 2006) and cognition (Grady et al., 1994; Cabeza et al., 1997; Rypma & D'Esposito, 2000; Persson et al., 2004), including the amygdala, insula and PFC, and these changes may affect social decision-making. The old have less amygdala activity to emotionally salient stimuli, such as negative faces, as compared to the young (Roalf et al., in press; Gunning-Dixon et al., 2003; Iidaka et al., 2002; Mather et al., 2004), but more anterior insula activity to negative emotional faces (Fischer et al., 2005). The young and the old show no difference in amygdala activity, but the old did have more insula activity when choosing between risky or safe monetary gambles where there is no social component (Lee et al., 2008). Higher insula activity in the old may be a safety signal that guides older adults away from choices with a potentially negative outcome (Lee et al., 2008). However, another study that examined anticipation of positive (i.e., gain) or negative (i.e., loss) outcomes found that older adults have similar insula activity to the anticipation of positive outcomes but reduced activity to anticipation of negative outcomes as compared to the young (Samanez-Larkin et al., 2007). Overall, this suggests that the anterior insular may help guide decisions in older adults.

Older adults show more activation of the DLPFC than younger adults during a number of cognitive operations, including during reward-based decision-making (Mell et al., 2009). Higher prefrontal activity in the old is compensatory as it is associated with normalizing performance so that the old perform more like the young (Grady et al., 1994; Cabeza et al., 1997; Rypma & D'Esposito, 2000; Persson et al., 2004). For example, older adults have bilateral activation of the prefrontal cortex during verbal recall tasks (Cabeza et al., 1997); working memory tasks (Reuter-Lorenz et al., 2000), word and face recognition tasks (Madden et al., 1999; Grady et al., 2005) and emotion recognition tasks (Roalf et al., in press; Gunning-Dixon et al., 2003), that is not seen in the young. Other studies suggest that higher prefrontal activity imposes greater cognitive control of behavior, particularly during emotionally salient tasks (Mather & Knight, 2005; Isaacowitz et al., 2009) and this may be one source of the improved behavior (Paxton et al., 2008; Buckner, 2004). It is unknown whether changes in activation of the PFC affect the outcome of decisions during the UG. However, we suspect that more activity of the DLPFC and the anterior insula in the old guide older adults to reject more unfair offers in the UG.

To the best of our knowledge, no study has investigated the effects of old age on the neural substrates of social decision-making, nor investigated their neural response to generosity. We used functional magnetic resonance imaging (fMRI) to compare brain activity in young and old adults during the UG while participants accepted or rejected unfair, fair and generous monetary offers from both human and computer partners. We hypothesized that the old would have more activity in the DLPFC and anterior insula, but less in the amygdala, and that this activity will be associated with higher rates of rejection for offers that deviate in fairness.

Materials and Methods

Participants

Thirteen healthy younger adults (7 female; 6 male) and 14 healthy older adults (7 female; 7 male) were recruited from an urban population. Health status and eligibility were obtained via phone interview. Criteria for participation were similar to our previous studies (Roalf et al., under review). The young were between 24 and 45 years of age and the older adults were between 65 and 85 years of age (Table 1). These age ranges permitted recruitment of relatively healthy elderly, and groups that significantly differed in age but had experienced relatively comparable life styles, including similar levels of education and a history of employment. All subjects understood English and had adequate hearing and vision (with correction if necessary). Older and younger participants did not differ in formal education or on the vocabulary sub-test of the Wechsler Adult Intelligence Scale-Revised (WAIS-R), which controls for cohort-related differences in education environments. This sub-test provides a standardized approximation of functional intelligence and is highly correlated with IQ (Wechsler, 1981). The two groups reported similar levels of income.

-----Insert Table 1 here-----

Exclusion criteria were similar to our previous studies (Roalf et al., in press; Roalf et al., under review). Participants were excluded if they had a self-reported history of neurological problems (e.g., stroke, seizure, or head trauma), significant medical problems (e.g., uncontrolled hypertension), current or previous psychiatric conditions (e.g., schizophrenia), or current use of medications likely to affect mood or cognition such as anti-anxiety agents (e.g., SSRIs). Participants were also excluded if they had conditions contrary to MRI such as internal metal, risk of metal in the eyes, non-removable hearing aids or implants, pacemakers or reported claustrophobia. Older

participants were screened for dementia and depression using the Mini-Mental Status Examination (MMSE; scores <26; Folstein et al., 1975) and Geriatric Depression Scale (GDS; scores >10 Sheikh et al., 1991), respectively. No older subjects had abnormal MMSE or GDS scores nor did MMSE or GDS scores correlate with any measure of brain activity. All participants provided written informed consent and were paid for their time and participation in the study. This study was approved by the OHSU IRB and all participants provided written informed consent.

Social Decision Making Task: The Ultimatum Game

We used a modified version of the UG (Figure 1) that was similar to that employed by Sanfey et al., (2003 & 2005). The game was played between a proposer, controlled by a computer, and a responder played by the participant. In this game, the proposer (a computer or a person) proposed a split of a sum of money that was either accepted or rejected by another, the responder. If the proposal was declined, neither player received any money (Figure 1). Briefly, each trial began with a photograph of the proposer, which lasted 4 seconds. Next, the offer was presented for 4 seconds, followed by a 4 second response period during which the participant could accept or decline the presented offer. Then the participants saw a 4 second outcome screen, which was based upon their response. Each trial ended with cross-hair presentation that remained on the screen for a variable amount of time (4, 6, or 10 seconds). A jittered trial length was used to reduce the predictability of the stimuli and reduce the correlation among the regressors during fMRI scanning, thus increasing the efficiency for separating the brain's activity to stimuli and to response (Rosen et al., 1998; D'Esposito et al., 1999; Wager & Nichols, 2003). Participants completed four sessions of the UG. There were 28 rounds per session, 14 interactions with a human partner and 14 interactions with a computer partner that were presented in pseudo-random sequence. No more than three

consecutive interactions with human or computer partners were permitted. Human proposers were each depicted by a photograph (Minear & Park, 2004) and a name on the screen, and in other trials non-human proposers were depicted by a photograph of a computer. Participants were told that responses with any one proposer would not affect subsequent interactions. Ten dollars was proportionally divided on every trial (e.g., “\$4 for You; \$6 for Joe”). Prior studies have used only fair and unfair offers. We sought to also examine responses and brain activity during generous offers. Twenty-one percent (21%) of offers were split generously (\$1 for proposer: \$9 for responder, \$2:\$8, \$3:\$7, \$4:\$6), 21% of offers were fair (\$5:\$5), and 58% of offers were unfair (\$6:\$4, \$7:\$3, \$8:\$2, \$9:\$1). The percentage of unfair offers was similar to a previous neuroimaging study (Sanfey et al., 2003). Generous offers have not typically been used in the UG as it is assumed these offers would always be perceived similarly to the fair (\$5:\$5) offers, thus, the remaining 42% of offer was divided equally for generous and fair offers. Prior to scanning, participants completed a training session where they were exposed to one of each offer type and became familiar with the button box used during scanning. The percent of offers accepted was the main outcome measure for the behavioral data and percent signal change from baseline was the main outcome measure for the neuroimaging data.

-----Insert Figure 1 here-----

Payment procedures were similar to our previous study (Roalf et al., under review).

Participants were paid \$10 in cash for participation, however to make the economic nature of the tasks realistic, participants were told that additional compensation could be earned based on their performance. The additional compensation was a one-time payment based on the earnings from a randomly drawn trial from each of the fMRI block of trials. Participants were reminded they were

playing for actual money before beginning the task and were informed of their total earnings at the completion of all decision-making tasks.

Imaging acquisition

Anatomical and functional imaging data were acquired using a Siemens TIMS Trio 3T MR scanner (Erlangen, Germany) with a 12-channel head-coil at the Advanced Imaging Research Center at Oregon Health & Science University. Participants were positioned supine on a padded scanner bed and wore foam earplugs and ear protection headphones. Non-paramagnetic plastic glasses with corrective lenses were available for participants needing vision correction and picture adjustment was made by focusing the lens on the projector. To minimize head movement, each participant's head was stabilized with expandable foam cushions. The protocol included an initial localizer series for orientation and slice positioning. High-resolution, T1-weighted images (3D Magnetization Prepared RAPid Gradient Echo; MPRAGE) were collected for anatomic coregistration with the fMRI data. The parameters of the MPRAGE were: 144 axial slices, TR (repetition time) = 1800ms, TE (echo time) = 2.56 ms, flip angle (FA) = 12°, field-of-view (FOV) = 256 mm², matrix = 512 X 512, voxel size = 0.5 X 0.5 X 1.0 mm. Functional data was acquired via an EPI-BOLD pulse sequence with the following parameters: (TR) = 2000 ms, (TE) = 30 ms, FA = 90°, FOV = 220 mm², matrix = 384 x 384. Thirty-six axial slices (3.44 mm in plane resolution with 4 mm slice thickness, no skip) oriented to the AC-PC line were collected covering the entire cerebrum. The stimuli were back-projected into the MR scanner using a video projector (PLC-XP50L, Sanyo, Inc.) fitted with a custom long-throw lens and viewed via a mirror mounted on the head-coil. Picture and timing were controlled using Presentation Software (version 11.1, Neurobehavioral Systems, Albany, CA, USA).

Imaging Data Analysis

FMRI Preprocessing:

The fMRI data was processed and analyzed using Brain Voyager QX (Brain Innovations, Version 2.11.1542; <http://www.brainvoyager.com>). The first four image volumes were discarded to permit magnet stabilization. Prior to statistical analysis, each subjects' functional data underwent slice scan time correction, high-pass temporal filtering (GLM with Fourier basis set including linear trend removal) to remove low frequency oscillations in the signal time-course in each voxel, 6-parameter rigid body motion correction and spatial smoothing with a Gaussian kernel of 5mm FWHM (Hamann et al., 2004). The individual fMRI data were normalized and then co-registered to the individual's high resolution T1 (MPRAGE) anatomical brain scan and re-sampled into 3 mm³ voxels. Next, each brain dataset was convolved into standard stereotaxic coordinate system (Talairach & Tournoux, 1988) to allow the pooling of data across subjects. Results of the spatial normalization were visually inspected to ensure acceptable anatomical registration with the standard brain.

FMRI Statistical Analysis:

Blood oxygen level dependant (BOLD) activity during the UG was analyzed in two steps. First, general linear model (GLM) was performed for each participant. The GLM included the following 18 regressors: two generous offer regressors (computer/human); two fair offer regressors (computer/human); 8 unfair offer regressors (\$4:\$6; \$3:\$7; \$2:\$8; \$1:\$9 computer/human) and 6 residual motion parameters were modeled with a canonical hemodynamic response function. Next, a whole-brain analysis across all subjects was performed using a Random Effects (RFX) Analysis of Variance (ANOVA) within GLM. Whole brain contrasts of interest were determined. Primary contrasts of interest included 1) Unfair vs. Fair; 2) Unfair vs. Generous; and 3) Fair vs. Generous

offers. Activation was considered significant for a contrast at $p < .0025$ with a cluster-threshold of 9 contiguous voxels, as determined through Monte-Carlo simulation (Poline & Mazoyer, 1993; Forman et al., 1995). These methods are similar to previous research on the UG (Sanfey et al., 2003; Koenigs & Tranel, 2007; Mehta & Beer, 2009).

Subsequently, *a priori* hypotheses regarding amygdala, insula and DLPFC activity were tested using a region of interest (ROI) analysis similar to a previous studies (Wright et al., 2002; Wedig et al., 2005; Williams et al., 2006) including some of our previous work (Roalf et al., in press). The amygdala (center: $X = \pm 23$, $Y = \pm 5$, $Z = \pm 15$) and anterior insula (center: $X = \pm 37$, $Y = \pm 10$, $Z = \pm 5$) ROIs were defined using Talairach coordinates generated from Talairach Daemon Client 2.42 (Lancaster et al., 1997; Lancaster et al., 2000). The DLPFC ROI was a hand-drawn cube centered at $X = \pm 35$, $Y = 19$, $Z = 29$ in Talairach space, which was used in previous study of emotion in younger and older adults (Roalf et al., in press). The ROIs are depicted in Supplemental Figure 1. We chose to anatomically, not functionally define ROIs to extract activity as previous studies in the young and old find similar effects using either method (Wright et al., 2006).

Percent signal change time courses were extracted for the significant voxels in each ROI for each individual. Average percent signal change was determined for individual subjects for the following contrasts: 1) Unfair vs. Fair offers and 2) Unfair vs. Generous offers. Data was not analyzed for Fair vs. Generous comparison as there were no significant differences in activity for this comparison at the given threshold at the group level. Human vs. Computer proposers were compared, however there were no age-group differences in behavioral performance. Thus, fMRI data is reported across all participants for this comparison. Accepted vs. Rejected offers were compared in an exploratory analysis using fixed-effects (FFX) as only 6 young (46%) and 8 old (57%)

participants rejected offers, which limited the use of a random effects (RFX) analysis. Peak signal change was also determined for each comparison, however, only the average data is reported here, as both outcome measures showed similar effects. The latency to the peak percent signal change was determined for each contrast. Finally, grand average percent signal time course plots are reported for each condition for young and old groups for the amygdala, insula and DLPFC. Independent sample t-tests were used to compare activation between groups at each time point following an offer. This study provided an extremely rich data set, thus some exploratory analyses are included in supplemental material.

