



Review

Neuroeconomics and aging: Neuromodulation of economic decision making in old age

Peter N.C. Mohr^{a,b,*}, Shu-Chen Li^a, Hauke R. Heekeren^{a,b}^a Max Planck Institute for Human Development, Berlin, Germany^b Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

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ABSTRACT

Economic decision making is a complex process of integrating and comparing various aspects of economically relevant choice options. Neuroeconomics has made important progress in grounding these aspects of decision making in neural systems and the neurotransmitters therein. The dopaminergic and serotonergic brain systems have been identified as key neurotransmitter systems involved in economic behavior. Both are known to be prone to significant changes during the adult lifespan. Similarly, economic behavior undergoes significant age-related changes over the course of the adult lifespan. Here we propose a triadic relationship between (a) economic decision making, (b) dopaminergic and serotonergic neuromodulation, and (c) aging. In this review, we describe the different relationships around this triad in detail and summarize current evidence that supports them. Based on the reviewed evidence, we propose new research agendas that take the entire triad into account.

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1. Introduction

Neuroeconomics is a new field of interdisciplinary research that emerged around the turn of the 21st century. It calls for new

conceptual, theoretical, as well as methodological developments in combining cognitive neuroscience, computational neuroscience, psychology, and economics to carry out in vivo investigations of the brain processes involved when individuals make economically relevant decisions (Camerer, 2007; Camerer et al., 2005; Glimcher et al., 2009; Glimcher and Rustichini, 2004; Loewenstein et al., 2008; Montague, 2007; Sanfey et al., 2006). Neuroeconomics has its root in behavioral economics, a scientific subfield of economics that has adopted psychological research on social, cognitive, and emotional factors to better understand economic decisions.

* Corresponding author at: Neurocognition of Decision Making Group, Max Planck Institute for Human Development, Lentzeallee 94, 14195 Berlin, Germany. Tel.: +49 30 824 06 240; fax: +49 30 824 06 616.

E-mail address: mohr@mpib-berlin.mpg.de (Peter N.C. Mohr).

Shortly after cognitive and affective psychology started to use neuroscientific methods such as functional magnetic resonance imaging (fMRI), behavioral economists also teamed up with cognitive neuroscientists to form the new field of neuroeconomics.

In the past few years, neuroeconomics has made important progress in grounding economic behavior in neural processes (Glimcher et al., 2009). This progress includes further linking of such subfields of economics as finance (Knutson and Bossaerts, 2007) and marketing (e.g., Plassmann et al., 2007) with neuroscientific research methodologies. A wide range of studies in animals and humans have identified neural mechanisms underlying the representations of value, reward, and risk, which are important factors affecting economic behavior (see d'Acremont and Bossaerts, 2008; Platt and Huettel, 2008; Rangel et al., 2008; Schultz, 2006 for reviews). Most of these studies, however, focus only on young adults, neglecting possible age differences in economic behavior and the associated neurocognitive mechanisms.

Many developed countries are now faced with aging populations, due to an increase in average life expectancy and a decrease in birth rate (Beddington et al., 2008). The prosperity of societies generally depends heavily on its ability to profit from the cognitive resources of its constituent members, both economically and socially. Thus, in aging societies it is crucial to understand how brain mechanisms affecting cognitive abilities and decision making change over the adult lifespan in order to guide strategies for cognitive interventions at the individual level and social policies at the societal level.

Theories of lifespan development posit that the gain–loss dynamics of fundamental developmental resources (e.g., brain, cognitive, emotional, social, temporal, and financial resources) vary dynamically across the lifespan. Individuals thus need to adaptively regulate their behaviors and actions throughout life for optimal development (Baltes and Baltes, 1990; Baltes et al., 1999; Carstensen, 1995). During the process of aging, losses in different types of developmental resources gradually outweigh gains. For instance, the age-related decline of fluid intelligence has a steeper slope than the growth of crystallized intelligence over the same period (e.g., Li et al., 2004). Therefore, it is of particular importance for individuals in midlife and old age to adjust their preferences and behaviors in different domains of life, including economical and financial practices, for successful aging.

