Social economic decision-making across the lifespan: An fMRI investigation

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ABSTRACT

Recent research in neuroeconomics suggests that social economic decision-making may be best understood as a dual-systems process, integrating the influence of deliberative and affective subsystems. However, most of this research has focused on young adults and it remains unclear whether our current models extend to healthy aging. To address this question, we investigated the behavioral and neural basis of simple economic decisions in 18 young and 20 older healthy adults. Participants made decisions which involved accepting or rejecting monetary offers from human and non-human (computer) partners in an Ultimatum Game, while undergoing functional magnetic resonance imaging (fMRI). The partners' proposals involved splitting an amount of money between the two players, and ranged from $1 to $5 (from a $10 pot). Relative to young adults, older participants expected more equitable offers and rejected moderately unfair offers ($3) to a larger extent. Imaging results revealed that, relative to young participants, older adults had higher activations in the left dorsolateral prefrontal cortex (DLPFC) when receiving unfair offers ($1–$3). Age group moderated the relationship between left DLPFC activation and acceptance rates of unfair offers. In contrast, older adults showed lower activation of bilateral anterior insula in response to unfair offers. No age group difference was observed when participants received fair ($5) offers. These findings suggest that healthy aging may be associated with a stronger reliance on computational areas subserving goal maintenance and rule shifting (DLPFC) during interactive economic decision-making. Consistent with a well-documented "positivity effect", older age may also decrease recruitment of areas involved in emotion processing and integration (anterior insula) in the face of social norm violation.

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1. Introduction

As the average life expectancy continues to rise, an increasing number of senior citizens are faced with the regular challenge of making decisions in an ever so complex social environment. Despite well documented changes in cognitive resources and brain function in older adults, surprisingly little is known on how healthy aging impacts cognitively demanding processes such as social economic decision-making (Sanfey & Hastie, 2000). Several neuropsychological investigations of normal aging point to declines in speed of processing (Salthouse, 1996; Van Der Werf et al., 2001), episodic memory (Moscovitch & Winocur, 1992), attention and working memory (Belleville, Peretz, & Malenfant, 1996; Gazzaley, Sheridan, Cooney, & D'Esposito, 2007; West, 1999) and executive control

processes (Glisky, Rubin, & Davidson, 2001), which have been linked to reduced neuronal density and neurochemical function in the prefrontal and medial-temporal cortices (Hedden & Gabrieli, 2004). However, such neuropsychological investigations may not fully capture the executive functioning of older adults in activities of daily living, for instance in situations where social and affective factors are more salient. In that regard, a neuroeconomic approach to assessing decision-making in healthy older adults may be valuable in assessing more subtle types of decision-making biases, and may offer insights into potential weaknesses, compensatory mechanisms, and strengths characteristic of older adults' decision-making (Mohr, Li, & Heekeren, 2010).

1.1. A dual-system model of decision-making

Indeed recent research in this field has proven useful in refining our understanding of decision-making in an interactive, social context (Sanfey, 2007). For instance, one major insight emerging from such research is that decision-making may be best understood as the interaction of two primary subsystems, including an

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affective/intuitive system ("System 1") and a computational, deliberative component ("System 2"; Kahneman, 2003; Stanovich & West, 2000). Importantly, such interactive framework appears to have validity at the neural level, as separate functional correlates of these subsystems have been identified (Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003). For instance "social emotions", such as disgust in the face of social norm violation or social reward (i.e. being treated unfairly or generously by a peer), have been shown to engage neural systems associated with more primary emotions (e.g. pain, physical disgust, food; Mohr et al., 2010; Sanfey, 2007). Thus, potential changes in decision-making associated with aging could presumably reflect a modulation of the deliberative system (e.g. regulatory/inhibitory processes, working memory, goal maintenance), but also, or alternatively, a biasing of the affective system (e.g. changes in emotional saliency of various stimuli). In light of such neuroeconomic framework, a growing literature suggesting that these cognitive and neural systems can indeed be partially impacted by aging is of particular interest in predicting potential age differences in decision behavior.

1.2. Deliberative system and aging

Deliberative processes, such as those supporting working memory and executive control processes (e.g. goal maintenance and adaptation to shifting rules), appear to be more affected by age than affective processes. Studies have shown that older adults tend to be slower at processing and learning new information, and less able to inhibit irrelevant information and automatic response sets (Peters, Hess, Västfjäll, & Auman, 2007). Such findings are consistent with the well documented structural and functional changes in the prefrontal cortex (PFC) observed in healthy older adults (Braver et al., 2001; Marschner et al., 2005), and particularly with recent evidence that such age-related alterations in memory and executive functioning may be specifically linked to functional deficits in the dorsolateral prefrontal cortex (DLPFC) rather than in other prefrontal areas such as the ventromedial PFC (MacPherson, Phillips, & Della Sala, 2002). Thus, in terms of economic decision-making, these age-related changes could negatively impact older adults' deliberative processing, which depends on the DLPFC, for instance their ability to maintain multiple and competing decision goals in working memory, or to compute and flexibility modulate utility estimation in complex and dynamic social environments. Interestingly, however, healthy older adults show minimal cognitive deficits in everyday decision-making (e.g. grocery shopping) or even on some economic decision-making tasks that involve computations such as "willingness to pay" estimation (Denney, 1981; Kovalchik, Camerer, Grether, Plott, & Allman, 2005). In addition, some research suggests that older adults may neurally compensate for subtle cognitive changes by recruiting the PFC to a larger extent. This seems to hold for various executive tasks, such as working memory and inhibition, and particularly so in high functioning seniors (Cabeza, 2002).

1.3. Affective system and aging

An important body of research further suggests a modulation of the affective system in older age, including a reduced negative affective experience and more focus on positively valenced information, coupled with functional changes in cortical and subcortical areas. According to socioemotional selectivity theory (SST; Carstensen, 1992), approaching death results in a shift in motivation, whereby older adults become more focused on maintaining well-being and positive affective experience, and less focused on exploration and risk-taking. From this point of view, older adults may be more prone to avoid or down-regulate negative affect and to prefer positive information ("positivity bias"). Importantly, such

research is supported by behavioral and neural evidence relevant to social decision-making. For instance, recent behavioral studies suggest that older adults may be more avoidant of conflicting and risky (thus negatively arousing) situations in interactive economic decision-making tasks. Specifically, older age has been associated with lower levels of risk-seeking attitudes and risk tolerance, more generous financial offers to others (Roalf, Mitchell, Harbaugh, & Janowsky, 2011), lower degree of competiveness (Mayr, Wozniak, Davidson, Kuhns, & Harbaugh, 2011), and higher returns of trust investments (Sutter & Kocher, 2007). Older adults also appear to process faces differently in that they have more difficulties in identifying and distinguishing negative facial expressions, such as fear and anger (Keightley, Winocur, Burianova, Hongwanishkul, & Grady, 2006). They also show a reduced activation of the amygdala in response to negative facial expressions (Iidaka et al., 2002) and to other negatively valenced stimuli (Mather et al., 2004). Such reduced neural response to negative emotion appears to be coupled with an increased engagement of the lateral and medial prefrontal cortex, suggesting a heightened effort to regulate negative information in a social context (Williams et al., 2006).