Statistical analyses

Mixed-model repeated-measures analyses of variance (ANOVA; SPSS, v17.0) and follow-up t-tests were used to analyze UG responses and ROI data. In these analyses age-group was the between-subjects factor and offer (generous, fair, unfair) was the within-subjects factor. All measures were tested for sphericity and equal variances (Levene's test). When appropriate statistical corrections (i.e., Greenhouse-Geisser) were used and are noted in the results. Degrees of freedom are reported at the nearest whole number. Similar analyses were performed to analyze the response to proposer type (human or computer). Non-parametric between group chi-square analysis was used to compare UG responses of each offer type (i.e., \$1:\$9) since the young accepted 100% of some offers types while the old did not. For this analysis, if a participant accepted more than 90% of a given offer they were considered an 'acceptor' of that offer; those that did not meet these criteria were considered 'rejecters' for that offer. Pearson correlations were performed within each offer category for young and old groups separately to assess for associations between brain activity and choices, and for

associations in activity among brain regions. Bonferroni corrections were used to adjust for multiple comparisons in correlation analyses.

Results

Ultimatum Game:

Overall the young accepted more offers than the old [$F(1,25)=4.59$, $p=.04$]. Acceptance rates were affected by offer type [$F(1.20,29.97)=27.32$, $p<.02$; Figure 2A]. Unfair offers were accepted less than fair ($p<.01$) and generous ($p<.01$) offers, but acceptance rates of fair and generous offers did not differ. There was no interaction between offer type and age group. Because the young never rejected generous offers we used a non-parametric between-group analyses of the number of participants that accepted each offer type. Fewer older adults were considered acceptors of generous offers than the young (\$9:\$1 [$\chi^2(1)=5.69$, $p=.02$]) and \$8:\$2 [$\chi^2(1)=5.69$, $p=.02$]; Figure 2B). Older adults' range of acceptance rates for generous offers was between 66% and 100%. In addition, fewer older adults were acceptors of mildly unfair offers [\$3:\$7 ($\chi^2(1)=3.64$, $p=.05$)] and marginally fewer older adults were acceptors of very unfair offers \$ as compared to the young [2:\$8 ($p=.08$)]. Similar numbers of young and old accepted mild generous offers (\$7:\$3, \$6:\$4), fair offers (\$5:\$5) and mild unfair offers (\$4:\$6) and extremely unfair offers (\$1:\$9; Figure 2B). There was no age group difference in median reaction time to respond between young and old, nor any difference based on offer type or proposer type. However, participants responded faster when accepting offers than when declining offers [$F(1,25)=10.42$, $p<.01$].

-----Insert Figure 2 here-----

We also examined whether the proposer type affected responses in exploratory analyses. Proposer type (human or computer) did not affect acceptance rates and there was no interaction

between proposer type and age group. The effect of proposer type on responses to each offer type was also measured. There was an interaction between offer and proposer [$F(1, 35)=3.79, p=.03$]. Overall, unfair and fair offers were accepted equally from computer or human proposers, however, more generous offers were accepted from computers than from humans ($p=.04$). Exploratory paired samples t-test showed that older adults were more likely to accept generous offers from computers as compared to human proposers [$t(13)=2.27, p=.04$]. Unfair offers from human and computer proposers were accepted less than fair ($p<.01$) or generous ($p<.01$) offers. Generous human offers were accepted less than fair offers ($p=.05$), but not for computer proposers.

Functional Imaging Results

Ultimatum Game Offers

Whole Brain Analyses

Overall, whole brain analysis showed that contrasts of unfair vs. fair, and unfair vs. generous offers activated a similar network of brain regions (Table 2). There was more activation of bilateral insula, occipital cortex, cingulate gyrus, and medial frontal cortex for unfair as compared to fair or generous offers. Fair and generous offers resulted in more activation of the post-central gyrus and middle frontal cortex as compared to unfair offers. These analyses resulted in significant activation within the anterior insula and DLPFC ROIs but not the amygdala ROI (Figure 3A). Thus, ROI analyses were conducted only in the anterior insula and DLPFC.

-----Insert Table 2 here-----

Region of Interest Analysis

Anterior Insula

Overall, older adults had more insula activity to all offers than the young [$F(1,25)=5.32$, $p=.03$]. There was an offer by age group interaction [$F(1,36)=4.90$, $p=.02$, Figure 3B]. The old had greater anterior insula activation to generous ($p<.01$), but not fair or unfair offers, as compared to the young. The young had marginally more activity for unfair offers as compared to generous ($p=.08$) offers, but similar activity for unfair and generous offers compared to fair offers. The old had similar activation of the anterior insula for generous and unfair offers; generous offers resulted in more activation than fair offers ($p=.02$) and unfair offers elicited marginally more activation than fair offers ($p=.07$). There were no differences in the latency to peak measurement for activity in the insula for generous, fair or unfair offers. Time course analyses confirmed that the old had sustained activation longer in the anterior insula as compared to the young for generous offers ($ps<.05$; Figure 4A). These results remain the same when proposer type was included in the analysis.

-----Insert Figure 3 here-----

DLPFC

The old had more DLPFC activity as compared to the young [$F(1,25)=8.92$, $p<.01$]. There was no main effect of offer, however the offer by age group interaction was significant [$F(2,37)=4.08$, $p=.02$, Figure 3C]. The old had greater DLPFC activity to generous ($p<.01$) and unfair ($p<.03$), but not fair offers as compared to the young. In the young, DLPFC activity was similar for all three offers. In contrast, the old had marginally more activation to generous ($p<.06$) and more activation to unfair ($p<.03$) offers as compared to fair offers; activity to generous and unfair offers did not differ. Time course analysis showed that the old had more DLPFC activity for generous and unfair, but not fair, offers as compared to the young ($ps<.05$;

Figure 4B). There were no differences in the latency to peak measurement for activity in the DLPFC for generous, fair or unfair offers. Including proposer type in the analysis resulted in more activation in the DLPFC to computer than human proposers [$F(1,25)=11.87, p<.01$], but there were no interactions with age-group or offer type.

-----Insert Figure 4 here-----

Correlations between anterior insula and DLPFC for offers

Correlations between the anterior insula and DLPFC were performed within each age group for generous and unfair offers. Activity for generous, fair, and unfair offers in the anterior insula was positively correlated with more DLPFC activity for both young and old ($r>.56, p<.05$), regardless of proposer type. Including proposer type in the analysis showed that more anterior insula activity was associated with more DLPFC activity for human, unfair offers in the young ($r=.79, p<.01$) and marginally so in the old ($r=.50, p=.06$). Only the old also had a positive relationship between these two regions for unfair computer offers ($r=.60, p=.02$).

Correspondence between Ultimatum Game responses and brain activity

Correlation analyses for generous offers were limited to old participants only as none of the young declined generous offers. Acceptance rates of generous offers were negatively related to anterior insula and DLPFC ($r>-.53, p\leq.05$), regardless of proposer type. Acceptance rates for unfair and fair offers were not related to either anterior insula or DLPFC in the young or the old and assessing this relationship by proposer type did not change this result.

Human versus Computer Proposers

This analysis was performed to determine the neural structures engaged by different partners (human or computer) in the UG.

Whole brain analysis

Overall, subjects had more activation of the fusiform gyrus, amygdala and medial prefrontal cortex to offers made by human as opposed to computer proposers. In contrast, offers made by computer proposers activated occipital cortex, middle and lateral prefrontal cortex more than human proposers did (Table 3). This analysis resulted in significant activation within the amygdala and DLPFC ROIs (Figure 5A). There was no significant activation of the anterior insula.

-----Insert Table 3 here-----

Region of Interest Analysis

Amygdala

There was no difference in percent signal change between young and old participants. Overall, there was more amygdala activity to human proposers as compared to computer proposers [$F(1,25)=35.73$, $p<.01$; Figure 5B]. There was no interaction between proposer type and age group. Time course analyses confirmed that the young and the old showed more activation of the amygdala for human than computer proposers (Figure 6A), but no difference between groups for either proposer type. There were no differences in the latency to peak measurement for activity in the amygdala for human versus computer proposals.

-----Insert Figure 5 here-----

DLPFC

Older adults had marginally more activity in the DLPFC ROI as compared to young ($p=.10$). Overall, there was more DLPFC activity to computer proposers as compared to human proposers [$F(1,25)=12.85$, $p<.01$; Figure 5C]. There were no interactions between proposer type

and age group. Time course analysis confirmed these findings (Figure 6B). An exploratory time course analysis indicated that computer proposers elicited more early DLPFC activation while human proposers elicited more late DLPFC activation (Supplemental Figure 2; see Supplemental Data for detailed analysis).

Correspondence between amygdala and DLPFC activity to proposer type

There were no significant correlations between amygdala and DLPFC activation for human or computer proposers.

Correspondence between Ultimatum Game responses and brain activity to proposers

More amygdala activity to human proposers correlated with higher acceptance rates ($r=.40, p<.05$), however this relationship did not exist for computer proposers. More DLPFC activity, to either human or computer proposers, corresponded to lower acceptance rates ($r>-.40, p<.04$).

-----Insert Figure 6 here-----

There were no significant group differences in ROI activation or time course analyses for Accepted vs. Declined offers, nor interactions with proposer or offer type.

Discussion

We found age-related changes in social economic decision-making and in the associated neural activity. To our knowledge, this is the first paper that quantified neural responses during the UG in older adults and measured responses to generous as well as unfair UG offers. The old rejected more unfair UG offers and surprisingly, also rejected more generous offers as compared to the young. In fact, 42% of older adults rejected generous offers, while none of the young rejected those same offers. The behavioral response to these offers coincided with

significant changes in neural activity of the anterior insula and DLPFC. Specifically, the old had greater neural responses to UG offers than the young, and this was most apparent in the anterior insula for generous offers. In addition, older adults had more DLPFC activity to both generous and unfair offers as compared to the young. Interestingly, in the old, more activity in both of these regions corresponded with lower acceptance rates to generous offers. Finally, offer type did not influence amygdala activity however, across both age groups, there was more amygdala activity to offers made by human proposers than computer proposer, but more DLPFC activity to computer than human proposers. Exploratory analyses suggest that the DLPFC neural response to human proposers occurs later than the response to computer proposers.

These behavioral data confirm our previous findings that the old focus more on equity during social economic decisions than the young (Roalf et al., under review). The old reject more unfair offers than the young and this indicates that the old are willing to forgo financial rewards to maintain equity in social relationships. This is made all the more apparent by the finding that the old also reject more generous offers than the young. Thus, older adults forgo disproportionate gains particularly when it reduces the potential gain for another person. This suggests that older adults are focused on equity or fairness in decision outcomes. Older adults' behavior fits with two similar decision theories that are based on equity or equality in decision outcomes. First, classic equity theory (i.e., distributive fairness) proposes that individuals who perceive themselves as either under-rewarded or over-rewarded will experience distress (Adams, 1965; Goodman, 1977). This distress leads to attempts to restore equity within a given relationship (Adams, 1965). Hence, older adults may find unequal outcomes more distressful

than younger adults and attempt to relieve this distress by declining unequal generous and unfair offers. Furthermore, older adults' decisions correspond with the equality heuristic which suggests that decisions should yield an equilibrium outcome in which each individual shares equally and alternatives that differ from a 50-50 distribution will be discarded (Messick, 1993). Thus, equal outcomes may be the 'foundation' for beliefs about equity, and provide a baseline for fairness decisions in the UG. Taken together, these data suggest that the need for equity, or fairness, in older adults results in distress for and subsequent rejection of offers that deviate in equality in the UG.

Rejection of unequal offers also reflects differences in emotion in older adults. Rejecting unequal offers reduces negative emotional experiences in older adults, supporting older adults' bias towards positive emotion experiences (Carstensen et al., 2000; Gross et al., 1997; Lawton et al., 1992; Magai et al., 2009; Mroczek & Kolarz, 1998) and greater control over their moods (Gross et al., 1997; Lawton et al., 1992), which results in improved social-emotional well being. In fact, Socioemotional Selectivity Theory (SST) suggests that older adults optimize their emotional well-being by increasing positive emotional experiences and decreasing negative emotional experiences (Carstensen et al., 1999). In this case, forgoing gain to maintain social equity maybe more emotionally gratifying than decision outcomes that results in unequal distributions. Thus, age-related changes in social-emotional goals may mediate older adults' focus on equity.