Recently, cognitive neuroscience has made important progress in linking age-related changes in cognitive abilities (e.g., working memory, episodic memory, and processing robustness) to structural and functional changes in the brain (Cabeza et al., 2005, for review). Further, it was found that many cognitive functions are heavily influenced by the neurotransmitter dopamine, which typically undergoes a substantial decline with regard to many aspects of its functioning during healthy aging (Erixon-Lindroth et al., 2005; Kaasinen and Rinne, 2002; Suhara et al., 1991). In light of clear age-related declines in dopaminergic modulation, neurocomputational studies (Li et al., 2001; Li and Sikstrom, 2002) as well as a range of empirical findings (e.g., Bäckman et al., 2000) indicate a correlative triad between dopaminergic neuromodulation, cognition, and aging, as Bäckman and colleagues recently conceptualized (Bäckman et al., this volume; Bäckman et al., 2006).

Importantly, basic research on the neuromodulation of reward processing (Schultz, 2006; Schultz et al., 1997) indicates that economic decision making (e.g., reward processing) is also influenced by dopamine (Fiorillo et al., 2003). Furthermore, related research suggests that another neurotransmitter, namely serotonin, also plays an important role in economic decision making. Like dopamine, serotonin also undergoes significant changes during the adult lifespan (McEntee and Crook, 1991); therefore, these two

neurotransmitters likely both modulate age-related changes in economic behavior.

Neuroeconomics has the potential to shed light on how biological, psychological, and social changes across the adult lifespan may influence economic behavior in old age. Observed adult age differences in brain activation patterns would indicate not only where the change happens but also what might underlie age-related differences in economic decision making. Such findings would broaden the basis for aiding older adults in making economic decisions, in light of the fact that the aging brain functions with less efficient neuromodulation of reward processing. In this review, we relate neuroeconomics and aging by reviewing evidence around a new correlative triad consisting of (a) dopaminergic and serotonergic neuromodulation, (b) economic decision making, and (c) aging.

In the following, we first introduce factors known to influence economic decisions. Here we focus on factors influencing economic decisions under risk; whereas factors (e.g., mentalizing) that solely influence strategic interactions of decision making are not within the purview of this article. We then review how some of the factors relevant for decision making under risk, namely (a) reward, (b) risk, and (c) delay of reward, are represented in the brain and how they are affected by dopamine and serotonin. Afterwards, we illustrate how the dopaminergic and serotonergic system change over the adult lifespan and describe how economic behavior changes during healthy aging. Finally, we review how some of these changes are paralleled by changes in brain activity associated with the described factors and give an outlook of potential research regarding the neural foundations of economic decisions across the adult lifespan.

2. Factors influencing economic behavior

Economic decision making is usually seen as a type of value-based decision making, where the values of different actions are first compared, and the action selected is that corresponding to the highest value (e.g., Weber and Johnson, 2009). Two main competing classes of models in economic decision making have been proposed (d'Acremont and Bossaerts, 2008; Glimcher, 2008; Rangel et al., 2008). The first class of models, utility-based models, which includes Expected Utility Theory (EUT) and Prospect Theory (PT) (Kahneman and Tversky, 1979; von Neumann and Morgenstern, 1953), proposes that decision makers first determine the value and the relative weight of each possible reward and then calculate the overall value of a choice option as the weighted sum of possible outcome values. The second class of models, namely risk-return models (RRM), proposes that decision makers first determine the expected reward of each of the alternatives and the associated risk (e.g., variance of rewards), and then calculate the value of the alternative as the risk-corrected expected reward (Bell, 1995; Sarin and Weber, 1993). Both classes of models take reward and risk into account, which is explicitly defined in risk-return models and implicitly influences the value of an alternative in utility-based models via the curvature of the utility function. Importantly, however, a third factor influences the value of a choice alternative, namely the possible delay between action and reward delivery, which is specified in models of intertemporal choice (Ainslie, 1974; Kirby, 1997; Laibson, 1997).

Besides these factors that are explicitly specified in models of risky decision making, there is a number of additional second-order factors that usually do not affect the value directly. These include subject-related factors such as anticipatory emotions (Loewenstein et al., 2001) and cognitive abilities as well as object-related factors like the framing (Tversky and Kahneman, 1981). Cognitive abilities like working memory capacity and processing speed influence the integration of information while estimating

risk or expected reward. Anticipatory emotions and the framing of the decision or choice options likely influence perceptions of risk and reward, respectively.