These findings suggest that, when making economic decisions in a social context, older adults may be less susceptible to the influence of negatively valenced signals, such as partner's negative emotions or intentions, or impending negative economic outcomes, as an adaptive response to avoid negative emotion and to focus on positive information (positivity bias). Consistent with this hypothesis, recent work shows that, relative to younger peers, older adults are experiencing less negative affect when anticipating monetary losses and less positive affect when avoiding losses (Nielsen, Knutson, & Carstensen, 2008), as well as a reduced activation in the anterior insula (Samanez-Larkin et al., 2007), a region associated with aversive emotional states (Calder et al., 2007; Denson, Pedersen, Ronquillo, & Nandy, 2009; Ploghaus et al., 1999). Interestingly, older adults have been shown to make more risk-taking mistakes in a financial investment task (Samanez-Larkin, Kuhnen, Yoo, & Knutson, 2010) and showed reduced ability to avoid high-loss card decks in the Iowa Gambling Task (Denburg, Recknor, Bechara, & Tranel, 2006), which could partly reflect a diminished sensitivity to potential losses in relation to such positivity effect. In fact, physiological data in this latter study suggest that older adults may primarily rely on positive somatic markers to match younger adults' performance in the IGT (as indexed by their stronger physiological responses to *advantageous* decks), which contrasts with the negative markers to risky/disadvantageous decks commonly observed in younger samples.

1.4. The present study

Based on the above mentioned research, we may expect to see age-related differences in social economic decision-making. Thus the present study sought to investigate such age differences at the behavioral and neural level, using a well know economic task, the Ultimatum Game (UG; Guth, Schmittberger, & Schwarze, 1982). Indeed, such task encompasses a dual-system framework of decision-making, combining computational processes (e.g. goal maintenance, utility estimation) as well as affective influences (e.g. salient negative social signals), reflected by the recruitment of specific neural systems (Sanfey et al., 2003). In this game, one player (the "proposer") is endowed a sum of money and makes an offer to another player (the "responder") on how to split this money between the two of them. The responder can either accept the offer, in which case the money is split as proposed, or reject the offer, in which case neither player receives anything and the money is returned to the experimenter. Whereas standard game theoretic models of decision-making would predict that responders should accept any non-zero offers (as even trivial amounts are preferable

to no gain at all), most individuals typically tend to reject about half of the unfair offers they receive (defined as 30% or less of the pot; Camerer, 2003), and report a negative emotional response (e.g. anger, disgust) and increased arousal when receiving unfair offers (Sanfey et al., 2003; van't Wout, Kahn, Sanfey, & Aleman, 2006). Thus, the responder role in the UG provides a good decision-making paradigm to examine how both deliberative and affective influences are potentially altered with age.

As noted earlier, behavioral differences may be subtle or may reveal age-related strengths in healthy older adults. Thus, we expected modest or no behavioral differences between young and older age groups. At the neural level, however, we expected to see differential recruitment in the PFC and the anterior insula. Firstly, we conjectured that some level of cognitive deficit associated with reduced PFC function in older adults may lead to age differences in computational and goal maintenance processes while making decisions. The DLPFC is typically recruited in the UG, particularly when receiving unfair offers, with higher DLPFC activation leading to more acceptance of these offers (Sanfey et al., 2003). Thus, this region may be instrumental in moderating affective influences that would lead to rejection of unfair offers, for instance by maintaining task rules and goals online (e.g. making money). Based on the above literature, older adults may be less likely to successfully implement such DLPFC-dependent processes, which could lead to lower acceptance rates of unfair offers. At the neural level, we could expect lower activation of the DLPFC in older adults, reflecting more pronounced deficit, or stronger activation, reflecting compensatory mechanisms (Cabeza, 2002).

Secondly, based on SST, a positivity bias and tendency to avoid negative affect could lead to a reduced focus on the negative social signal conveyed by unfair offers, which could in turn diminish the negative emotional experience of older adults when receiving these offers. Thus neural differences between young and old participants could be observed, reflecting the differential processing of such negative information. We predicted that, relative to young participants, older adults would show lower activation of the anterior insula when presented with unfair offers. Indeed, not only has this region been consistently linked to the experience and anticipation of aversive emotional states (Calder et al., 2007; Denson et al., 2009; Ploghaus et al., 1999), it has been implicated in the anticipation of negative economic outcomes in decision-making tasks (Paulus, Rogalsky, Simmons, Feinstein, & Stein, 2003; Samanez-Larkin et al., 2007). Importantly, activation of this region has been associated with the processing and subsequent rejection of unfair offers it the UG (Sanfey et al., 2003). Thus, presumably, a reduced insular activation may reflect a lower negative emotional reaction to unfairness in older relative to young participants. This could in turn be associated with a lower likelihood to reject unfair offers (i.e. higher acceptance rates). However, such affective biases may not necessarily be predictive of behavior, particularly in the context of potentially more significant age-related weaknesses in deliberative DLPFC-dependent processes (Peters et al., 2007).

2. Materials and methods

2.1. Participants

A total of 18 young adults (10 females; age 18–27, $M = 22.4$) and 20 older adults (13 females; age 55–78, $M = 64.1$) were recruited on the University of Arizona campus and in the community with flyers and newspaper ads. Participants were screened twice for typical magnetic resonance safety criteria (i.e. to rule out presence of metal in the body). In addition, participants were screened for and excluded if reporting any current or past neurological events or illnesses, psychiatric condition, or the use of psychotropic medications. All participants gave written informed consent.

2.2. Experimental procedures

Prior to the scanning session, participants were invited to participate in an introductory session during which they were instructed about the task they would be performing inside the scanner (i.e. Ultimatum Game). Their pictures were taken and they were told their partners in the task would see their de-identified picture when making their offer. To ensure that subjects were sufficiently motivated to make real decisions, they were told they would be paid a proportion of their earnings in the game in addition to their participation fee (i.e. typically a total of about $30, which they received upon completing the scanning experiment). Participants also completed a questionnaire asking them about what offer they would make as a proposer. Older adults also completed a short battery of neuropsychological tests to rule out any potential cognitive impairment above and beyond what would be expected for their age (see below) and to explore potential relationships between these neuropsychological constructs and the decision task.

2.2.1. Decision task (Ultimatum Game)

At the beginning of the scanning session, participants were asked to report their expectations of what offer amounts they would receive in the game, and in what proportions. They were also briefly reminded about the UG. Inside the scanner, each participant played in the role of the responder and received 36 one-time monetary offers from various human partners[1] as well as 12 randomly generated computer offers. Each offer involved a $10 split and both human and computer offers included equal proportions of $5, $3, $2, and $1 offers. To ensure participants' sustained attention, these offers were presented in random order in the course of 3 separate blocks of 16 offers. At the beginning of each trial, a jittered fixation cross was presented for an average of 6 s. Next, a picture of the proposer for that trial was presented (i.e. human partner's mug shot or a computer picture) for 4 s. The pictures that participants saw were de-identified and were selected from a pool of actual UG players' photographs from previous studies (Chang & Sanfey, 2009; Harlé & Sanfey, 2007) as well as from volunteers in the community. Participants then saw the offer and had up to 10 s to either accept or reject the offer by way of a button press. Finally, the decision outcome was presented for 4 s (Fig. 1a).