Older adults' focus on equity in social decision-making was reflected in the neural responses of the affective system. In the old, more activation to generous offers and marginally more activation to unfair offers was associated with lower acceptance rates in the old,

suggesting that this activity guides UG choices. These data are similar to studies that show aging results in more anterior insula activity to aversive emotional faces (i.e., disgust; Fischer et al., 2005) and during decisions with potential aversive outcomes (Lee et al., 2008), but less amygdala activity (Fischer et al., 2005) as compared to the young. Previous studies in younger people confirm that unfair UG offers elicited disgust and anger (Straub & Murnighan, 1995; Pillutla & Murnighan, 1996), and are associated with activation of the anterior insula (Sanfey et al., 2003; Tabibnia et al., 2008; Guroglu et al., 2010). Thus, more anterior insula activity during older adults' decisions for generous and, to some extent, stingy offers suggest they feel more disgust for these offers as compared to the young. In addition, anterior insula activity signals aversive outcomes (Lee et al., 2008), painful stimuli (Derbyshire et al., 1997), disgust (Calder et al., 2001) and harm avoidance (Paulus et al., 2003). Thus, we suggest that older adults' use of an equity rule is guided by the disgust response elicited by unequal offers. Interestingly, disgust recognition is relatively preserved in aging as compared to other negative emotions (Gross et al., 1997) and is also preserved in age-related neurodegenerative conditions (Henry et al., 2008). Hence, older adults may have stronger inequality aversion as registered by more anterior insula as compared to younger adults (Bolton & Ockenfels, 2000; Fehr & Schmidt, 1999), and thus, may guide social decision-making in older adults.

The prefrontal cortex, including the DLPFC, is necessary for executive functioning, reasoning, and flexible, situation-dependent responses (Ochsner & Gross, 2005), all of which are necessary during the UG and most of which decline with aging (Sanfey et al., 2003). In older adults, DLPFC activity reflects the cognitive control over emotional responses or the regulation of self-interested impulses. Indeed, DLPFC activity during the UG in younger adults is

associated with maintenance of the cognitive demands or goals of the task (Sanfey et al., 2003). Older adults have more DLPFC activity to generous and unfair offers as compared to the young, and more DLPFC activity was associated with lower acceptance rates. More DLPFC activity may reflect increased cognitive demands of goal maintenance in older adults during social decision-making. In fact, older adults recruit prefrontal brain regions to meet cognitive-processing needs (Gutchess et al., 2005) and inhibit goal-irrelevant information (Earles et al., 1997). Thus, it is possible that in older adults, more DLPFC activity to unequal offers reflects the effortful, controlled processes that are necessary to determine and implement equity during social decisions. This control may be reflected in differing decision goals between the young and the old. Sanfey et al. (2003) suggest that a younger participant's goal in the UG is to maximize reward. In order to accomplish this, young adults must accept offers that they find unfair and do so by engaging the DLPFC, which suppresses negative emotional responses elicited by unfair offers (Sanfey et al., 2003; Knoch et al., 2006). Younger adults show an inverse relationship between anterior insula activity and DLPFC activity for offers that were subsequently accepted or rejected (Sanfey et al., 2003). This suggests that the DLPFC may be involved in cognitive control over the emotional impulse to reject some aversive, unfair offers, but these data are only correlative in nature. If this relationship holds, older adults should show more DLPFC activity to unequal offers that were accepted. Yet, in the current study, older and younger adults did not show this differential pattern of response to offers that were subsequently accepted or rejected, however, this analysis was limited due to a small sample size.

Alternatively, DLPFC activity may modulate self-interested impulses. Support for this idea comes from a recent study that disrupted DLPFC activity during the UG. Direct disruption

of the DLPFC, through the use of repetitive transcranial magnetic stimulation (rTMS), during the UG leads to an increase in the acceptance of unfair offers, even though participants still viewed these offers as unfair (Knoch et al., 2006). Consequently, less DLPFC activity lead to more selfish behavior in the UG. These findings suggest another mechanism by which older adults may implement their equity rule. More DLPFC activity in older adults to unequal offers may enable them to overcome selfish impulses to accept these offers. Instead they are able to employ their equity rule as guided by the anterior insula. In contrast, younger adults have less DLPFC activity and thus are more likely to be self-interested as reflected by their lower rejection rates in the UG. Thus, it possible that more regulation of self-interested impulses enable older adults to 'implement their fairness goals' (Knoch et al., 2006, pg 833). The current data do not allow us to determine which role the DLPFC is playing in social economic decision-making, however, future studies can directly address this question.

We also asked whether social decisions with humans are special interactions as compared to interactions with a computer. Behaviorally, we found that proposer type only affected acceptance rates of generous offers, but not fair or unfair offers. This was only seen in older adults since no young adults rejected generous offers. The current data is in contrast to a previous study that found younger adults were more likely to reject unfair offers from a human than a computer proposer due to their aversion to these offers, and that this was mediated by the anterior insula, not amygdala (Sanfey et al., 2003). It is unclear why our behavioral results differ from this previous study with respect to proposer type. One explanation of the difference may be that participants in our study played more rounds of the UG (112 vs. 20) than in the previous study, providing participants with more experience. One possibility is that more

experience builds an emotional response to unknown humans, but decreases aversion.

Neuroimaging showed that the amygdala was more active to human as compared to computer proposers and more amygdala activity was associated with higher UG acceptance rates in both young and old. The amygdala activates to both positive (Hamann et al., 2002) and negative emotional stimuli (Adolphs & Tranel, 1999). Amygdala activity is associated with increased physiologic arousal (skin conductance response; Williams et al., 2001) when rejecting unfair UG offers in younger adults (van't Wout M. et al., 2006). This pattern was only observed for offers proposed by human partners, but not for offers from computers partners (van't Wout M. et al., 2006), which is similar to our findings here. This implies that human interactions are special in the UG. Taken together, these data provide direct support for economic models that acknowledge the role of affective brain systems in decision-making.

Limitations of the current study include our inability to perform a parametric analysis of specific offer type (i.e., \$9:\$1 vs. \$5:\$5) as we included fewer generous offers (6 per condition) as compared to unfair offers (14 per condition). However, this does not affect the finding that old rejected generous offers and this was never seen in the young. Fewer subjects were utilized in the analysis of rejected offers because some participants chose not to reject any offers and therefore could not be included. Thus, we do not know if differential brain activity between younger and older adults to accepted versus rejected offers might be found with a larger sample. One method to optimize data collection in the future would be to behaviorally identify individuals who reject some UG offers prior to neuroimaging so that acceptance and rejection of unfair and generous offers can be fully compared.

The present study expands upon previous research in decision-making in older adults by providing behavioral and neural evidence of age-related changes in social decision-making. We report that older adults make social economic decisions based upon an equity rule as shown by their rejection of more unequal offers in the UG. Interestingly, older adults have this response in the face of generosity as well as unfairness and this is reflected in neural responses of both affective and deliberative regions of the brain. The old devote more cognitive, emotional, and, we show, neural resources to make social economic decisions than the young. These findings imply that older adults may have difficulty with decisions that involve fairness, particularly in social contexts, as older adults must both *think and feel* their way through social decisions in order to achieve the goal of equity.

Disclosure statement:

The authors certify that they have no actual or potential conflicts of interest including any financial, personal or other relationships with other people or organizations within three years of beginning the work submitted that could inappropriately influence our work. The Institutional Review Board at Oregon Health & Science University approved this experiment for ethical treatment of human participants and all participants provided written consent.

Tables

Table 1: Participant Characteristics

	N	Age	Gender Male/Female	Education	WAIS-R Scaled Score	MMSE	Income % > 40K
Young	13	27.92 (2.66)	6/7	16.00 (2.45)	11.78 (3.56)	---	38%
Old	14	71.71 (3.29)	7/7	16.64 (3.22)	13.69 (2.75)	29.23 (0.92)	35%

Age and Education are reported in years. Age, education and WAIS-R are expressed as: Means (SD).

Table 2: Brain activation results for the unfair vs. fair and unfair vs. generous offers for all participants.

Hemisphere	Structure	BA	t	X	Y	Z	Cluster size
<i>Unfair>Fair</i>							
L	Insula	*	9.29	-33	14	13	5883
R	Insula	*	10.37	36	17	1	6494
L	Medial Frontal Gyrus	6	10.60	-6	-4	55	27771
R	Cingulate Gyrus	24	8.79	6	-4	31	508
R	Medial Globus Pallidus	*	5.92	12	-7	-8	334
R	Superior Occipital Gyrus	19	10.10	33	-70	25	12276
R	Inferior Occipital Gyrus	18	14.20	27	-88	-8	126122
R	Cuneus	18	5.72	12	-97	22	477
<i>Fair>Unfair</i>							
L	Middle Frontal Gyrus	8	5.61	-24	20	46	542
R	Postcentral Gyrus	5	5.78	21	-43	64	546
<i>Unfair>Generous</i>							
L	Insula	*	9.51	-30	23	13	4772
R	Insula	*	9.47	36	17	1	5770
L	Medial Frontal Gyrus	6	10.92	-3	-4	58	14635
R	Cingulate Gyrus	24	6.74	6	-4	31	482
R	Middle Frontal Gyrus	46	6.25	51	32	25	1323

R	Precentral Gyrus	6	8.52	42	-1	31	9208
R	Medial Globus Pallidus	*	5.89	12	-7	-8	328
L	Middle Temporal Gyrus	21	5.76	-54	-43	7	450
R	Superior Occipital Gyrus	19	11.45	33	-70	25	11468
R	Inferior Occipital Gyrus	18	13.76	33	-85	-8	126738
R	Precuneus	7	6.16	9	-76	43	1539
<i>Generous>Unfair</i>							
L	Middle Frontal Gyrus	8	6.24	-24	20	46	977
R	Postcentral Gyrus	5	6.05	21	-43	64	487

BA, Brodmann's Area; L, left hemisphere; R, right hemisphere; x, y, z in Talairach coordinates. Cluster size in mm³.

Table 3: Brain activation results for the human vs. computer offers for all participants.

Hemisphere	Structure	BA	t	X	Y	Z	Cluster size
<i>Human>Computer</i>							
R	Amygdala	*	6.41	18	-7	-11	727
R	Fusiform Gyrus	37	7.02	39	-43	-17	4874
L	Parahippocampal Gyrus	34	5.89	-21	-1	-11	395
R	Inferior Frontal Gyrus	47	6.08	36	29	-8	362
L	Medial Frontal Gyrus	9	6.39	-3	50	34	2014
R	Medial Frontal Gyrus	10	5.87	3	44	-8	290
L	Inferior Occipital Gyrus	19	5.41	-45	-70	-8	871
L	Culmen	*	5.43	-39	-40	-20	356
<i>Computer>Human</i>							
L	Parahippocampal Gyrus	19	5.64	-30	-40	-5	353
L	Cingulate Gyrus	23	7.03	-3	-31	28	1280
R	Middle Frontal Gyrus	8	6.34	42	26	37	1822
R	Middle Frontal Gyrus	10	6.57	33	41	22	773
L	Medial Frontal Gyrus	6	7.64	-3	-4	52	1551
L	Middle Frontal Gyrus	6	4.95	-27	-7	58	297
L	Middle Frontal Gyrus	10	5.34	-39	44	16	353

L	Middle Frontal Gyrus	8	7.78	-36	29	43	1923
L	Inferior Parietal Lobule	40	5.68	-30	-52	37	1225
L	Precuneus	7	9.47	-9	-76	49	36589
L	Culmen	*	6.04	-9	-49	-2	265

BA, Brodmann's Area; L, left hemisphere; R, right hemisphere; x, y, z in Talairach coordinates. Cluster size in mm³.

Figure Captions

Figure 1:

Timeline for a single round of the Ultimatum Game. Each round began with cross-hair presentation that was jittered in length (4-10 seconds). The participant then saw the photograph and name the proposer or the photograph of a computer and the label “computer” for 4 seconds. Next, participants saw the offer proposed for 4 seconds, followed by a 4 second interval during which they could accept or decline the offer. Outcomes (4 seconds) were then revealed based upon the response of the participant.

Figure 2:

Behavioral results from the Ultimatum Game. (A) On average, older adults accepted fewer offers as compared to younger adults. (B) Older adults accepted fewer generous (\$9:\$1;\$8:\$2) and unfair (\$3:\$7;\$2:\$8) offers as compared to the young. * ($p < .05$); # ($p < .10$).

Figure 3:

Anterior insula and DLPFC activity related to Ultimatum Game offers. (A) An example of a statistical map of the t statistic for the contrast [unfair offer – fair offer] in all participants showing activation of bilateral anterior insula and DLPFC. Areas in orange show greater activity to unfair than fair ($p < .0025$). Statistical maps for the contrast [unfair offer – generous offers] were very similar to the map displayed. (B) Average percent signal change in the anterior insula. Older adults had more activation to generous offers as compared to the young. (C) Average percent signal change in the

DLPFC. Older adults had more activation to generous and unfair offers as compared to the young. * (p<.05).

Figure 4:

Time course of activation in the anterior insula and DLPFC for offers. (A) Older adults show more sustained activation as compared to the young for generous offers. (B) Older adults show more activation as compared to the young for generous and unfair offers. * (p<.05); # (p<.10).

Figure 5:

Amygdala and DLPFC activity related to human or computer proposers in the Ultimatum Game. (A) Statistical map of the t statistic for the contrast [human proposer – computer proposer] in all participants showing activation of bilateral amygdala and DLPFC. Areas in orange show greater activity to human as compared to computer proposers; areas in blue show the opposite (p<.0025). (B) Average percent signal change in the amygdala. Participants, regardless of age, had more activation of to human proposers as compared to computer proposers. (C) Average percent signal change in the DLPFC. Participants, regardless of age, had more activation of to computer offers as compared to human offers. * (p<.05).

Figure 6:

Time course of activation in the amygdala and DLPFC for offers. (A) Participants show more sustained amygdala activation to human as compared to computer proposers. (B) Participants show more sustain activation for computer offers as compared to human offers. * (p<.05); # (p<.10).