2.1. Reward

Rewards can be described as positive outcomes or events from which individuals can benefit subjectively or objectively. One can, furthermore, distinguish between primary and secondary rewards. Primary rewards include those that are necessary for survival of the species, such as food, water, and sex (Schultz, 2006, for review). Secondary rewards derive their beneficial value from primary rewards and include, for instance, monetary gains, pleasant touch, beauty, and music. Humans are usually reward-seeking, thus, the possibility of reward as a consequence of an action will increase the value of this action (compare Fig. 1A). Usually, however, the marginal value of a reward is not linear, that is, doubling the reward will not necessarily double the value ascribed to an action.

Furthermore, reward is not only an important aspect in the valuation process of an action, but it also drives learning in uncertain environments. By its reinforcing nature it helps us to learn what to go for and what to refrain from. However, this process only works if the expected rewards are properly updated with information regarding actual rewards. The most important information in this context is the so-called “prediction error,” the difference between an expected (predicted) and an actual reward. Animal learning and classical temporal difference reinforcement learning models are based on the assumption that individuals learn from prediction errors (Rescorla and Wagner, 1972; Sutton and Barto, 1981).

2.2. Risk

Risk in the economic sense refers to uncertainty about the possible consequences of an action. Whereas risk describes uncertainty with known probabilities about possible consequences, ambiguity, in contrast, describes a form of uncertainty where probabilities are unknown or less well defined. In financial economics risk is usually measured by the standard deviation of possible outcomes, a measure of the variation around the average outcome. Recent research has highlighted the role of affect for risk perception and risk-related behavior (Finucane et al., 2000; Loewenstein et al., 2001; Slovic et al., 2005). The so-called risk-as-feelings hypothesis postulates that responses to risky situations result in part from direct, emotional influences, including feelings such as worry, fear, dread, or anxiety (Loewenstein et al., 2001). Depending on the risk attitude of an individual, risk can increase or decrease the value of an action (compare Fig. 1B). Whereas risk-averse individuals try to avoid risk, risk-seeking individuals are attracted by risk. Risk-neutral individuals are not affected by risk, thus for these individuals risk has no influence on the value of an action.

2.3. Delay of reward

Whereas most theories of decision making under risk include reward and risk explicitly or implicitly (e.g., EUT or RRM), they neglect a third factor, namely the possible delay between action and reward delivery, and treat every reward as an immediate one. In most situations, however, the relation between the action of deciding for a given option and goal attainment is not always immediate. Many decisions involve the valuation of rewards or costs that will only occur much later in time. In such situations it is crucial that information about the temporal extent of the outcome is also reflected in outcome-based prediction signals. Behavioral results show that given a fixed reward, actions leading to