#### 2.2.2. Neuropsychological measures

On their first behavioral session, older adults completed a battery of neuropsychological tests to assess overall cognitive functioning and rule out any cognitive impairment. Tests included the Mini Mental Status Exam (MMSE; Folstein, Folstein, & McHugh, 1975), the Wechsler Abbreviated Scale of Intelligence (WASI; Wechsler, 1999), including all four subtests (block design, matrix reasoning, vocabulary, and similarities), Parts A and B of the Trail Making Test (TMT; Reitan, 1958), the Stroop Color Word Test (SCWT; Stroop, 1935), and the California Verbal Learning Test (CVLT-II, Standard Form; Delis, Kaplan, Kramer, & Ober, 2000). All tests were scored correcting for age. Older adults' MMSE scores ranged from 29 to 30 out of 30 ($M = 29.6$, SD = 0.6). Relative to peers of similar age, their mean WASI Verbal IQ ($M = 119$, SD = 11.1) and Performance IQ ($M = 116$, SD = 7.5) were in the high average range and individual percentile scores ranged from the average to superior range. Older participants' performance on the TMT (Trails A: $M = 23.9$ s, SD = 5.1; Trails B: $M = 54.2$, SD = 18.1; percentile range: 43–98%) and SCWT (Color-Word: $M = 38.7$ items, SD = 8.9; percentile range: 16–99%) were within normal limits relative to peers of similar age groups ruling out any abnormal executive functioning. Participants' working memory and delayed memory were also intact based on CVLT scores for 1st learning tials (List A 1st trial: $M = 6.5$, SD = 2.3; List B: $M = 5.7$, SD = 1.4; percentile range: 16–98%) and delayed free recall ($M = 10.7$, SD = 3.5; percentile range: 16–98%). Thus the overall neuropsychological profile of older adult participants in this study was within normal limits of intellectual and psychological functioning.

2.3. fMRI acquisition

Functional images were acquired on a GE 3.0 Tesla full-body scanner with a standard bird-cage head coil, and participants' heads were stabilized with foam pads. E-prime software was used to present the decision task on a computer interface, which was projected onto goggles worn by participants via a fiber-optic cable. Participant's responses were recorded using a 2-button-press response box. Each scanning session started with a 20 s 3-D localizer scan, followed by an 8 min T1-weighted scan (TR = 2000 ms, TE = 25 ms, slice thickness = 1.5 mm, gap = 0 mm, 120 sagital slices) to obtain high-quality structural images. Three T2-weighted functional scans of about 6 min long were then conducted while participants played the Ultimatum Game. Functional scans used a 3-shot echo planar imaging (EPI) sequence to maximize signal in regions associated with high susceptibility artifact such as the orbitofrontal cortex (Weiskopf, Hutton, Josephs, & Deichmann, 2006; TR = 2000 ms, TE = 25 ms, FOV = 24 mm, slice thickness = 2.6 mm, gap = 0.4 mm, 42 axial slices).

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[1] Human partner trials for older adults included an equal number of young adult partners and older adults to assess potential role of partner age in this population. Young participants received human offers from young partners only. UG acceptance rates of older participants for young and older proposers were not statistically different and therefore both trial types were combined as human partner trials.
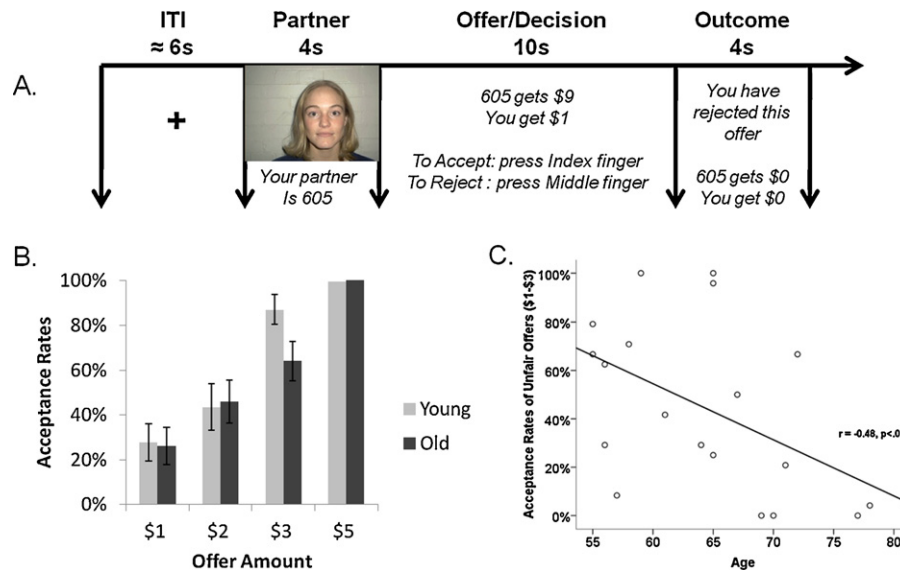
Fig. 1. (a) Ultimatum Game (UG) trial timeline (each trial lasted a total of 24 s); (b) aggregate acceptance rates of UG offers by age group and offer amount (error bars: ±1 S.E.M.); (c) correlation plot of average acceptance rates of unfair offer ($1–$3) and age in the older adults participants ($r = -0.48$, $p < .05$).

2.4. fMRI analysis

Image pre-processing and analyses were conducted using Brain Voyager software (Version 1.10). The first three volumes of the functional runs (6 s total) were discarded to account for T1 equilibrium effects. Image preprocessing for functional images included 6-parameter, 3D motion-correction, slice scan time correction using linear interpolation, spatial smoothing with a 4 mm full width at half minimum Gaussian kernel, voxel-wise linear detrending, and high pass filter of frequencies below 3 cycles per time course. Motion correction parameters were visually inspected to ensure that participants' head motion was not over 3 mm in each spatial axis. Three functional runs (one in a young participant, two in one old participant) were removed from data analyses for severe head motion.

To minimize potential confounding variables in assessing age group differences, each individual's structural and functional images were inspected for abnormalities, with particular attention to a priori regions of interest. Spatial normalization was performed using the standard 9-parameter landmarks method of Talairach and Tournoux (1988), landmarks which were manually placed for each individual brain. Levene tests were performed to compare between-group signal variance in each condition, and revealed no between-group heteroscedasticity. Finally, statistical analyses focused on the interaction of age and within-subject conditions such as offer amount. Such statistical approach is likely to further minimize confounding factors in comparing age groups (Samanez-Larkin & D'Esposito, 2008).

A two-level random-effect general linear model (GLM) was used to analyze functional data. The model included first-level fixed regressors defined for each subject and for each epoch of the time course. These regressors modeled the BOLD response to partner presentation, outcome, and a decision phase of 2 TR from offer presentation ($n = 8$: $1 Human Offer, $1 Computer Offer, $2 Human Offer, $2 Computer Offer, $3 Human Offer, $3 Computer Offer, $5 Human Offer, and $5 Computer Offer). Each regressor was convolved with a standard gamma model of the hemodynamic impulse-response function, and the resulting general linear model was corrected for temporal autocorrelations using a first-order autoregressive model. To create whole-brain statistical maps, voxel-wise BOLD response associated with predictors of interest (decision phase) was examined in a mixed ANOVA, with age group (young or old) as a between-subject predictor, and offer amount and partner type as within-subject factors. The whole brain search focused on identifying clusters tracking a significant offer amount by age group interaction (for human offers). To correct for multiple comparisons, all statistical maps were cluster-size thresholded using a Monte Carlo simulation-based estimator to protect against overall FWE rate of $p < .05$ (Forman et al., 1995). To tease apart any significant age group by offer interactions, averaged brain activation was extracted from these identified clusters and compared using t-tests. Bonferonni corrections for multiple comparisons were applied to specific contrasts of interests.

3. Results

3.1. Decision-making

A linear mixed model with random intercept at the subject level and with age group, offer amount, and partner type as independent variables was fit to the data. A significant main

effect of offer amount ($F(3,260) = 123$, $p < .001$) and a significant offer amount × age group interaction ($F(3,260) = 4.9$, $p < .005$) were revealed. Parameter estimates for this model revealed a significant age group difference in acceptance rates for $3 offers, but not for $1, $2, or $5 offers. Specifically, older adults were less likely to accept $3 offers (beta $= -27.3\%$, $p < .005$) relative to young adults (Fig. 1b). There were no significant main effects or interactions involving partner type (Aggregate acceptance rates: Young/Human Offers = 60.4%, Young/Computer Offers = 68.5%, Old/Human Offers = 56.8%, Old/Computer Offers = 57.0%).