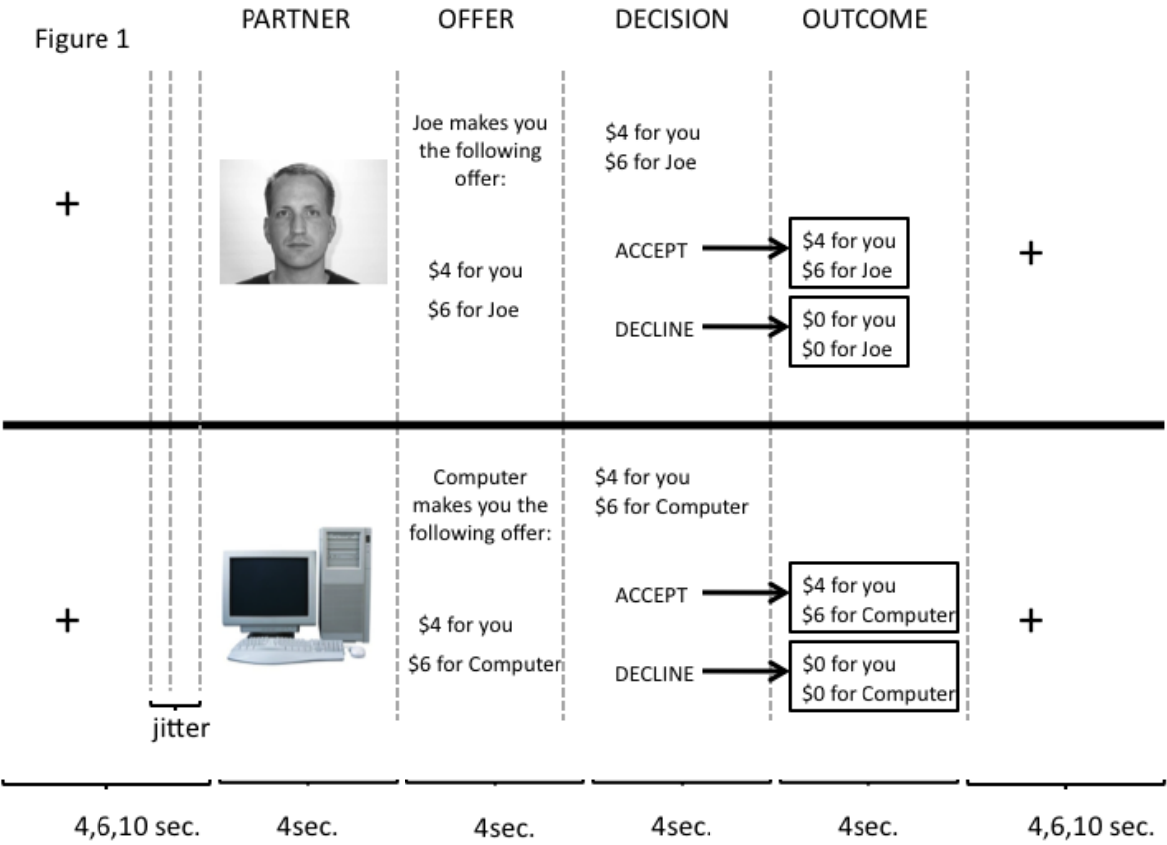


Figure 2A

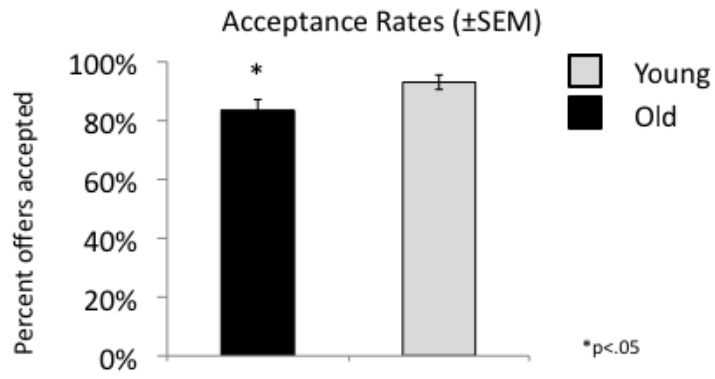


Figure 2B

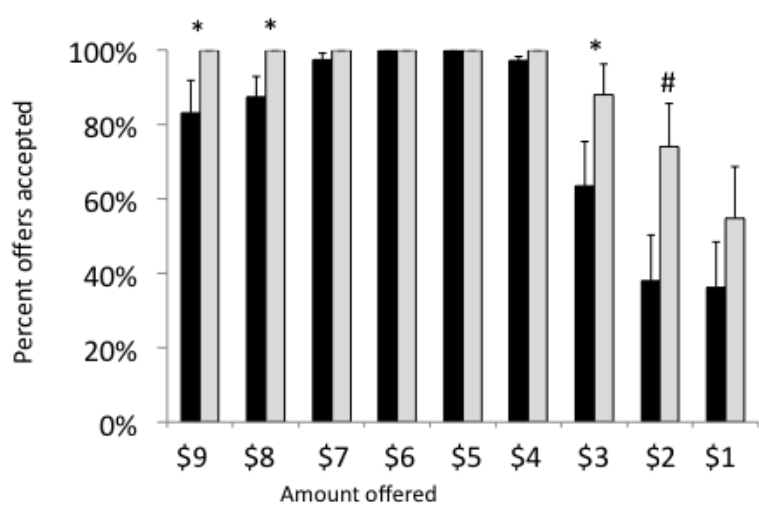


Figure 3A

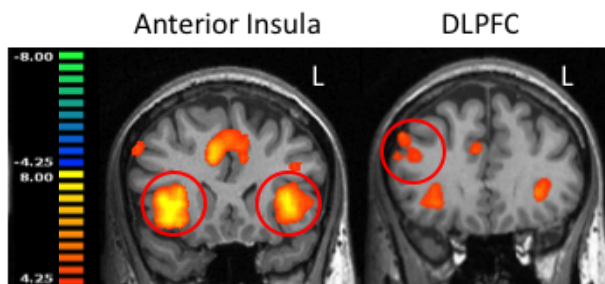


Figure 3B

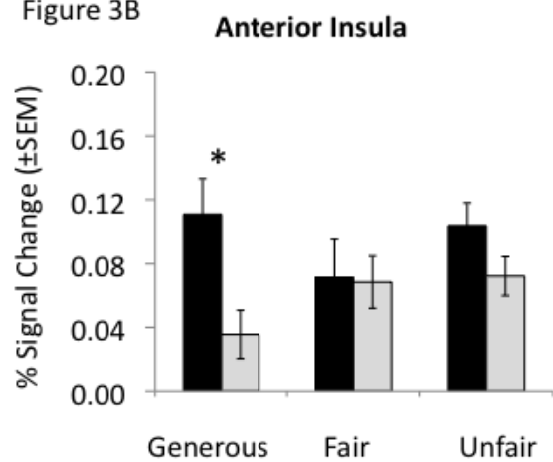


Figure 3C

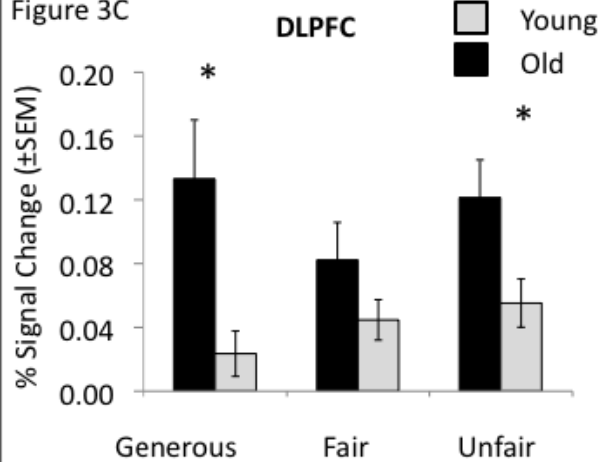


Figure 4A Anterior Insula Activation Time Course

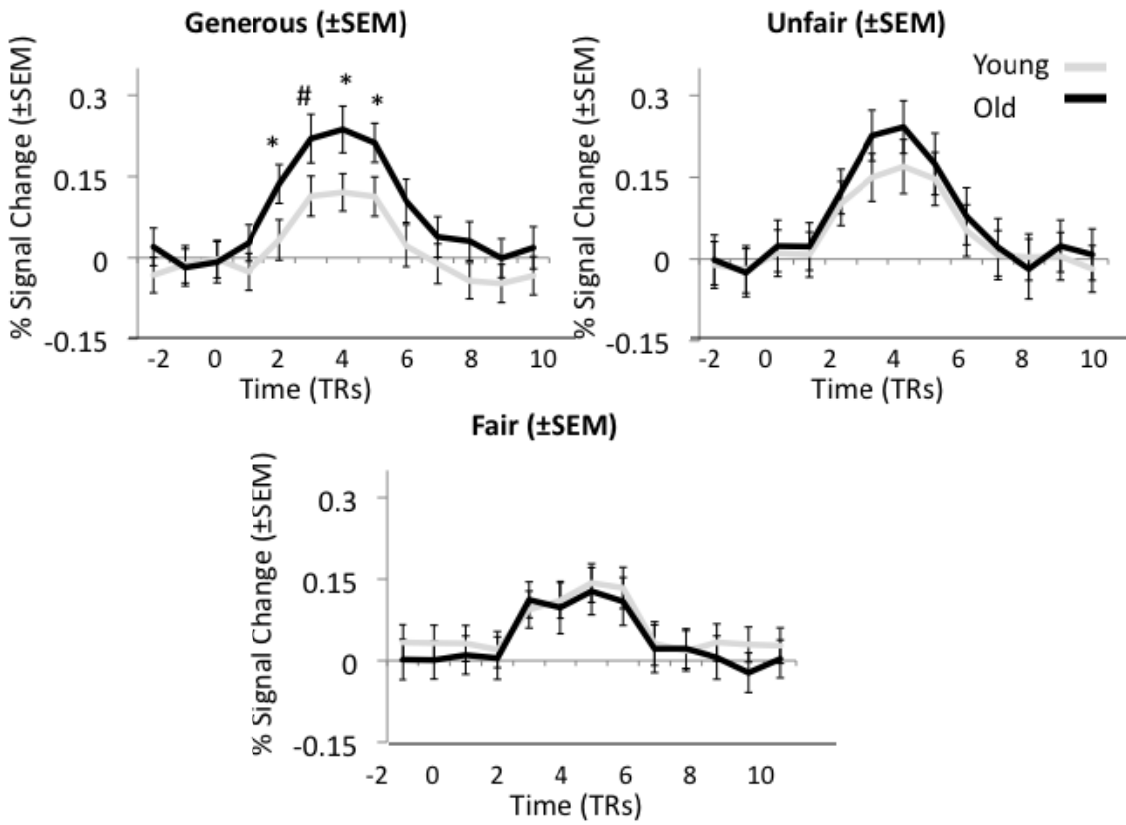


Figure 4B DLPFC Activation Time Course

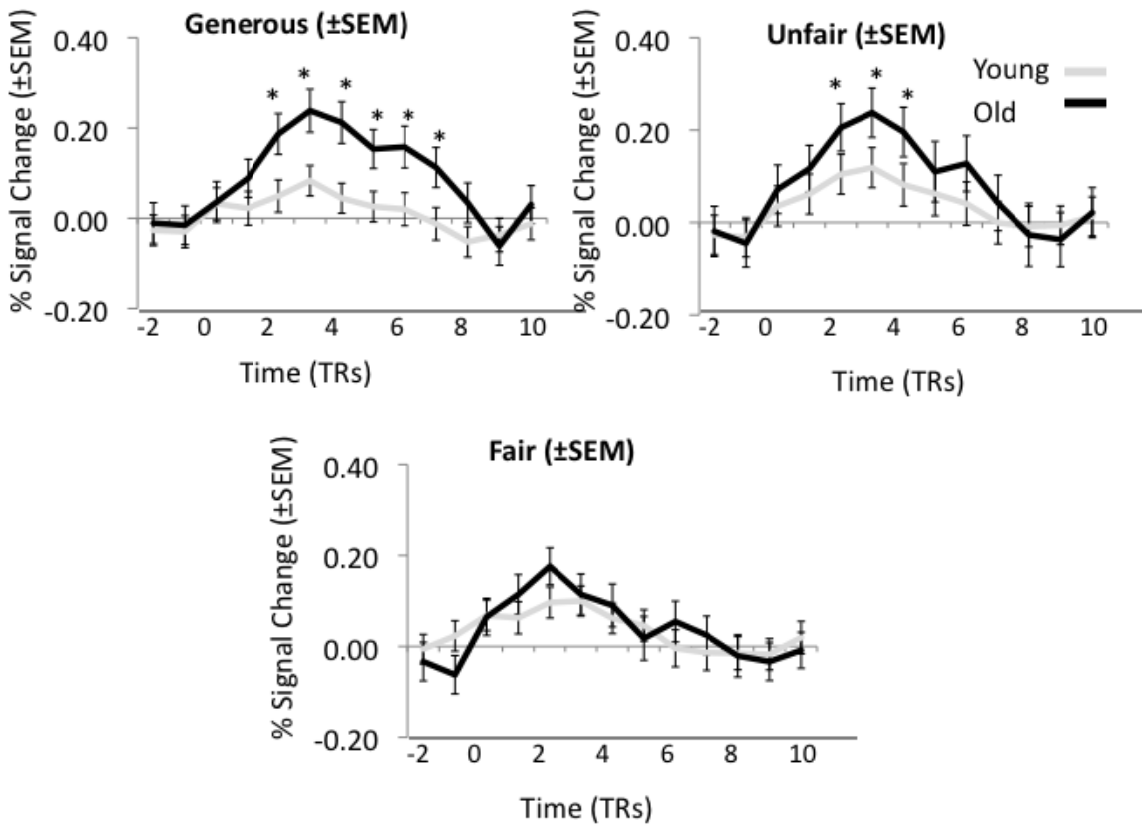


Figure 5A

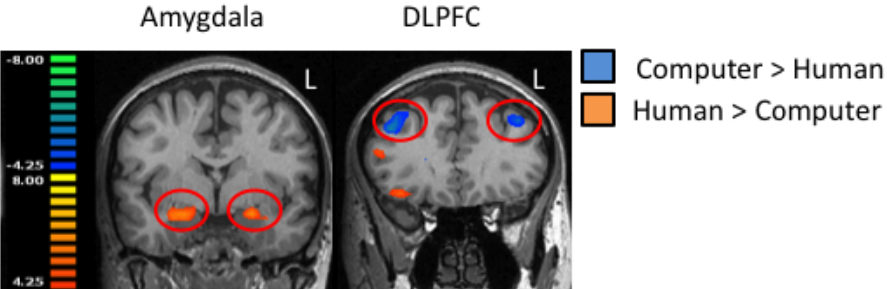


Figure 5B

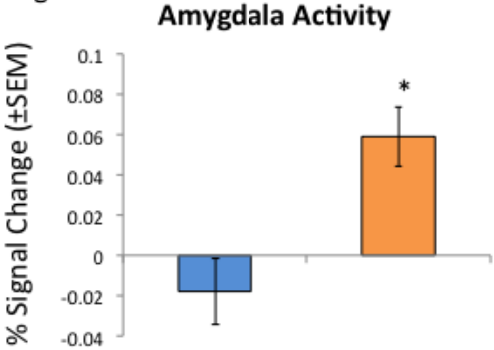


Figure 5C

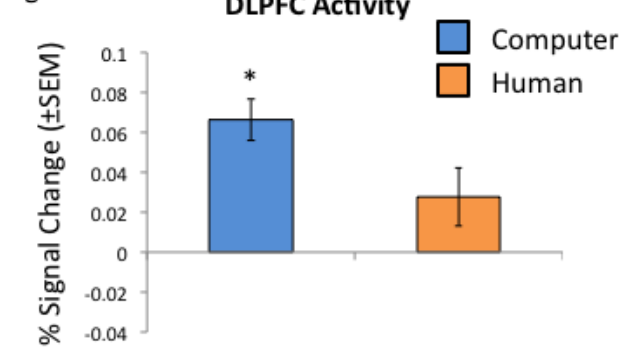


Figure 6A

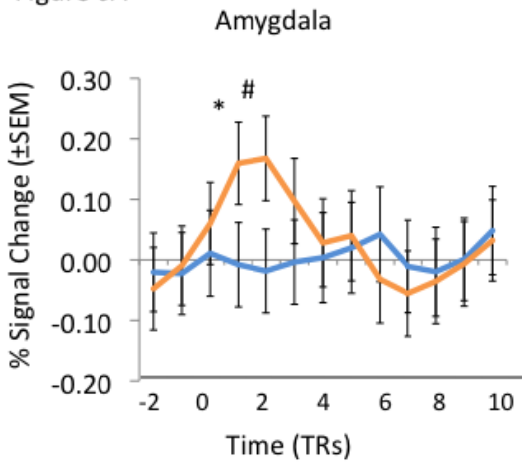
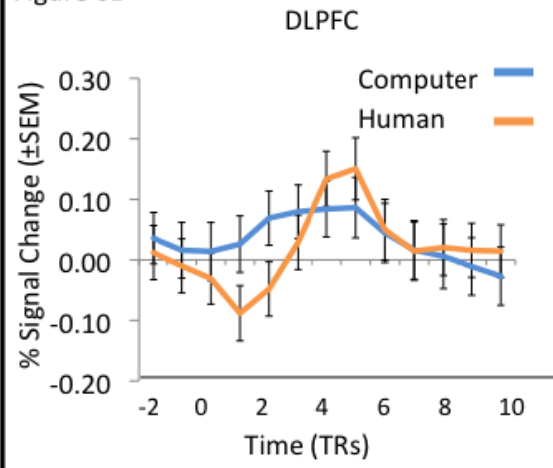


Figure 6B



Supplemental Results

Exploratory analysis of Human vs. Computer (Early vs. Late DLPFC activation)

An exploratory follow-up analysis of early (0-6 seconds) and late (6-16 seconds) DLPFC percent signal change was performed. These time windows were selected based upon the extracted group time course data. The young had marginally less activation ($p=.07$) as compared to the old for the first 6 seconds after an offer. However, there was a no age group difference for late DLPFC average percent signal change. Computer proposers elicited more DLPFC activity early in the time course as compared to human proposers [$F(1,25)=27.05$, $p<.01$; Supplemental Figure 2]. In contrast to the early period, human proposers elicited more late activity of the DLPFC as compared to computer proposers [$F(1,25)=21.87$, $p<.01$]. There were no interactions between proposer type and age group for early or late DLPFC activity.

Time course activation

As a follow-up analysis, one-sample t-tests were used to determine significant activation from zero for each group for each comparison (Generous vs. Unfair vs. Fair; Human vs. Computer; Accepted vs. Rejected)

Human vs. Computer

Young and old adults showed significant amygdala activity above baseline to offers made by human, but not computer proposers (Supplemental Figure 3A). Initially, DLPFC activity to offers made by human proposers was suppressed, but increased significantly more than baseline in the young (Supplemental Figure 3A). This same DLPFC activity pattern was seen in the old for human proposer, however the initial suppression was not significant. The young showed no significant activity as compared to baseline within the DLPFC for offers made by