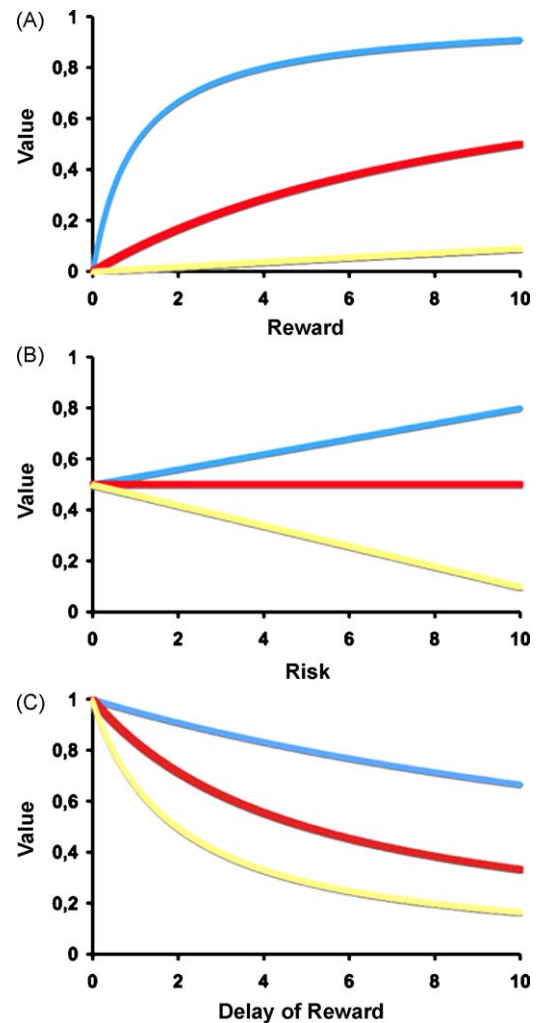


Fig. 1. Relationship between value and reward, risk, or delay. (A) The value of an action usually increases as the reward associated with it increases. The marginal value of the reward, however, usually decreases with increasing reward. Whereas the relationship between reward and value is mostly assumed to be linear in risk-return models the curvature of this function can be non-linear in utility-based models, indicating the risk attitude of an individual (convex = risk-seeking; concave = risk-averse). Different lines in this graph (as also in B and C) represent different individuals and aim to illustrate individual differences in the relationship between value and reward (risk, delay). (B) Depending on the risk attitude of an individual the amount of risk (e.g., the variance of rewards) associated with an action can increase or decrease the value of this action in risk-return models. In risk-seeking individuals risk has a positive impact on value, whereas its impact is negative in risk-averse subject and does not affect value in risk-neutral individuals. (C) Delayed rewards are usually valued lower than immediate rewards. The value of an action decreases with an increasing delay between the action and reward delivery. This temporal discounting of rewards can be described with hyperbolic or quasi-hyperbolic discount functions (hyperbolic functions are plotted here).

immediate rewards are usually preferred over actions that only yield rewards in the future (Laibson, 1997; Loewenstein and Prelec, 1992). Thus, value usually decreases if the delay of reward increases (compare Fig. 1C). This has led to models that described the observed temporal discounting with hyperbolic or quasi-hyperbolic functions (Ainslie, 1974; Kirby, 1997; Laibson, 1997).

Although behavioral research has successfully investigated how economic behavior changes when the described factors change, it has limitations in finding answers about the underlying processes that produced these changes. In the next section, we will review neuroeconomics studies that related economic decision making, and, in particular, reward, risk, and delay of reward, to brain activity.

3. Neural systems involved in economic decision making

Neuroeconomics has the potential to shed light on the processes underlying economic decision making. Several neuroeconomics studies have already investigated reward, risk, and delay discounting (Knutson and Bossaerts, 2007; Platt and Huettel, 2008; Rangel et al., 2008). These studies used a variety of paradigms. Some of these paradigms directly mirror tasks applied in behavioral economics and consumer research (e.g., Kable and Glimcher, 2007; Kuhn and Knutson, 2005; McClure et al., 2004; Plassmann et al., 2008), providing a direct link to existing behavioral research. Other studies designed new tasks, directly targeting one of the factors influencing economic behavior (Huettel et al., 2005; Knutson et al., 2001, 2005; Paulus et al., 2003). As subjects in all of these tasks had to make decisions, which resulted in monetary outcomes, we consider these economic in nature although they are less directly connected to every day economic decision making.

Evidence from a range of fMRI studies indicates that the ventral striatum (VST) and the ventromedial prefrontal cortex (VMPFC) are implicated in the representations of reward (Delgado et al., 2000; Elliott et al., 2000, 2003). But these brain regions were not only shown to code for the reward itself at the time of its delivery, but also activated by reward-predicting stimuli in the anticipation of reward (compare Fig. 2A) (Heekeren et al., 2007; Knutson et al., 2001, 2005; O'Doherty et al., 2004; Preusschoff et al., 2006).

In the context of risk processing, many studies have shown four key regions to be involved—the anterior cingulate cortex (ACC), the anterior insula (aINS), the dorsolateral prefrontal cortex (DLPFC) and the VST (compare Fig. 2B) (Critchley et al., 2001; d'Acremont and Bossaerts, 2008; Grinband et al., 2006; Hsu et al., 2005; Huettel et al., 2005; Paulus et al., 2003; Preusschoff et al., 2006; Rolls et al., 2008; Rushworth and Behrens, 2008; Volz et al., 2003, 2004; Weber and Huettel, 2008). The aINS plays an important role in affective influences on decision making (see Winkielman et al., 2007, for review) and was often related to aversive emotions, such as disgust (Adolphs, 2002). Thus, risk-related activity in the aINS could reflect the processing of (aversive) affective responses to risk, as suggested by some theories on (perceived) risk (Loewenstein et al., 2001).