The same pattern was observed when age was used as a covariate instead of age group, revealing a significantly more negative slope between acceptance rates and age for $3 human offers (beta $= -.73$, $p < .005$) and $3 computer offers (beta $= -.86$, $p < .005$), but not for $1, $2, or $5 offers. Within the older adult group, a negative relationship was further observed between aggregate acceptance rates of unfair offers ($1–$3) and participants' age ($r = -.48$, $p < .05$; Fig. 1c).

3.1.1. Reaction times

A mixed effects generalized linear model was fit to reaction time data to explore any difference between age groups. Age group, decision type (accept or reject), partner type (human or computer) and offer amount were included as independent variables in the model, with subject modeled as a random factor. A main effect of offer amount was statistically significant (Wald Chi Square = 55.8, $p < .001$), with participants being significantly slower at responding to $1, $2, and $3 relative to $5 offers. A significant decision × offer amount × partner type × age group interaction (Wald Chi Square = 99.5, $p < .001$) was also revealed. No other main effects or interactions reached statistical significance. To unpack this interaction, separate generalized linear models were fit to assess age group differences for each offer amount, decision type and partner type. Such analyses revealed that older adults were significantly slower at rejecting $1 human offers ($B = +458$ ms, $p < .05$).

3.1.2. Pre-game expectations

On average, older adults expected to receive a higher amount ($M = \$4.6$) from a proposer than younger adults ($M = \$3.9$, $t(36) = 5.3$, $p < .001$). Consistently, they reported they would offer significantly more to a human partner ($M = \$4.8$) relative to younger participants ($M = \$4.1$, $t(36) = 2.1$, $p < .05$). Interestingly, such mean offer

Table 1
BOLD activation foci during decision phase: effect of age on fair vs unfair offers.

Region	Talairach coordinates ($x\ y\ z$)			z	p	Cluster size (voxels)
[Old (unfair–fair)] > [young (unfair–fair)]						
L dorsolateral prefrontal cortex	−27	23	46	3.000800	0.0026	17
L inferior parietal gyrus	−33	−43	46	4.241338	0.000022	300
L cerebellum	−15	−79	−24	4.530252	0.000006	109
R postcentral gyrus	42	−25	52	4.663828	0.000003	176
R supramarginal gyrus	60	−31	25	3.919183	0.000089	16
R occipital gyrus	27	−61	−24	3.549322	0.000386	40
R cuneus	6	−85	4	4.256602	0.000021	82
[Old (unfair–fair)] < [young (unfair–fair)]						
L anterior insula	−36	5	−8	−3.497950	0.000469	10
R anterior insula	42	14	−5	−3.688950	0.000225	17

Note: Human offers only; whole brain random effect analysis; corrected for cluster-wise significance: $p < .05$, minimum cluster size 10 voxels/270 mm^3.

estimate was negatively correlated with acceptance rates of human unfair offers ($1–$3) in young adults ($r = −.55$, $p < .05$) but not in older adults ($p = .82$). This suggests that while young adults may be less likely to accept an unfair offer closer in amount to what they would personally offer, older adults appear insensitive to such discrepancy despite in fact being more generous. Expected mean offer was not significantly related to acceptance rates in both groups.

3.1.3. Acceptance rates and neuropsychological measures (old sample only)

A marginally significant relationship ($r = −.44$, $p = .06$) was observed between acceptance rates of unfair offers ($1–$3) and Trails B scores on the Trail Making Test, a measure inversely related to executive control and cognitive flexibility (Arbuthnott & Frank, 2000) and associated with recruitment of the DLPFC (Stuss et al., 2001; Zakzanis, Mraz, & Graham, 2005). This relationship was even stronger for acceptance rates of the most unfair offers ($1; $r = −.49$, $p < .05$). Importantly a similar relationship was observed between acceptance rates of $1 offers and Part B–Part A difference scores of the TMT ($r = −.47$, $p < .05$), which may more readily control for visuospatial and psychomotor age differences that are unrelated to cognitive flexibility. Taken together, these results suggest that the more difficult it is to implement and cognitively support multiple cognitive demands, the less likely older adults are to accept unfair offers.

3.2. Neuroimaging

3.2.1. Whole brain analyses

The primary focus of this investigation was to assess how age groups differed in their response to various types of offers. Thus whole brain analyses focused on exploring brain areas in which

age interacted with offer amount (i.e. unfair vs fair) for human offers at the point of decision (see Appendix A for common unfair vs fair contrast activations across both age groups). A significant offer amount × age group interaction was revealed in several brain areas, including the right and left anterior insula, left DLPFC, left inferior parietal gyrus, right postcental gyrus, and right supramarginal gyrus (see Table 1 for all foci of activation).

Greater activation to human unfair offers ($1–$3) in old relative to young was observed in the left DLPFC (see Fig. 2a and b), left inferior parietal gyrus, right postcental gyrus, and right supramarginal gyrus. Activations in these areas to fair ($5) human offers did not reveal any age group difference.

The opposite pattern was observed in the right and left anterior insula, with lower activity to human unfair offers ($1–$3) in old relative to young participants in these areas, but no significant age group difference for fair ($5) human offers (see Fig. 3a, b, and d). Activations in these areas were negatively correlated with age (ant. right insula: $r = −.45$, $p < .05$; ant. left insula: $r = −.68$, $p < .05$; see Fig. 3c).

3.2.2. Brain–behavior relationships

To further explore how age may interact with the recruitment of specific brain areas to bias decision-making, we used regression analysis to examine how age group may moderate the relationship between acceptance rates for each unfair offer amount ($1, $2, $3) and their respective neural activation coefficients (betas) in our two regions of interest. Thus three moderated regression models were fit for activations in three functionally identified areas (left DLPFC, right anterior insula, left anterior insula).