computer proposers. In contrast to the young, old adults had more activation of the DLPFC to offers made by computer proposers as compared to baseline (Supplemental Figure 3A).

Generous, Fair & Unfair Offers

Both young and old showed significantly more insula and DLFC activation to generous, fair and unfair offers as compared to baseline (Supplemental Figure 3B).

Accepted vs. Declined

Both young and old showed significantly more insula activation to accepted and declined offers as compared to baseline (Supplemental Figure 3C).

Supplemental Table

Supplemental Table 1: Comparison of acceptance rates and effect sizes of unfair offers in two studies (Roalf et al. under review & the current study)

Study	Young Acceptance Rate	Old Acceptance Rate	Cohen's <i>d</i>	Effect Size <i>r</i>
Roalf et al., Under review	76.37% (24.33)	57.73% (33.18)	0.64	0.31
Current Study	79.23% (26.70)	58.67% (31.38)	0.72	0.34

Acceptance Rates are expressed as Means (SD).

Supplemental Figure Captions

Supplemental Figure 1:

Coronal brain slices documenting the midpoint of the three regions of interest: Amygdala (Left: -23, -5, -15; Right: 23,-5,-15); Anterior Insula (Left: -37,10,5; Right: 37,10,5); DLPFC (Left: -35,19,29; Right: 35,19,29).

Supplemental Figure 2:

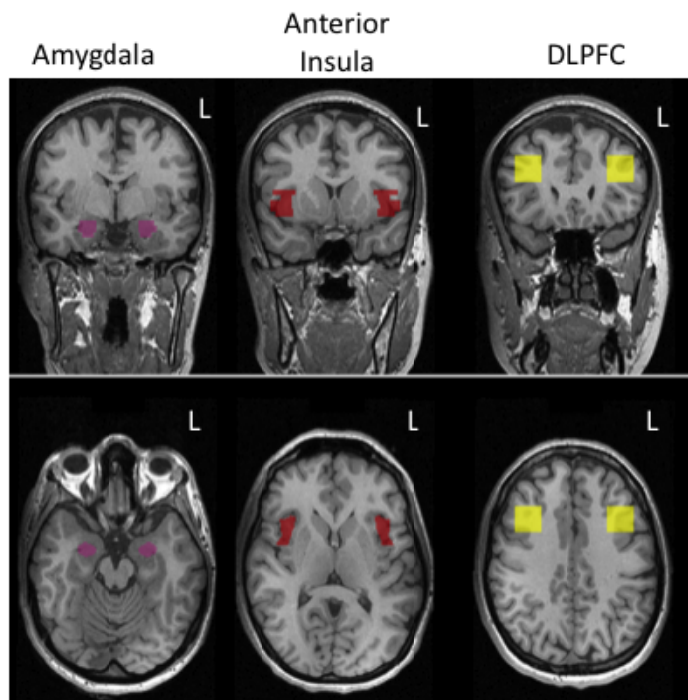
Average early and late DLPFC activation by group to offers by human and computer proposers.

Participants had more activation to computers early in the time course as compared to later in the time course. The opposite pattern, more activity later in the time course than earlier in the time course was found for offer from human proposers.

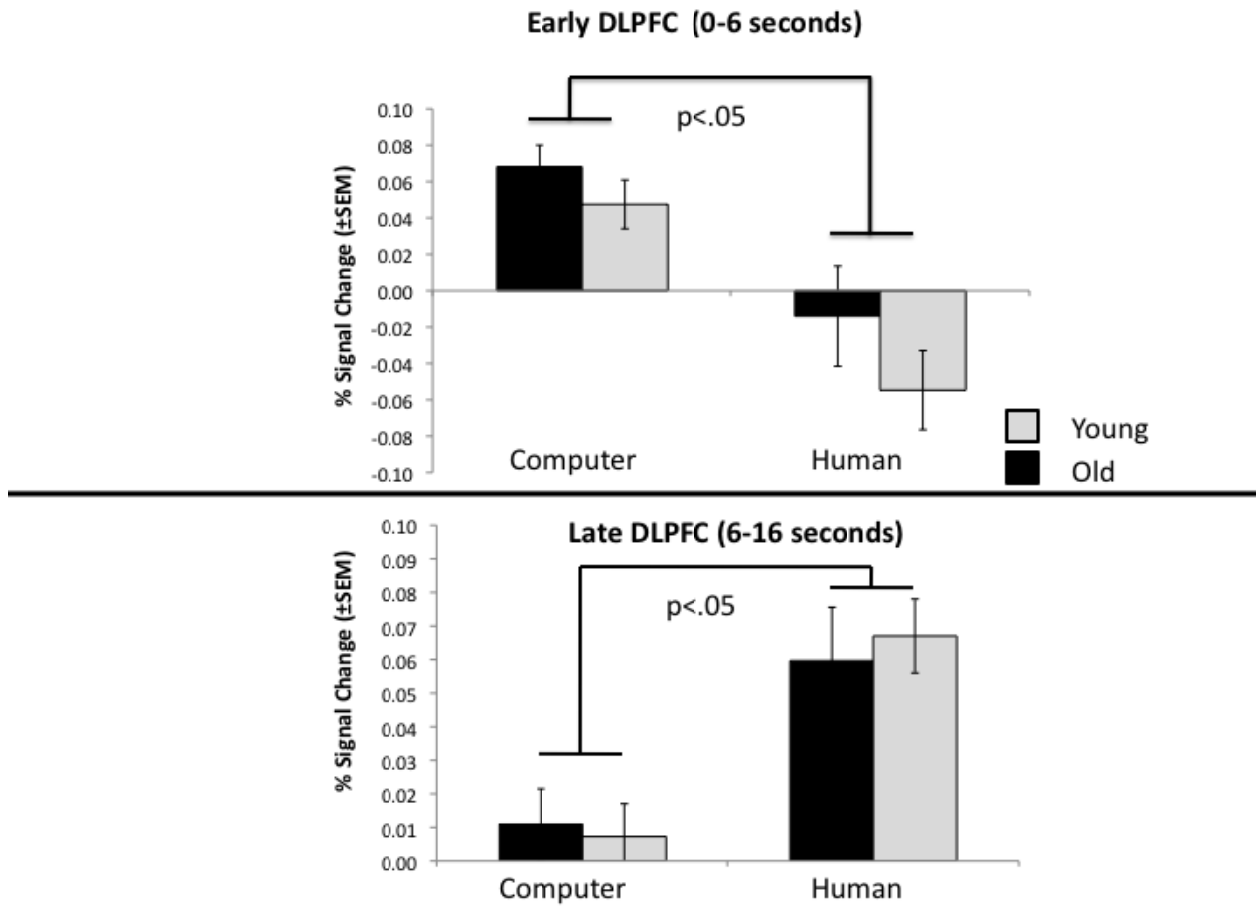
Supplemental Figure 3:

Significant time course activations as compared to baseline for (A) Human and computer proposers; (B) generous, fair and unfair offers; and (C) accepted and declined offers for older and younger adults. * $p < .05$, # $p < .10$.