Neuroeconomics has also started investigating the effect of delayed rewards resulting in partly ambiguous results (Ballard and Knutson, 2009; Kable and Glimcher, 2007; McClure et al., 2004, 2007). Initially McClure et al. (2004) identified distinct brain systems coding for immediate rewards and for all rewards, independent of delay. Whereas typical reward-related brain regions like VST, VMPFC, and PCC coded for immediate rewards, McClure et al. identified the DLPFC and LOFC as brain regions that are engaged uniformly by intertemporal choices (choices between rewards that will be delivered at different time points). These findings were replicated using primary rewards (McClure et al., 2007). In contrast, Kable and Glimcher (2007) found that VST, VMPFC, and PCC code not only for immediate rewards but also for the subjective value of delayed rewards. Additionally, the VMPFC was inversely correlated with the delay of reward (compare Fig. 2C). These authors applied hyperbolic discount functions with individual discount parameters to determine the subjective value of rewards.

Although different networks have been identified for reward processing, risk processing, and delay discounting, the VST appears to be implicated in all three processes. This indicates that this brain region may play an important role in integrating the different aspects of value into a single value signal. This hypothesis is supported by different studies that found a correlation between value and brain activity in the VST (Kable and Glimcher, 2007; Kuhn and Knutson, 2005; Tom et al., 2007). Other studies,

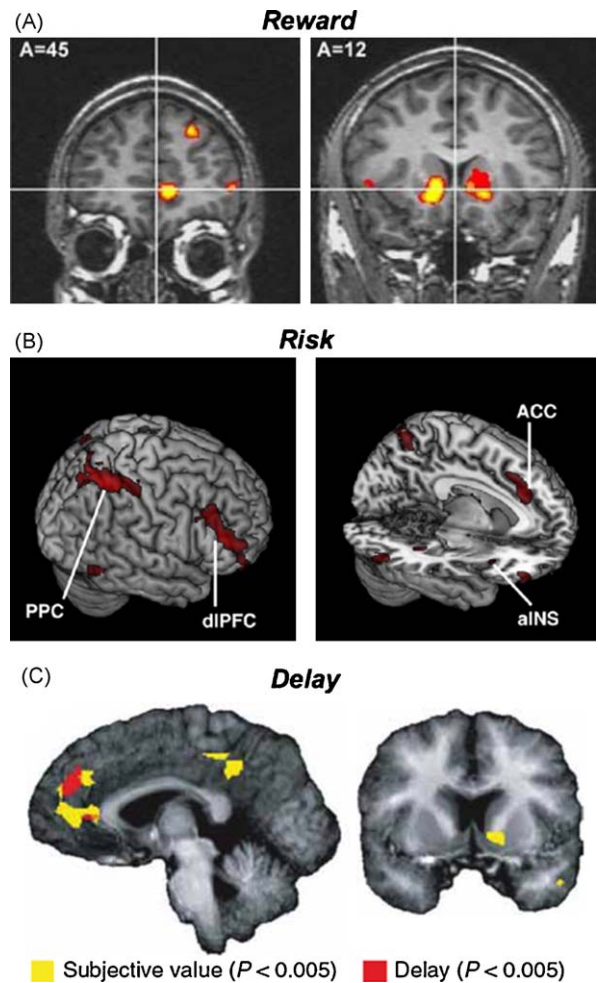


Fig. 2. Brain regions involved in economic decision making. (A) Expected reward correlates significantly with brain activity in the VST and VMPFC during anticipation of an outcome (adapted with permission from Knutson et al. (2005), Copyright Society for Neuroscience). (B) Activations in ACC, DLPFC, and aINS are significantly higher in risk conditions compared to control conditions (adapted with permission from Weber and Huettel, 2008, Copyright Elsevier). (C) Delay is inversely correlated with brain activity in the VMPFC (red), whereas the subjective value of rewards correlates irrespective of the delay with brain activity in VMPFC, VST, and PCC (adapted with permission from Kable and Glimcher, 2007, Copyright Nature). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

however, suggest that value is also represented in the VMPFC (see Kable and Glimcher, 2007; Plassmann et al., 2007, 2008; Seymour and McClure, 2008, for review). To date, however, no neuroeconomics study has investigated value while varying all three parameters (reward, risk, and delay of reward) simultaneously.