A moderated regression model revealed a significant interaction between age group and activation of the left DLPFC in predicting
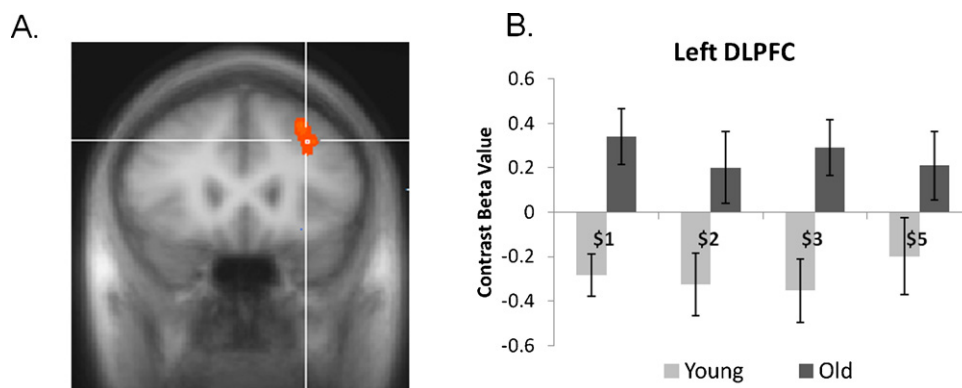
Fig. 2. (a) Coronal view of BOLD response in left dorsolateral prefrontal cortex (DLPFC) at offer presentation (initial 4 s) for human offers (whole brain analysis, corrected for cluster-wise significance: $p < .05$, minimum cluster size 270 mm^3); (b) activation (contrast beta value) in left DLPFC for each offer amount and age group during initial decision phase (4 s). Stronger activation in the old relative to young age group was observed for $1, $2, $3 offers ($p < .05$). No significant age group difference was found for $5 offers ($p > .05$); error bars: ±1 S.E.M.
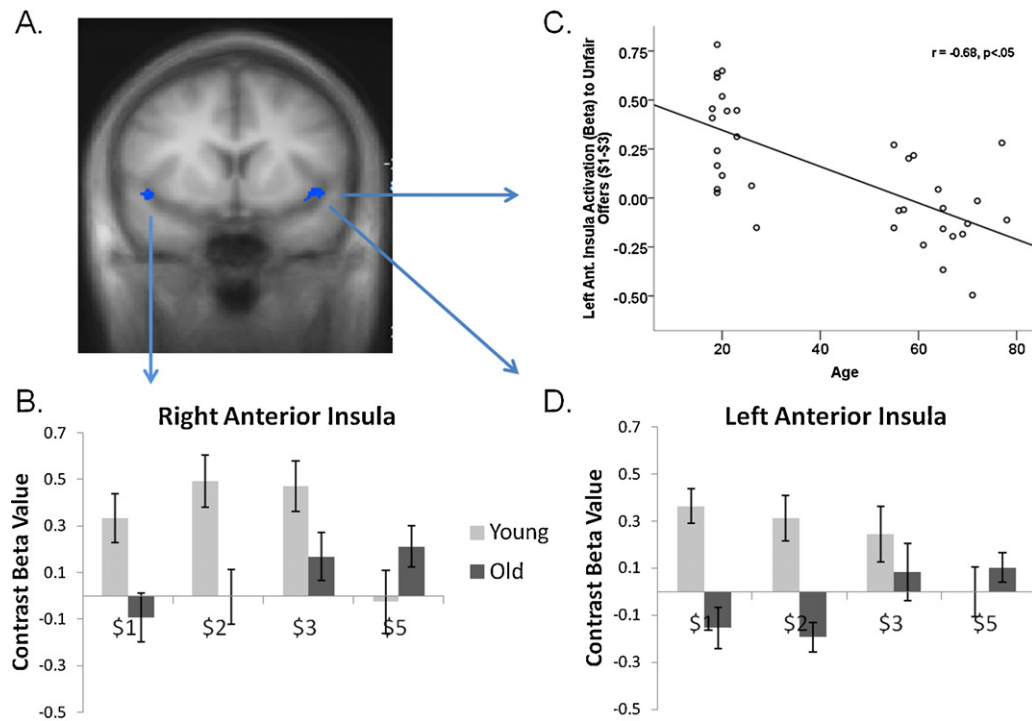
Fig. 3. (a) Coronal view of BOLD response in left and right anterior insula at offer presentation (initial 4 s) for human offers (whole brain analysis, corrected for cluster-wise significance: $p < .05$, minimum cluster size 270 mm^3); (b) activation (contrast beta value) in right anterior insula for each offer amount and age group during initial decision phase (4 s). Stronger activation in the old relative to young age group was observed for unfair offers $1, $2, and $3 offers ($p < .05$) but not for $5 offers ($p > .05$; error bars: ± 1S.E.M.); (c) correlation plot between average activation in the left anterior insula to unfair offers ($1–$3) and participant's age (both age groups); $r = -0.68$, $p < .05$; (d) activation (contrast beta value) in left anterior insula for each offer amount and age group during initial decision phase (4 s). Stronger activation in the old relative to young age group was observed for unfair offers $1 and $2 offers ($p < .05$) but not for $3 and $5 offers ($p > .05$; error bars: ± 1 S.E.M.).

acceptance rates of the most unfair offers ($1; $F(1,34) = 6.7$, $p < .05$; $R^2 = .16$). Specifically, a significant positive relationship was observed between activation in this region and acceptance rates in the older adult group ($r = +0.58$, $p < .05$; Fig. 4a) but not in the young adult group ($p = .35$; Fig. 4b). Interestingly, such DLPFC activation coefficient for $1 offers was marginally related to Trails B time to completion measures in older adults ($r = -.43$, $p = .06$). No other moderated regression model reached statistical significance (i.e. age did not moderate the relationship between acceptance rates

of other offer amounts with DLPFC activation or with activations in the left or right anterior insula). Of note, no significant relationship was observed between acceptance rates of unfair offers and anterior insula activations, even in the younger group ($p > .05$).

4. Discussion

The present study used a neuroeconomic approach to compare young and older adults in a well-known social economic decision
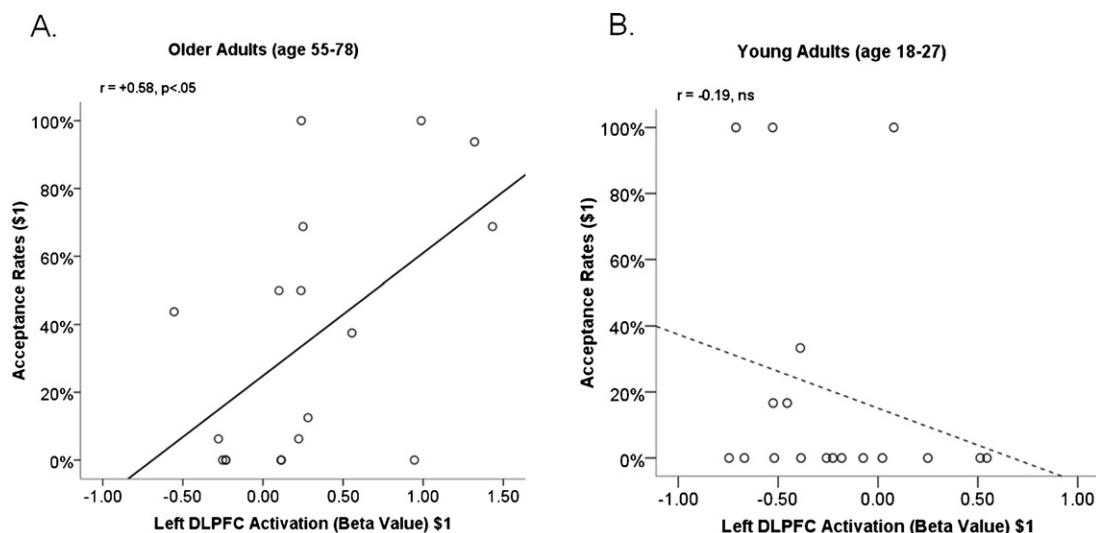
Fig. 4. Relationship between acceptance rates of the most unfair offers ($1) and activation in the left DLPFC by age group. A significant positive correlation between acceptance rates and DLPFC activation was observed in older adults ($r = +0.58$, $p < .05$), but no significant relationship was found for young adults ($p > .05$).

task, with particular attention to age difference in recruiting specific neural systems. Participants played the Ultimatum Game (UG), in which they had to decide whether to accept or reject monetary offers from various partners who proposed how to split an amount of money between the two. Of particular interest was how age groups may differ in their response to "unfair" offers (i.e. less than 30% of the pot), as such offers have been shown to engage both computational/deliberative and affective systems (recruiting the DLPFC and the anterior insula, respectively; Sanfey et al., 2003). Decision tasks that rely on such dual-system process may indeed help to capture more subtle biases in the type of dynamic and interactive decision-making young and older adults face in everyday life.