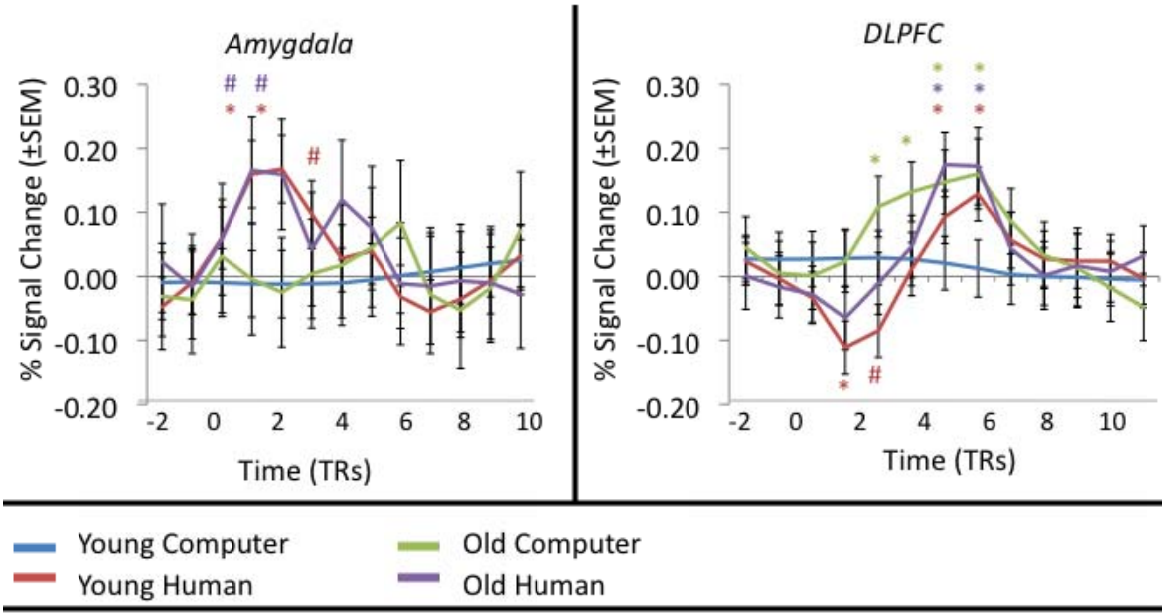
Supplemental Figure 1



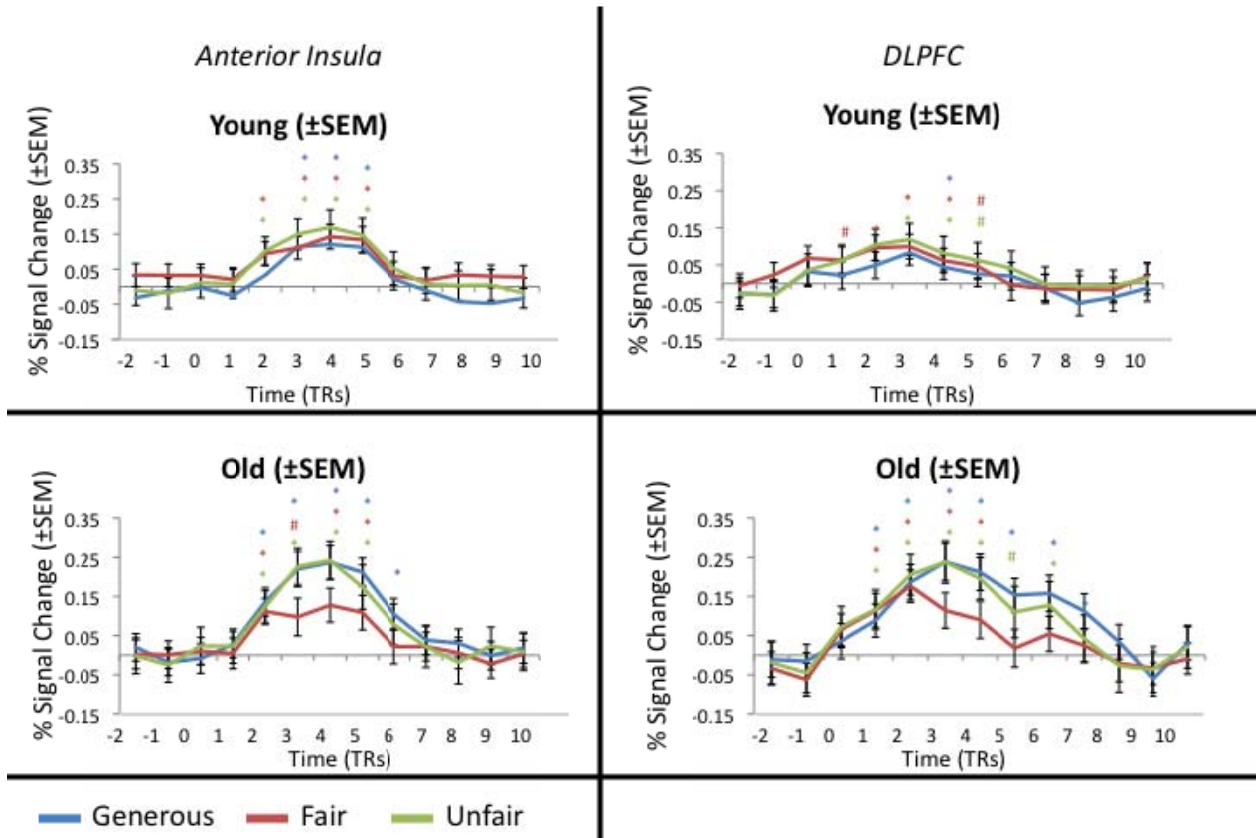
Supplemental Figure 2



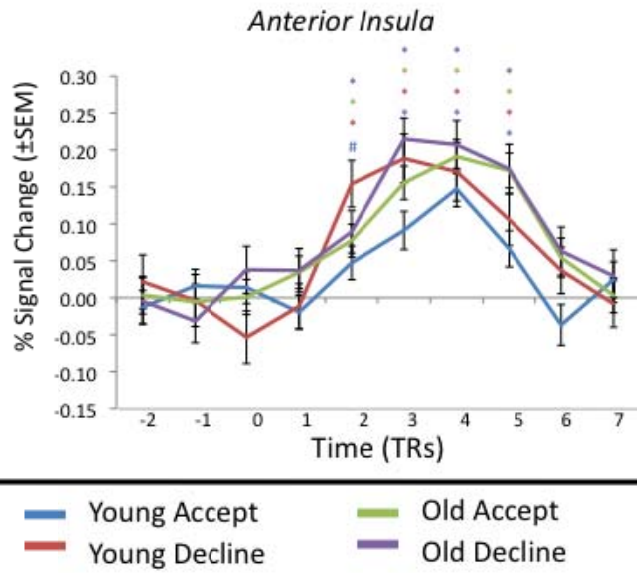
Supplemental Figure 3A



Supplemental Figure 3B



Supplemental Figure 3C



Chapter 4

General Discussion

Summary of Experimental Findings

Age-related changes in non-social and social decision-making were studied using behavioral and neuroeconomics methods. Self-report questionnaires indicated that older adults were more risk-averse and less risk-seeking than younger adults. The young and the old weighed risk and reward similarly in a non-social economic decision-making task (delay-discounting). In contrast, older adults differed from the young during social economic decision-making. When making economic offers, older adults were more likely than the young to equally share a sum of money. Furthermore, when accepting offers from others, older adults were more likely to reject offers that deviated in equity. In older adults, greater rates of rejection in the UG were accompanied by more neural activity in two regions associated with emotional and cognitive processes of decision-making, the anterior insula and dorsolateral prefrontal cortex. Taken together, these data suggest that older adults have no difficulty recognizing activities that involve risk and perform as well as the young in complex non-social decisions. However, when decisions involve socio-emotional components, older adults are more likely to use an equity rule even when it results in fewer rewards. Moreover, older adults had more activity of the anterior insula, which is associated with aversive behavioral responses (Singer et al., 2009), to both unfair and generous offers as compared to young adults. The old also had more DLPFC activity as compared to the young and activity in this region is associated with cognitive resources necessary to make complex decisions (Hare et al., 2009). I argue that the source of age-related differences in social decision-making lies in improved control of

social-emotional experiences that occurs in aging. In the following sections, I discuss the role of affective and deliberative information processing in decision-making and how these systems mediate social decision-making in older adults.

Multiple systems guide decision-making

The study of decision-making examines the mechanisms that underlie choices, preferences and judgments (Peters et al., 2007). Decisions are made between alternative courses of action based on cognitive evaluation of the potential outcomes. Economic models provide the foundation for rational decisions and judgments. However, real-world decisions often violate the principle of rationality (Fehr & Camerer, 2007). The reliance of these models on several assumptions is the source of their failure. For instance, they assume that people take the time to calculate values for each option or that they know the actual outcome probabilities. In reality, humans rarely, if ever, have all the information necessary to make a decision or foresee all the possible outcomes, so when making choices, people often balance what they *know* about a decision with what they *feel* about a decision. In fact, people rely on affect to guide judgments and decisions in everyday life (Slovic et al., 2002). For example, when purchasing a new car, people report to relying on emotional responses (i.e., exhilaration when driving), not rational economic choices (i.e., price; Sheller, 2004). This suggests that decision-making is not a unitary process, but that both cognitive and emotional processes contribute to choice, preference and judgments. The dual system that has received the most attention in decision-making is the affective/deliberative system (Loewenstein & O'Donoghue, 2004; Sloman, 1996). The affective system is responsible for automatic, associative, fast, effortless, thoughts and feelings. The affective system provides information about the valence

("goodness" or "badness") of decision options, which can motivate choice (Bechara et al., 1994). Affect serves or substitutes for information that would otherwise guide decisions (Kahneman, 2003), it diverts attention to salient features of decisions, and motivates one to take action (Peters et al., 2007). In addition, affect can be used as a 'common currency' that permits comparisons and contrasts among decision alternatives (Peters et al., 2007). Mood that is incidental or unrelated to the decision also impacts choice behavior (Forgas, 1995; Isen & Patrick, 1983). The affective system is mediated by both cortical (i.e., prefrontal cortex, anterior insula) and subcortical (i.e., amygdala, nucleus accumbens) brain regions. In contrast, the deliberative system is responsible for controlled, reason-based, slow, effortful behavior that assesses options in a goal-based manner and monitors the quality of the affective information and its impact on decisions. Deliberative processes are used for comparisons among choices based on explicit features (i.e., reward-value). Furthermore, the deliberative system is flexible and provides effortful control over the thoughts and feelings generated by the affective system. This system is primarily comprised of anterior and dorsolateral regions of the prefrontal cortex and posterior parietal cortex (Miller & Cohen, 2001; Duncan et al., 1996; Smith & Jonides, 1999; Stuss & Knight, 2002).

Age-related changes in dual system processing and decision-making

Deliberation and affective experience change with age. Older adults show deficits in deliberation, such as problem solving (Diehl et al., 1995; Cornelius & Caspi, 1987). In addition, older adults have poorer attention and memory, which impact deliberative processes (Somberg & Salthouse, 1982; Salthouse & Kersten, 1993; Salthouse, 2006). Concurrently, older adults have improved emotional experiences (Carstensen et al., 1999), as negative affect decreases

and positive affect increases or remains stable (Carstensen et al., 2000; Gross et al., 1997; Lawton et al., 1992; Magai et al., 2009; McConatha et al., 1997; Mroczek & Kolarz, 1998). For example, older adults focus more on positive than negative stimuli (i.e., Mather et al., 2004), and have shorter bouts of negative mood throughout the day as compared to the young (Carstensen et al., 2000). This is in the face of the fact that older adults report experiencing emotions with the same intensity as younger adults (Carstensen et al., 2000; Levenson et al., 1991; Mikels et al., 2005; Tsai et al., 2000). In the following sections, I argue that these age-related enhancements in affective experience lead older adults to make decisions using equity during social decision-making. I also discuss the impact that age-related deficits of the deliberative system (i.e., cognitive decline) may have on decision-making and suggest these deficits lead to changes in decision strategy, but are not sufficient to cause specific changes in decisions that occur in a social context.

Age-related change in the affective system and decision-making.

Why do older adults focus more on equity than younger adults during social decision-making in the UG? In the following section, I argue that the reliance on an equity rule in older adults occurs because of increased reliance on emotional experiences. This argument is based on the following: 1) UG decisions are associated with emotional responses that are accompanied by more neural activity in emotion brain regions in older adults; 2) older adults are better at cognitive regulation of their emotions; 3) emotional experiences, particularly positive experiences, are more salient in older adults; and 4) social-emotional interactions are more important to older adults than to the young; 5) decisions without a social context are

similar in the young and old, at least as measured by delay discounting and 6) that older adults expect others to be equitable during social economic interactions.