Many of the brain regions reviewed above are known to be influenced by the neurotransmitters dopamine and serotonin (e.g., VST, VMPFC, and DLPFC), indicating the implication of these neurotransmitters in economic decision making. In the following section we will review evidence for a direct relationship between dopamine and serotonin on the one hand, and reward, risk, and delay discounting on the other hand.

4. The role of dopaminergic and serotonergic neuromodulation in economic decision making

Economic decision making is heavily influenced by the modulation of different neurotransmitter systems (e.g., dopamine, serotonin, and norepinephrine). Neurotransmitters are chemicals that are used to relay, amplify, and modulate signals between

neurons. Here, we focus on dopamine and serotonin because these two neurotransmitters so far show the clearest relationship with economic behavior (Doya, 2008, for review).

Neural representations of reward and prediction error rely on dopaminergic neurons. The majority of midbrain dopamine neurons (75–80%) show rather homogeneous, phasic activations to unpredicted food and liquid rewards (Schultz, 2009). The response increases monotonically with reward magnitude, e.g., the amount of liquid volume (Tobler et al., 2005). During the course of learning, however, the dopamine response to the reward decreases gradually, and a response to the reward-predicting stimulus develops. At the time of reward delivery dopamine no longer codes for the reward itself but for the prediction error (Schultz et al., 1997). Similarly, activations of midbrain dopamine neurons shift from the time of reward delivery to the onset of the reward-predicting stimulus when the probability of being rewarded increases (compare Fig. 3 (Fiorillo et al., 2003)). Moreover, there is also a direct link between risk and dopamine release (Fiorillo et al., 2003; St Onge and Floresco, 2009). More than one-third of midbrain dopamine neurons in monkeys show a relatively slow, moderate activation that increases gradually between the reward-predicting stimulus and reward. This increase varies monotonically with risk (compare Fig. 3). Recent evidence also suggests that reward delays directly affect the response of dopamine neurons (Kobayashi and Schultz, 2008).

Studies that investigated the relationship between dopamine and economic factors like reward, risk, and delay discounting mostly used single-cell recordings in monkeys. In contrast, studies

that related serotonin to economic behavior are mostly based on pharmacological interventions in humans. Rapid tryptophan depletion (RTD) is a research technique for transiently reducing brain serotonin levels by the ingestion of an excess of large, neutral amino acids in the absence of tryptophan, the precursor of serotonin. Studies using RTD frequently found differences in economic behavior between RTD-depleted individuals and controls. RTD significantly altered decision making in a gambling task such that depleted subjects chose the more likely of two possible outcomes more often than controls (Talbot et al., 2006). Tryptophan-depleted individuals also discriminated less well between the magnitudes of expected rewards (only gains) associated with different choices (Rogers et al., 2003).

The results from studies that investigated the relationship between levels of serotonin and risk attitudes are quite ambiguous. Some studies did not find differences in risk attitudes or risk-taking behavior between levels of serotonin (Rogers et al., 2003; Talbot et al., 2006), whereas other studies identified serotonin-related differences in neuroticism, harm avoidance, and loss aversion, individual characteristics that are strongly related to risk aversion (Gonda et al., 2008; Murphy et al., 2008). One study investigated the effect of serotonin and dopamine on risk-taking in a genetic approach and found significant influence of both neurotransmitter systems (Kuhnen and Chiao, 2009).