A significant behavioral difference was observed between young and senior participants in the UG. Overall, relative to younger participants, older adults accepted less moderately unfair offers, specifically $3 (out of $10), but had similar acceptance rates for the most unfair offers ($1–$2) and for fair offers ($5). At the neural level, whole brain analyses revealed distinct interactive patterns between age and type of offers in two sets of regions. Firstly, relative to young participants, older adults had significantly less activation in the left and right anterior insula in response to unfair offers. Secondly, the opposite pattern was observed, namely more activation in older adults relative to young adults in frontal and parietal regions, including the left DLPFC and the left inferior parietal gyrus. Thus a double dissociation pattern was revealed, highlighting age differences in recruiting two hypothesized cortical regions, the anterior insula and the DLPFC. In contrast, age was not significantly related to neural activations to fair offers.

Our subtle behavioral findings are not inconsistent with previous reports that performance on everyday problem-solving (Denney, 1981; Kovalchik et al., 2005) is similar or show only minor differences across age groups, despite potential differences in cognitive processing and neural recruitment. Nonetheless, it is notable that older adults did respond differently to the most ambiguous, intermediate offers (i.e. neither very unfair nor fair), and that acceptance rates for these offers were negatively related to age. Indeed, such level of UG offer has been shown to elicit the most variance in acceptance rates (Chang & Sanfey, in press) and it is therefore not surprising that such offer level prompted the most notable behavioral difference. Acceptance of $3 offers also tends to be sensitive to differences in expectations and social norms in this game (Chang & Sanfey, in press), and thus could suggest that the present discrepancy in acceptance rates reflects the observed age difference in expectations and proposer strategy in the game. Indeed, we found that older adults expected to receive about $0.70 more from their UG partners than young adults did. Senior participants also reported a preference to make higher offers as a proposer. However, while expected offer was related to acceptance rates in young adults, this was not the case in older adults, despite their preference for a more equitable game. Therefore, it is unlikely that a difference in expectations alone accounts for the distinct acceptance and neural patterns.

The flatter slope for acceptance rates of unfair offers as a function of offer amount fits with research suggesting that older adults tend to be more consistent in their choices (e.g. as evidenced by less susceptibility to the attraction effect; Kim & Hasher, 2005) and are more likely to rely on heuristics, compared to young adults who are more likely to use analytic strategies for the same decisions (Johnson, 1990). In other words, older adults tend to process less information in complex shifting scenarios and may exhibit less cognitive flexibility in such contexts (Peters et al., 2007). In support of such interpretation, acceptance rates of the most unfair offers was correlated with performance on a neuropsychological measure of executive control and switching cognitive demands (Trail B from the TMT), with higher acceptance rates associated with better performance. Thus, in the UG, a reduced ability to flexibility adapt to

shifting rules (as determined by various offer levels and partner type) may lead to less change in acceptance pattern across a range of unfair offers, or at least for offers below what they expect and prefer in the game.

Such interpretation is consistent with the typically observed age-related decline in cognitive functions subserved by the DLPFC, including working memory as well as rule maintenance and set shifting. More importantly, our present finding that older adults exhibited more activation in the DLPFC relative to younger participants, activation which was also inversely related to Trail B measures (as for acceptance rates), lends credence to the hypothesis that older adults' reliance on the DLPFC may be higher and that the processing and executive control of various decision-related information, such as game rules and goals, may be more effortful for older adults. Specifically, such decreased flexibility in acceptance of unfair offers may relate to a DLPFC-driven decline in the maintenance, selection, or integration of the game's competing rules (e.g. making as much money as possible vs responding to an offensive social signal from inequitable offers) or of the of the various strategies employed for different categories of offers.

Our behavioral results are also consistent with accumulating evidence of altered reward processing in older adults in relation to declines in dopaminergic and serotonergic neuromodulation. These age effects in the dopamine and serotonin systems have been linked to changes in fronto-striatal functional interaction and to decreased efficiency in reward signaling, which in turns leads to less flexible behavior among older adults, particularly in the context of changing stimulus-reward contingencies (see Eppinger, Hämmerer, & Li, 2011, for a review). Thus, in the present study, the lower variability in acceptance rates towards unfair offers (i.e. a flatter slope) observed in older adults could reflect such inefficiencies in flexibly modulating decision-making to various levels of reward, most evident here in a failure to switch to "accept" responses for intermediate offers ($3). The fact that older adults exhibited similar acceptance rates for both human and computer offers lends further credence to this hypothesis. Indeed, this pattern would be consistent with older adults' reduced efficiency in updating stimulus-reward and/or reward-action signaling based on the degree of social norm violation (which typically leads to higher acceptance rates for computer offers).

The fact that more – as opposed to less – DLPFC activation was observed in older adults during the decision phase is further consistent with a "compensatory" hypothesis, whereby higher DLPC activation in older adults may serve to counteract neurocognitive inefficiency, rather than a "de-differentiation" hypothesis, whereby aging promotes difficulties in recruiting specific neural areas (Cabeza, Anderson, Locantore, & McIntosh, 2002). Indeed, an important body of research suggests that neurologically intact older adults exhibit a reduced prefrontal hemispherical asymmetry in the context of various PFC dependent cognitive tasks, including some that are very relevant to decision-making such as episodic memory retrieval, working memory, and inhibitory control (Cabeza, 2002; Nielson, Langenecker, & Garavan, 2002). Interestingly, such reduced asymmetry appears to stem from higher prefrontal activation in the left hemisphere in older adults (as found in the present study), with similar right prefrontal activations across age groups. This may reflect a stronger need in older adults to spread neural recruitment across both hemispheres to achieve a similar degree of performance (Cabeza, 2002). In the present study, stronger left DLPFC activation in the context of the obtained behavioral differences in the UG may reflect such compensatory mechanism, for instance in inhibiting response sets (e.g. rejecting offers) or maintaining and/or flexibly shifting across various game rules. The fact that older adults showed a significant relationship between Trail B measures, acceptance rates, and DLPFC activation supports a compensatory mechanism in inhibitory control, as performance on

the TMT Trail B has been shown to correlate with such function (Leimkuhler & Mesulam, 1985).

It is further noteworthy that, relative to young participants, older adults showed stronger activation in the left inferior parietal lobule when receiving unfair offers. A recent study of age differences in inhibitory control, as measured with a simple response inhibition task, revealed a similar neural pattern in that older adults had stronger activations in both the left DLPFC and left inferior parietal gyrus during successful inhibition (Nielson et al., 2002). It has been suggested that involvement of the inferior parietal region in this type of response inhibition task reflects additional motor control demands needed to assist in preventing a prepotent motor response (Garavan, Ross, & Stein, 1999). In the UG, this activation may reflect age-related compensatory mechanisms to inhibit a given response set in the game, such as rejecting unfair offers.

Another main neural finding was that, as hypothesized, older adults had lower activations of the anterior insula bilaterally when processing unfair offers. In fact, older adult demonstrated no differential activation in this area across levels of offer fairness, and activity in this area did not predict their decisions. Such age difference in anterior insula activation was particularly apparent for the most unfair offers ($1–$2), with no age group difference present for fair offers. Previous research has linked the anterior insula with the integration of emotional information and the experience of aversive states such as disgust (Calder et al., 2007), anger (Denson et al., 2009), and pain (Ploghaus et al., 1999). Importantly, activation in this region is observed when receiving unfair offers in the UG, and has been shown to predict rejections of these offers (Sanfey et al., 2003). This finding and other work showing that responders to unfair offers tend to report negative emotional states (Harlé & Sanfey, 2007; Xiao & Houser, 2005) and stronger physiological arousal (van't Wout et al., 2006), provide converging evidence that activation of the anterior insula in response to unfair UG offers reflects a negative emotional response to these offers, perhaps due to a form of moral disgust or anger when being treated unfairly. Thus, the present age difference in recruiting this region suggests older adults may process unfair offers as less aversive relative to their younger peers. This is particularly interesting given their higher offer expectations in the game and preference for more equitable offers. Nonetheless, such interpretation is consistent with socioemotional selectivity theory (SST; Carstensen, 1992) and more recent work showing lower negative affect (Nielsen et al., 2008) and anterior insular activation (Samanez-Larkin et al., 2007) in older adults in the context of anticipated economic loss.