A critical aspect of the UG is that it requires individuals to make decisions that involve another person. This introduces a social-emotional component (Sanfey, 2007). In younger adults, unfair UG offers elicit negative emotional responses about the actions of the other person (i.e., disgust/anger; Pillutla & Murnighan, 1996). Rejection of unfair offers in other studies was associated with activation of the anterior insula, a brain region involved in processing aversive emotional information (Sanfey et al., 2003; Knoch et al., 2006). This brain activity may be related to younger adults' self-interested goals, as more unfair offers were associated with more anterior insula activity and lower acceptance rates (Sanfey et al., 2003). I found a similar pattern in younger adults' behavior and brain response. They rejected unfair offers and had more activation of the anterior insula to unfair offers, but less activity to fair or generous offers. However, older adults showed different behavioral and neural patterns in the UG. Older adults rejected more unfair and generous offers as compared to the young. Furthermore, they showed a u-shaped response of the anterior insula, with more activity in response to generous and unfair offers. These data imply that deviations in equity in the UG elicit greater aversive emotional responses in older adults as compared to younger adults, regardless if they are positive or negative, during the UG.

Older adults are better at controlling their emotions as compared to the young. Older adults remain in negative moods (i.e., anger) for shorter periods of time and reflect on negative incidents less than the young (McConatha et al., 1997). In addition, older adults are better at restoring positive affect after negative mood induction (Kliegel et al., 2007). Accumulating

evidence suggests that older adults' positive bias results from a change in time perspective (Carstensen et al., 1999; Lang & Carstensen, 2002). Older adults view time as more constrained than younger adults and are motivated by goals that increase emotional well-being (Carstensen et al., 1999). This is reflected in older adults' 'positivity effect' in memory and attention where they attend to and remember disproportionately more positive than negative material (Carstensen & Mikels, 2005; Mather & Carstensen, 2003). Interestingly, when younger adults are faced with limited time perspectives such as during a terminal illness, they also increase their interest in positive social activities and relationships (Carstensen & Fredrickson, 1998; Fung et al., 1999). Finally, the brain regions that subserve emotion undergo far less age-related change than brain regions associated with deliberation (Raz et al., 2004; Allen et al., 2005; Grieve et al., 2005; Mu et al., 1999; Salat et al., 1999; Salat et al., 2001). Some studies show that older adults have proportionally less amygdala activity to negative emotional stimuli (Gunning-Dixon et al., 2003) and more activity to positive stimuli (Mather et al., 2004). However, increasing positive or suppressing negative emotion requires activation of cognitive control regions of the prefrontal cortex (Ochsner & Gross, 2005). Taken together, these results suggest that emotion is preserved, and possibly enhanced, in that there is a bias toward positive emotions in older adults. This positive bias may drive older adults to make decisions that increase positive feelings, such as decisions that result in equity. Importantly, equal outcomes result in less distress (Adams, 1965; Goodman, 1977) and presumably more positive affect, which may be reflected by less anterior insula activity to fair offers as compared to generous or unfair offers in the current data. Older adults may work to maintain these positive feelings by rejecting offers that do not match their equity rule. Thus, age-related

enhancement of affective information may lead older adults to replace or supplement cognitive 'rules' with emotional 'rules' when making decisions.

Older adults also emphasize social-emotional relationships more than the young, which influences social decision-making in the UG. Older adults emphasize creating meaningful relationships or contributing to society when describing their life goals. In contrast, younger adults emphasize learning and engaging in new life challenges (Bauer & McAdams, 2004). These emotional changes also guide older adults' views of others. In describing the qualities of the ideal person, older adults indicate that a positive view about life and positive social relationships are important, whereas younger adults mention being career-oriented and productive (Ryff, 1989). Changes in emotion also affect social relationships. Older adults spend more time and have a stronger emotional closeness with family members (Carstensen, 1992). Despite the loss of loved ones, even the oldest old maintain strong social relationships (Lang & Carstensen, 2002). The risk-taking data from the DOSPERT supports this notion, as social decisions are the only domain in which the old report less risk-taking behavior than the young and this may carryover to their behavior in the UG. In summary, age-related changes in social-emotional goals motivate older adults to pursue different emotionally gratifying social experiences (Carstensen, 2006; Charles & Carstensen, 2007). Age-related changes in social relationships may affect decision-making, particularly when social interactions are involved.

Age-associated changes in the deliberative system and decision-making

Age-related cognitive decline could also explain why older adults focus more on equity. Disruptions in cognitive processing (i.e., attention, memory) may lead older adults to adopt simpler decision strategies than the young, such as focusing on equity rather than a more

complex cognitive processing such as weighing and maximizing rewards (Mata, 2007). In general, older adults' information-gathering is more simplistic and they use far less information during decision-making than the young (Mata et al., 2007; Johnson, 1990). For example, younger and older adults were shown a series of products (i.e., car) and were told that they could view specific information about each product (i.e., price). These features were displayed in a matrix of boxes on a computer screen. Participants could view as many of the boxes as they desired, for as long as they desired, but could only view one box of information at a time. Older adults viewed less information (fewer boxes), but viewed this information for longer as compared to the young prior to making a decision, however, their final decisions were similar to younger adults (Johnson & Drungle, 2000b; Riggle & Johnson, 1996). This suggests that older adults either have a limit to the amount of information that they can consider when making a decision, or that they prefer to base decisions on a narrower set of information. In fact, younger adults adopt similar, simple strategies when asked to make decisions when their deliberative system is challenged with a working memory task (Mutter & Pliske, 1996; Mutter & Williams, 2004). In the current data, it appears that younger adults employ a reward maximization strategy while older adults use an equity strategy. Younger adults only reject unfair offers and never reject generous offers in the UG. For example, younger adults may compare their actual reward (i.e., \$3) to the maximum attainable reward (i.e., \$10). The difference between the maximum reward and actual reward ($\$10 - \$3 = \$7$) may drive choice behavior such that large differences are equivalent to unfair offers, which are more likely to be rejected, and small differences are equivalent to generous offers, which are always accepted. In contrast, older adults' strategy may be more focused on equity. It remains unclear if a

change in decision strategy is the result of explicit deficits of the deliberative system, but the age-related shift to the use of an equity heuristic leads older adults to poorer reward outcomes during this social decision-making task.

Older adults are also more likely to rely on decision heuristics, or rules, as compared to the young (Johnson, 1990; Riggle & Johnson, 1996). Employing a decision heuristic is a strategy that allows for conservation of cognitive resources (Payne et al., 1988). For example, older and younger adults were asked to select the political candidate they would support based upon a variety of information (Riggle & Johnson, 1996). Older adults were more likely to eliminate potential candidates immediately when their decision criteria were not met. In contrast, younger adults rarely adopted this heuristic and continued to consider every candidate until information was gathered on all possible candidates (Riggle & Johnson, 1996). This suggests that older adults may compensate for their inability to hold large quantities of information in mind by employing an 'elimination' heuristic. Thus, older adults employ simpler decision rules and are more likely to use a rule as compared to younger adults.

It is logical to suggest that a change in decision-making reflects impaired cognitive processing in older adults. Older adults have reduced processing speed (Salthouse, 2000; Salthouse, 1996) and poorer explicit learning and memory (Salthouse, 2006) as compared to younger adults. Yet, numerous studies indicate that healthy older adults have preserved decision-making as compared to younger adults (for review see Peters et al., 2007), including the delay-discounting data reported here. Thus, age-related changes in deliberation alone may not be sufficient to affect delay-discounting. However, a pilot study of older individuals with mild cognitive impairment (MCI), a transition stage that signals impending Alzheimer's disease,

shows that impairment of the deliberative system does affect delay-discounting behavior. Those with MCI (N=9) are much less likely to discount delayed rewards as compared to healthy older (N=30) and younger adults (N=28;Figure 1). In fact, these patients focused on the reward magnitude and ignored the fact that there was a delay to the rewards. These data suggests that memory or other cognitive deficits affect decision-making during delay discounting, which has previously been shown in healthy adults (Shamosh et al., 2008; Hinson et al., 2003) and patients with substance abuse disorders (Hoffman et al., 2006). Studies in younger adults indicate that deliberative brain regions, including regions of the prefrontal cortex (vmPFC & DLPFC) and posterior parietal cortex are engaged during delay discounting choices (McClure et al., 2004; Kable & Glimcher, 2009), which differ from the regions of the brain engaged during the UG. Interestingly, Alzheimer’s disease results in more atrophy of the prefrontal (Salat et al., 2001) and parietal cortex (Foundas et al., 1997) as compared to age-matched controls. However, age-related changes in neural activity during delay discounting are unknown. It is possible that failure of the medial temporal lobe (i.e., hippocampus), disrupts memory for past experiences, or disruptions of the prefrontal cortex alters the ability to accurately represent future outcomes, may explain why MCI patients exhibit delay-discounting deficits.

-----Insert Figure 1 here-----

Does the balance between the affective and deliberative systems provide a mechanism for implementing or regulating decision ‘rules’ in social decision-making?

The question remains as to how younger and older adults implement their decision ‘rules’ in the UG. Recent studies suggest that the deliberative brain regions are important for controlling emotional impulses to reject unequal offers during the UG. First, the affective and

deliberative systems show differential activity to unfair offers. Higher activity of the affective system (i.e., anterior insula) was related to higher UG rejection rates and anterior insula activity was higher than DLPFC activity when participants rejected unfair offers (Sanfey et al., 2003). However, DLPFC activity was greater than anterior insula activity to unfair offers that were subsequently *accepted* by participants (Sanfey et al., 2003). This suggests that the DLPFC is involved in cognitive control over the emotional impulse to reject some aversive, unfair offers, but these data are only correlative in nature. In the current study, older and younger adults did not show this differential pattern of response to offers that were subsequently accepted or rejected. This may be due to a lack of power as only a subset of participants (9 old and 5 young) rejected unequal offers and were included in that analysis, or it is possible that the DLPFC is not directly modulating the anterior insula. Support for the latter idea comes from a recent study that disrupted DLPFC activity during the UG. Direct disruption of the DLPFC, through the use of repetitive transcranial magnetic stimulation (rTMS), lead to an increase in the acceptance of unfair offers, even though participants still viewed these offers as unfair (Knoch et al., 2006). In contrast to Sanfey et al., (2003), these data suggest that the DLPFC modulates self-interested impulses and enables people to ‘implement their fairness goals’ (Knoch et al., 2006, pg 831). Simply, less DLPFC activity leads to more selfish behavior in the UG. However, rTMS disruption is not focal and may result in disruption of nearby regions of the cortex as well. But, these findings suggest a mechanism by which older adults implement an equity rule. More DLPFC activity in older adults to unequal offers enables them to overcome selfish impulses to accept the money and instead they employ their equity rule, which is emotionally driven. In contrast, less DLPFC activity in younger adults results in more self-

interested behavior, which is reflected in their lower rejection rates in the UG. Of course, the current data are only correlative in nature and there is as yet no direct evidence that the DLPFC is modulating self-interested responses in the UG, thus this interpretation should be taken with caution. Together, these data suggest that aging may affect the implementation of fairness rules and self-interested choices in the UG. These data, in combination with recent evidence for affective-deliberative interactions in delay discounting (McClure et al., 2004) and engagement of other emotion regions (i.e., amygdala) in regulating framing effects (De Martino et al., 2006) in decision-making, suggest that decision-making involves critical interaction between the affective and deliberative systems.

Alternative explanations for age-related changes in social decision-making

It is possible that other mechanisms mediate the decisions of equity in aging. For example, older adults may change their decision rules because they have more experience with social interactions and social decisions (Peters et al., 2007). More expertise may result in different expectations of how others will act during social exchanges. Older adults are better at making inferences about unknown individuals and are more focused on the behavior of others (Hess & Auman, 2001; Hess, 1999; Hess & Pullen, 1994). Thus, older adults may develop expectations on how social interactions should play out and when those expectations are not met, as would be the case with generous or unfair offers in the UG, older adults simply reject those offers. Furthermore, incorporating emotional and cognitive information during social decision-making may result in unrealistic expectations that others will be fair. In fact, some pilot UG data suggests that older adults expect other players in the UG to be equitable, whereas younger adults expect people to be somewhat unfair. Using the method of Sanfey

(2009) we assessed whether younger and older adults had similar expectations of proposers in the UG. We found that younger adults expected people to make offers that would be less than equal, whereas older adults expected others to make equal offers (Figure 2). Furthermore, a direct comparison of expectation showed that younger adults had significantly lower UG offer expectations as compared to older adults ($p=.03$). Thus, deviation from expectation may also play a role in age-related changes in social decision-making. Other explanations as to why older adults show intact non-social decision-making include more overall decision experience and the preservation of implicit cognitive processing in aging. For example, when comparing over-the-counter drugs, older adults report having more experience with these drugs, are more organized in their searches and focused on more relevant factors, such as active ingredients and side effects, as compared to the young (Johnson & Drungle, 2000a). It is likely that older adults have more experience with making decisions with a delayed outcome than the young, and this may enable older adults to make 'good' decisions even if they have subtle cognitive impairments.

-----Insert Figure 2 here-----

Caveats:

Some limitations should be noted. First, the present set of studies was focused on the evaluation of a range of decision-making in older adults, and further research using convergent methods is necessary to fully characterize changes in decision-making associated with age. Second, while these are the first studies to provide a comprehensive picture of decision-making in old age, the findings are limited due to the cross-sectional nature of the data. Studies over the lifespan are needed to confirm these findings. However, it is encouraging that similar

behavioral results were found in the UG across the two studies, suggesting that age does affect decision-making, particularly social decisions. Third, to my knowledge these are the first studies of social economic decision-making in older adults and as such, the methods employed are very similar to previous studies of the young. For example, the photographs of proposers used in the UG were only those of younger and middle aged individuals. It is possible that younger adults view these proposers as peers, while older adults may not. In fact, group biases exist in the UG, which affect decision outcomes. For example, gender affects UG offers (Solnick, 2007). Men attract higher offers than females, particularly from female proposers. Furthermore, male and female responders choose higher minimum acceptable offers when facing a female, but not male, proposer (Solnick, 2007). Thus, there may be important differences in behavior when interacting with individuals that are either 'in-group' (i.e., young vs. young) or 'out-group' (i.e., old vs. young). Thus, older adults' UG behavior may change if they were to receive offers from older proposers rather than young proposers. Further study into the specific factors of social interactions that are important for decision-making should consider such biases. Finally, the assessment of social economic decision-making was limited to the Dictator and Ultimatum games, however, there are numerous other measures (i.e., Prisoner's Dilemma, Trust Game, etc.) that assess other aspects of social decisions. It is possible that age-related differences in equity may affect reciprocal exchange as measured by the Trust Game. This may lead older adults to 'invest' (i.e., give up) more money in order to equilibrate outcomes, alternatively, they may find it more difficult to 'invest' in situations where the endpoint may not result in equitable outcomes (i.e., market volatility). Furthermore,

differences in equity rules may lead older adults to cooperate more in situations where it may be more beneficial to defect (i.e., Public Goods Game, Prisoner's Dilemma).

Conclusion:

Overall, this work shows that aging results in subtle changes in decision-making and these are domain dependent. Delay discounting performance was identical for younger and older adults. Older adults consider themselves more risk-averse than the young. However, when decisions involve social-emotional features, such as interaction with another person, older adults and younger adults do not make similar decisions. Older adults were more likely to reject offers from other individuals that were too generous or mildly unfair in the UG as compared to the young and these behavioral differences are associated with changes in emotion and cognitive processing regions of the brain. I suggest that this occurs because older adults use a decision rule due to an alignment of decision outcomes with social-emotional goals. Furthermore, older adults' decision-making experience may be particularly important when making social decisions. These data suggest that older adults are not poor decision-makers, but that they use social-emotional information differently than the young, and appear to be driven more by equity. I suggest that understanding the balance between deliberative and affective processes during decision-making is fundamental to understanding choice behavior in the old. Plainly stated, older adults make decisions that involve both the heart and the head.

Figure Captions

Figure 1:

Mean indifference ($\pm 95\%$ CI) points for delay discounting in patients with mild cognitive impairment (MCI), healthy older and younger adults. MCI patients discount delayed rewards less than healthy older or younger adults.

Figure 2:

Expectations in the Ultimatum Game were determined using a method similar to Sanfey, 2009. Older and younger adults were asked how other individuals would distribute \$10 in the UG. Participants were asked the number of people out of 100 that they believed would make a \$0, \$1, \$2, \$3, \$4, \$5, \$6, \$7, \$8, \$9, or \$10 offer. An average expected offer was computed for each participant. Average expected offer in younger adults ($p < .01$) was significantly less than fair (\$5), but this was not the case for older adults ($p = .65$). Younger adults had significantly lower expectations than older adults ($p = .03$).

Figures

Figure 1

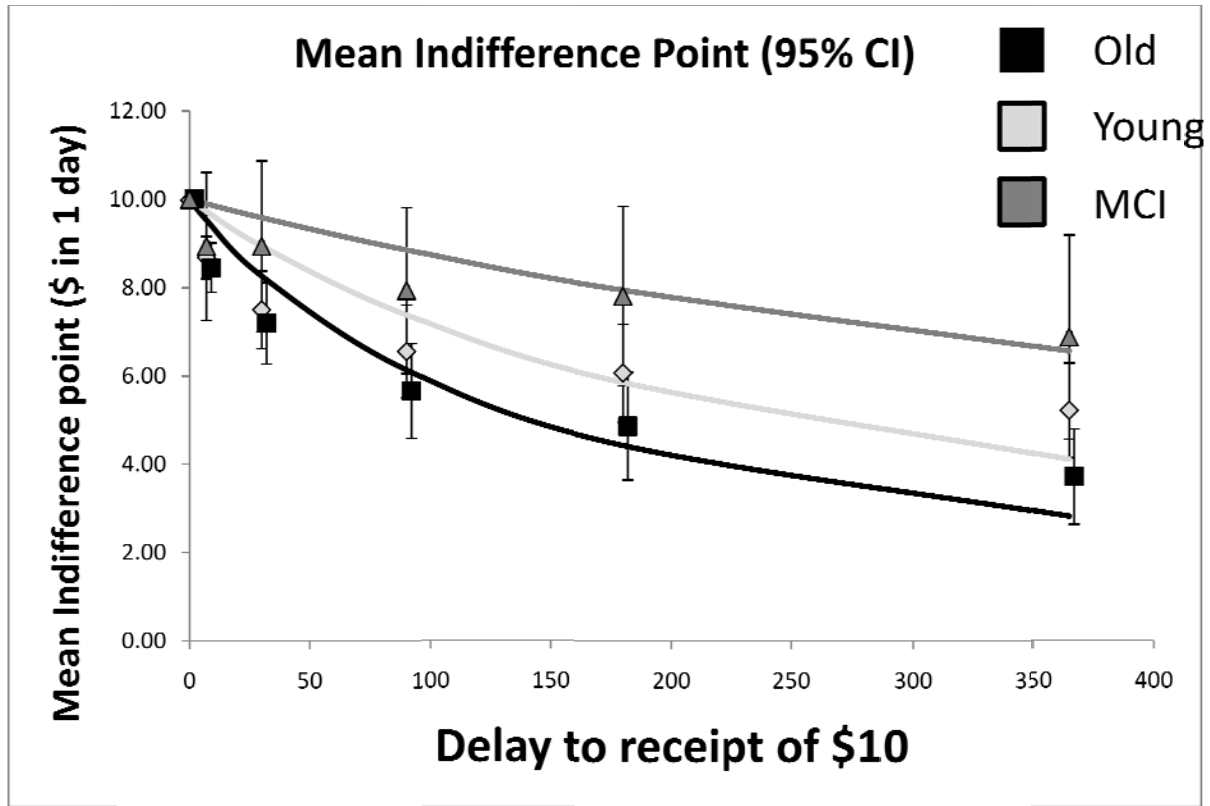
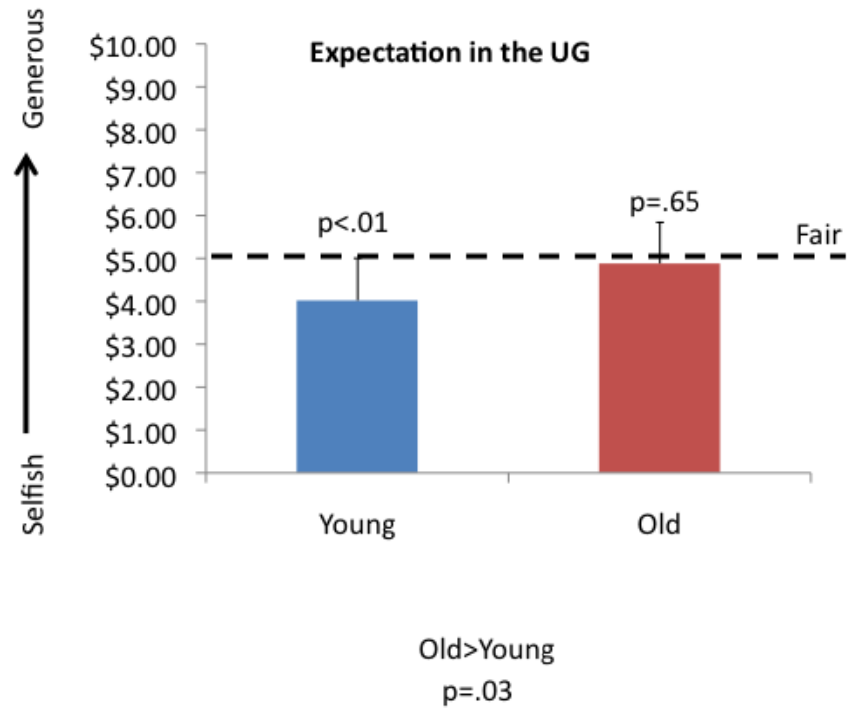


Figure 2



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Appendix
Decision-making task instructions:

(To be read to participant)

Thank you for coming in to help us out today. Today's visit will last about 2 hours.
Here is your \$10 for participating in today's study

(Pay subject \$10)

During today's visit you will participate in tasks and games in which you have to make decisions. For your participation today we have already paid you \$10 in cash. In some of these tasks and games you may earn an additional amount of money, which will be paid to you at a later date. It is important to keep in mind that some of the decision you make today will ONLY affect you and the amount of money that you might earn. Other decisions that you make will affect you (and the amount you can earn) and may affect other people that will participate in this study (and the amount of money that they can earn).

In some sections of this study you will be randomly paired with another participant. You will not find out who this person is, nor will he or she find out who you are, not now, nor after the experiment is over.

Remember that you will be making decisions for REAL money. You should understand that this not the researcher's money. The money is given to us by the university to use in a research study. ALL PAYMENTS WILL BE MAILED TO YOU AFTER THE COMPLETION OF THIS SESSION.

Ultimatum Game Instructions

Instructions: In this task you and another player have the opportunity to split \$10. The first player will make you an offer on how to split the \$10. You get the opportunity to accept or reject this offer. If you accept this offer you and Player 1 will split the \$10. If you reject the offer both players get nothing.

Examples:

Player 1 offer to split the money:

You \$5	Mover1 \$5
ACCEPT	REJECT
<hr/>	
You \$1	Mover1 \$9
ACCEPT	REJECT
<hr/>	
You \$2	Mover1 \$8
ACCEPT	REJECT
<hr/>	
You \$5	Mover1 \$5
ACCEPT	REJECT
<hr/>	
You \$0	Mover1 \$10
ACCEPT	REJECT

Dictator Game Instructions:

In this experiment you will be paired with another person who will play this game at a later date. You must decide how to split \$10 between yourself and your unknown partner. Each person who plays this game must decide how many dollars out of 10 (if any) they would keep and how many they would give to their unknown partner. Your response will be randomly paired with another participant. You will not find out who this person is, nor will he or she find out who you are, not now, nor after the experiment is over.

Example (1): Keep \$8 and Give \$2

Example (2): Keep \$5 and Give \$5

Example (3): Keep \$2 and Give \$8

These are examples only, the actual decision is up to each person. The amount you decide to keep is what you will earn and the amount that you decide to give is what your unknown partner will earn.

You will make your selection on the computer. You will be presented with options on how to divide the \$10. You will make your selection by using the UP and DOWN arrow keys. When you have made your choice press the SPACE bar to continue. You will then be presented with your unique CODE NUMBER. Please write this number down on the sheet provided. Please fill out the rest of the form, fold the sheet in half and place it in the DROP BOX. Also note that the experimenter will not know the personal decisions of those who participate in this experiment. A different member of the lab will view your response and pay you accordingly.

Delay Discounting Instructions

This task has 138 questions. For each question, you can choose between 2 options by clicking on it using the computer mouse. You can change your selection as often as you like and there is no right or wrong answer - we are interested in your personal preferences. Once you have finally decided which option you prefer you can register your preference and go on to the next question by clicking on the 'next question' box. One option will always be some amount of money available now. The other option will always be a fixed amount of money available after a waiting period. The waiting period will vary between 1 days (tomorrow) and 365 days. The choices you are making are real - if you choose 'money now' you would receive that amount of money at the end of the task and that if you choose 'money later' that you would actually have to wait before receiving the money.

Please try the demonstration below. When you are ready to begin the task, click on the 'begin task' box.

Abbreviations:

AARP – American Association of Retired Persons
ANOVA – Analysis of Variance
AUC – Area under the curve
BIS – Barratt Impulsiveness Scale
BOLD – Blood Oxygen Level Dependent
DLPFC – Dorsolateral Prefrontal Cortex
DOSPRT – Domain Specific Risk Taking Scale
FA – Flip Angle
FFX – Fixed Effects
fMRI – functional Magnetic Resonance Imaging
FOV – Field of View
FWHM – Full Width at Half Maximum
GDS – Geriatric Depression Scale
GDT – Game of Dice Task
GLM – General Linear Model
IGT – Iowa Gambling Task
MCI – Mild Cognitive Impairment
MMSE – Mini-Mental Status Examination
MPRAGE – Magnetization Prepared Rapid Acquisition Gradient Echo
MRI – Magnetic Resonance Imaging
OFC – Orbital Frontal Cortex
OHSU IRB – Oregon Health & Science University Institutional Review Board
PAG – Probability Associated Gambling Task
PFC – Prefrontal Cortex
RFX – Random Effects
ROI – Region of Interest
rTMS – repetitive Transcranial Magnetic Stimulation
SPSS – Statistical Package for the Social Sciences
SSS – Sensation Seeking Scale
SST – Socioemotional Selectivity Theory
TE – Echo Time
TR – Repetition time
UG – Ultimatum Game
VMPFC – Ventromedial Prefrontal Cortex
WAIS-R – Wechsler Adult Intelligence Scale - Revised