In summary, we observed a distinct age-driven signature in the processing of unfair UG offers within two hypothesized neural areas, namely the DLPFC and the anterior insula. From a dual-system perspective of economic decision-making, these results suggest that, when faced with these types of interactive economic decisions, neurally intact seniors may be more reliant on "System 2" to maximize executive control while less likely to engage "System 1" relative to their younger peers. Consistent with this dual-system framework, older adults had to recruit the DLPFC to a larger extent relative to young adults in order to achieve a similar performance level (i.e. acceptance rates). In contrast, older adults showed less recruitment of the affective/interoceptive system, as suggested by a lower activation in the anterior insula. Thus, overall, the observed age-dependent behavioral and neural patterns are more consistent with a compensatory recruitment of the deliberative system in older adults, implemented in the DLPFC, than with biases in the affective system. Indeed, in the later case, one would expect older adults to be less sensitive to the negative emotional saliency of being offered an offensive economic "deal" by a peer (which should lead to more acceptances of the most unfair offers given the observed lower insula activation). One possible explanation is that neural inefficiency in the DLPFC may simply

carry more weight in biasing behavior relative to diminished insular response to unfairness. Thus, although age-related differences in both neural systems may be significant in biasing behavior, they may cancel each other to a large extent, which is consistent with the subtle behavioral differences observed. Alternatively, such pattern could suggest that older adults are more likely to focus on a different type of negative outcome, namely foregoing a monetary gain rather than social norm violation. Thus their lower engagement of the anterior insula may result in a diminished sensitivity to the risk of losing money in the game, in which case they would be more likely to reject offers. Future research should seek to disentangle these hypotheses. In addition, the present results provide a framework to further assess how this neuro-cognitive signature in healthy seniors may be affected by neuronal insult and psychiatric conditions. For instance, neuro-degenerative or cerebro-vascular events in neural networks involving the DLPFC and/or the insular cortex, or over-activations in these areas as observed in depression (Fales et al., 2008) and anxiety disorders (Paulus & Stein, 2006), may lead to more substantial behavioral biases.

In conclusion, the present study suggests that a neuroeconomic framework can prove useful in refining our understanding of how healthy aging impacts decision-making in complex, socially interactive environments, by selectively biasing specific neuro-cognitive systems. Such approach may in turn help developing and improving neuropsychological methods to assess real-life executive functioning in both healthy aging and in various neurological conditions impacting these neural systems.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuropsychologia.2012.02.026.

References

Arbuthnott, K., & Frank, J. (2000). Trail Making Test part B as a measure of executive control: Validation using a set-switching paradigm. *Journal of Clinical Experimental Neuropsychology*, *22*, 518–528.

Belleville, S., Peretz, I., & Malenfant, D. (1996). Examination of the working memory components in normal aging and in dementia of the Alzheimer type. *Neuropsychologia*, *34*, 195–207.

Braver, S., Barch, D. M., Keys, B. A., Carter, C. S., Cohen, J. D., Kaye, J. A., et al. (2001). Context processing in older adults: Evidence for a theory relating cognitive control to neurobiology in healthy aging. *Journal of Experimental Psychology: General*, *130*, 746–763.

Cabeza, R. (2002). Hemispheric asymmetry reduction in older adults: The HAROLD model. *Psychology and Aging*, *17*, 85–100.

Cabeza, R., Anderson, N. D., Locantore, J. K., & McIntosh, A. R. (2002). Aging gracefully: Compensatory brain activity in high-performing older adults. *NeuroImage*, *17*, 1394–1402.

Calder, A. J., Beaver, J. D., Davis, M. H., Van Ditzhuijzen, J., Keane, J., & Lawrence, A. D. (2007). Disgust sensitivity predicts the insula and pallidal response to pictures of disgusting foods. *European Journal of Neuroscience*, *11*, 3422–3428.

Camerer, C. F. (2003). *Behavioral game theory: Experiments in strategic interaction.* New York: Russell Sage Foundation., pp. 46–117

Carstensen, L. L. (1992). Social and emotional patterns in adulthood: Support for socioemotional selectivity theory. *Psychology and Aging*, *7*, 331–338.

Chang, L. J., & Sanfey, A. G. (2009). Unforgettable ultimatums? Expectation violations promote enhanced social memory following economic bargaining. *Frontiers in Behavioral Neuroscience*, *3*, 36.

Chang, L. J., & Sanfey, A. G. Great expectations: Neural computations underlying the use of social norms in decision-making. *Social Cognitive Affective Neuroscience*, doi:10.1093/scan/nsr094, in press.

Delis, D., Kaplan, E., Kramer, J., & Ober, B. (2000). *California verbal learning test-II.* San Antonio, TX: The Psychological Corporation.

Denburg, N. L., Recknor, E. C., Bechara, A., & Tranel, D. (2006). Psychophysiological anticipation of positive outcomes promotes advantageous decision-making in normal older persons. *International Journal of Psychophysiology*, *61*, 19–25.

Denney, N. W., & Palmer, A. M. (1981). Adult age differences on traditional and practical problem-solving measures. *Journal of Gerontology*, 36, 323–328.

Denson, T. F., Pedersen, W. C., Ronquillo, J., & Nandy, A. S. (2009). The angry brain: Neural correlates of anger, angry rumination and aggressive personality. *Journal of Cognitive Neuroscience*, 21, 734–744.

Eppinger, B., Hämmerer, D., & Li, S. C. (2011). Neuromodulation of reward-based learning and decision making in human aging. *Annals of the New York Academy of Sciences*, 1235, 1–17.

Fales, C. L., Barch, D. M., Rundle, M. M., Mintun, M. A., Snyder, A. Z., Cohen, J. D., et al. (2008). Altered emotional interference processing in affective and cognitive-control brain circuitry in major depression. *Biological Psychiatry*, 63, 377–384.

Folstein, M. F., Folstein, S. E., & McHugh, P. R. (1975). Mini-mental state A practical method for grading the cognitive state of patients for the clinician. *Journal of Psychiatric Research*, 12, 189–198.

Forman, S. D., Cohen, J. D., Fitzgerald, M., Eddy, W. F., Mintun, M. A., & Noll, D. C. (1995). Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): Use of a cluster-size threshold. *Magnetic Resonance in Medicine*, 33, 636–647.

Garavan, H., Ross, T. J., & Stein, E. A. (1999). Right hemispheric dominance of inhibitory control: An event-related functional MRI study. *Proceedings of the National Academy of Sciences of the United States of America*, 96, 8301–8306.

Gazzaley, A., Sheridan, M. A., Cooney, J. W., & D'Esposito, M. (2007). Age-related deficits in component processes of working memory. *Neuropsychology*, 21, 532–539.

Glisky, E. L., Rubin, S. R., & Davidson, P. S. (2001). Source memory in older adults: An encoding or retrieval problem? *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 27, 1131–1146.

Guth, W., Schmittberger, R., & Schwarze, B. (1982). An experimental analysis of ultimatum bargaining. *Journal of Economic Behavior and Organization*, 3, 367–388.

Harlé, K. M., & Sanfey, A. G. (2007). Incidental sadness biases social economic decisions in the Ultimatum Game. *Emotion*, 7, 876–881.

Hedden, T., & Gabrieli, J. D. (2004). Insights into the ageing mind: A view from cognitive neuroscience. *Nature Reviews Neuroscience*, 5, 87–98.

Iidaka, T., Okada, T., Murata, T., Omori, M., Kosaka, H., Sadato, N., et al. (2002). Age-related differences in the medial temporal lobe responses to emotional faces as revealed by fMRI. *Hippocampus*, 12, 352–362.

Johnson, M. M. S. (1990). Age differences in decision making: A process methodology for examining strategic information processing. *Journal of Gerontology*, 45, 75–78.

Kahneman, D. (2003). A perspective on judgment and choice: Mapping bounded rationality. *American Psychologist*, 58, 697–720.

Keightley, M. L., Winocur, G., Burianova, H., Hongwanishkul, D., & Grady, C. L. (2006). Age effects on social cognition: Faces tell a different story. *Psychology and Aging*, 21, 558–572.

Kim, S., & Hasher, L. (2005). The attraction effect in decision making: Superior performance by older adults. *Quarterly Journal of Experimental Psychology: Section A: Human Experimental Psychology*, 58, 120–133.

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

Leimkuhler, M. E., & Mesulam, M. M. (1985). Reversible go-no go deficits in a case of frontal lobe tumor. *Annals of Neurology*, 18, 617–619.

MacPherson, S. E., Phillips, L. H., & Della Sala, S. (2002). Age, executive function and social decision making: A dorsolateral prefrontal theory of cognitive aging. *Psychology and Aging*, 17, 598–609.

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

Mather, M., Canli, T., English, T., Whitfield, S., Wais, P., Ochsner, K., et al. (2004). Amygdala responses to emotionally valenced stimuli in older and younger adults. *Psychological Science*, 15, 259–263.

Mayr, U., Wozniak, D., Davidson, C., Kuhns, D., & Harbaugh, W. T. (2011). Competitiveness across the life span: The feisty fifties. *Psychology and Aging*, doi:10.1037/a0025655 (Advance online publication)

Mohr, P. N., Li, S. C., & Heekeren, H. R. (2010). Neuroeconomics and aging: Neuromodulation of economic decision making in old age. *Neuroscience & Biobehavioral Reviews*, 34, 678–688.

Moscovitch, M., & Winocur, G. (1992). The neuropsychology of memory and aging. In F. I. M. Craik, & T. A. Salthouse (Eds.), *Handbook of aging: Cognition* (pp. 315–372). Hillsdale, NJ: Erlbaum.

Nielson, K. A., Langenecker, S. A., & Garavan, H. P. (2002). Differences in the functional neuroanatomy of inhibitory control across the adult life span. *Psychology and Aging*, 17, 56–71.

Nielsen, L., Knutson, B., & Carstensen, L. L. (2008). Affect dynamics, affective forecasting, and aging. *Emotion*, 8, 318–330.

Paulus, M. P., Rogalsky, C., Simmons, A., Feinstein, J. S., & Stein, M. B. (2003). Increased activation in the right insula during risk-taking decision making is related to harm avoidance and neuroticism. *Neuroimage*, 19, 1439–1448.

Paulus, M. P., & Stein, M. B. (2006). An insular view of anxiety. *Biological Psychiatry*, 60, 383–387.

Peters, E., Hess, T. M., Västfjäll, D., & Auman, C. (2007). Adult age differences in dual information processes: Implications for the role of affective and deliberative processes in older adults' decision making. *Perspectives on Psychological Sciences*, 2, 1–23.

Ploghaus, A., Tracey, I., Gati, J. S., Clare, S., Menon, R. S., Matthews, P., et al. (1999). Dissociating pain from its anticipation in the human brain. *Science*, 284, 1979–1981.

Reitan, R. M. (1958). Validity of the Trail Making test as an indicator of organic brain damage. *Perceptual and Motor Skills*, 8, 271–276.

Roalf, D. R., Mitchell, S. H., Harbaugh, W. T., & Janowsky, J. S. (2011). Risk, reward, and economic decision making in aging. *Journals of Gerontology Series B: Psychological Sciences and Social Sciences*, doi:10.1093/geronb/gbr099 (Advance online publication)

Salthouse, T. A. (1996). The processing-speed theory of adult age differences in cognition. *Psychological Review*, 103, 403–428.

Samanez-Larkin, G. G., & D'Esposito, M. (2008). Group comparisons: Imaging the aging brain. *Social Cognitive and Affective Neuroscience*, 3, 290–297.

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

Samanez-Larkin, G. G., Kuhnen, C. M., Yoo, D. J., & Knutson, B. (2010). Variability in nucleus accumbens activity mediates age-related suboptimal financial risk taking. *Journal of Neuroscience*, 30, 1426–1434.

Sanfey, A. G. (2007). Decision neuroscience: New directions in studies of judgment and decision-making. *Current Directions in Psychological Science*, 16, 151–155.

Sanfey, A. G., & Hastie, R. (2000). Judgment and decision making across the adult life span: A tutorial review of psychological research. In D. C. Park, & N. Schwarz (Eds.), *Cognitive aging: A primer* (pp. 253–273). New York, NY: Psychology Press.

Sanfey, A. G., Rilling, J. K., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2003). The neural basis of economic decision making in the Ultimatum Game. *Science*, 300, 1755–1758.

Stanovich, K. E., & West, R. F. (2000). Individual differences in reasoning: Implications for the rationality debate. *Behavioral and Brain Sciences*, 23, 645–665.

Stroop, J. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*, 18, 643–662.

Stuss, D. T., Bisschop, S. M., Alexander, M. P., Levine, B., Katz, D., & Izukawa, D. (2001). The trail making test: A study in focal lesion patients. *Psychological Assessment*, 13, 230–239.

Sutter, M., & Kocher, M. G. (2007). Trust and trustworthiness across different age groups. *Games & Economic Behavior*, 59, 364–382.

Talairach, J., & Tournoux, P. (1988). *Co-planar stereotactic atlas of the human brain*. Stuttgart/New York: Thieme.

Van Der Werf, Y. D., Tisserand, D. J., Visser, P. J., Hofman, P. A., Vuurman, E., Uylings, H. B., et al. (2001). Thalamic volume predicts performance on tests of cognitive speed and decreases in healthy aging: A magnetic resonance imaging-based volumetric analysis. *Cognitive Brain Research*, 11, 377–385.

van 't Wout, M., Kahn, R. S., Sanfey, A. G., & Aleman, A. (2006). Affective state and decision-making in the Ultimatum Game. *Experimental Brain Research*, 169, 564–568.

Wechsler, D. (1999). *Wechsler abbreviated scale of intelligence*. San Antonio, TX: Psychological Corporation/Harcourt Brace.

Weiskopf, N., Hutton, C., Josephs, O., & Deichmann, R. (2006). Optimal EPI parameters for reduction of susceptibility-induced BOLD sensitivity losses: A whole-brain analysis at 3 T and 1.5 T. *Neuroimage*, 33, 493–504.

West, R. (1999). Visual distraction, working memory and aging. *Memory & Cognition*, 27, 1064–1072.

Williams, L. M., Brown, K. J., Palmer, D., Liddell, B. J., Kemp, A. H., Olivieri, G., et al. (2006). The mellow years? Neural basis of improving emotional stability over age. *Journal of Neuroscience*, 26, 6422–6430.

Xiao, E., & Houser, D. (2005). Emotion expression in human punishment behavior. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 7398–7401.

Zakzanis, K. K., Mraz, R., & Graham, S. J. (2005). An fMRI study of the Trail Making Test (2005). *Neuropsychologia*, 43, 1878–1886.