Serotonin is also assumed to interact with dopamine in implementing prediction signals that reflect the temporal information about the outcome (Denk et al., 2005; Tanaka et al., 2007). The rate of discounting of delayed rewards is higher in low-serotonin conditions compared with high-serotonin conditions. Thus, low levels of serotonin accentuate delayed reward discounting in humans (Schweighofer et al., 2008). Both dopaminergic and serotonergic brain systems undergo significant changes over the adult lifespan. In the following section we will review empirical evidence for these changes as well as neurocomputational models that relate changes in cognition to changes in neuromodulation.

5. Age-related changes in dopaminergic and serotonergic neuromodulation

Brain aging involves neurofunctional, neuroanatomical, and neurochemical changes as well as dynamic interactions between these changes (Cabeza et al., 2005; Lindenberger et al., 2006). During the course of normal aging, dopaminergic systems undergo substantial decline. Much of the work on the relationship between aging and dopamine neurotransmission has focused on the caudate and the putamen, two major nuclei in the striatal complex with dense dopaminergic innervation from the substantia nigra. Thus, the conditions for reliable analyses of dopamine biomarkers are particularly favorable in the striatum. There is strong evidence for age-related losses of pre- and postsynaptic biochemical markers of the nigrostriatal dopamine system. Regarding pre-synaptic mechanisms, both PET and SPECT studies (Erixon-Lindroth et al., 2005; Mozley et al., 2001) indicate marked age-related losses of the dopamine transporter in the striatum (compare Fig. 3), with the average decline estimated to be 5–10% per decade from early to late adulthood. For postsynaptic mechanisms, molecular imaging work reveals age-related losses of both striatal D1 (Suhara et al., 1991; Wang et al., 1998) and D2 (Antonini and Leenders, 1993) receptor densities of comparable magnitude, as found for the dopamine transporter.

A similar downward age trajectory is seen for the mesocortical and mesolimbic dopaminergic pathways. Thus, marked age-related losses in D2 receptor binding have been observed throughout the neocortex as well as in hippocampus, amygdala, and thalamus (compare Fig. 4) (Inoue et al., 2001; Kaasinen and Rinne, 2002). The fact that similar age patterns are seen for the

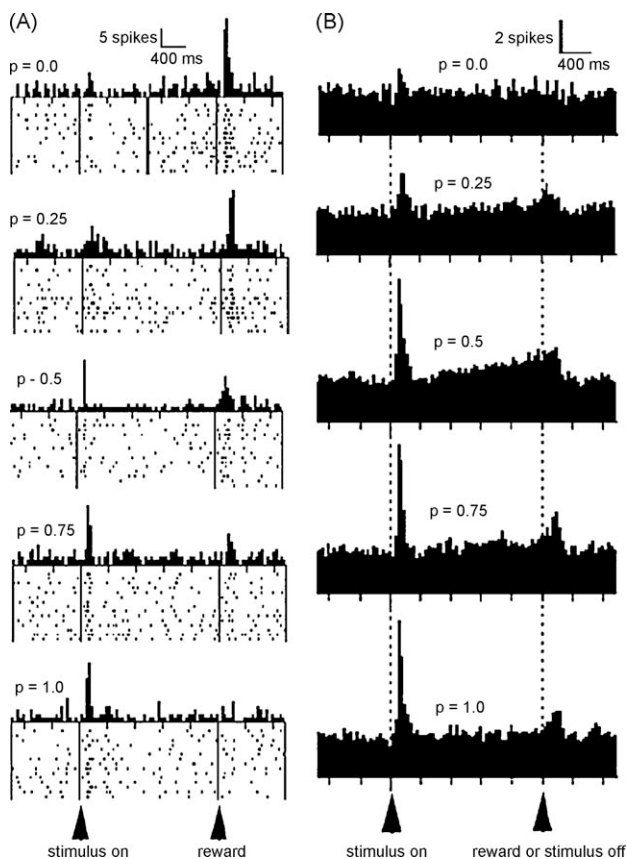


Fig. 3. Reactivity of midbrain dopamine neurons to predicted reward and risk. (A) Activations of midbrain dopamine neurons shift from the time of reward delivery to the onset of the reward-predicting stimulus when the probability of being rewarded increases. (B) Slow increase in firing of dopamine neurons between stimulus and reward delivery that is modulated by risk (both figures adapted with permission from Fiorillo et al., 2003, Copyright Science).

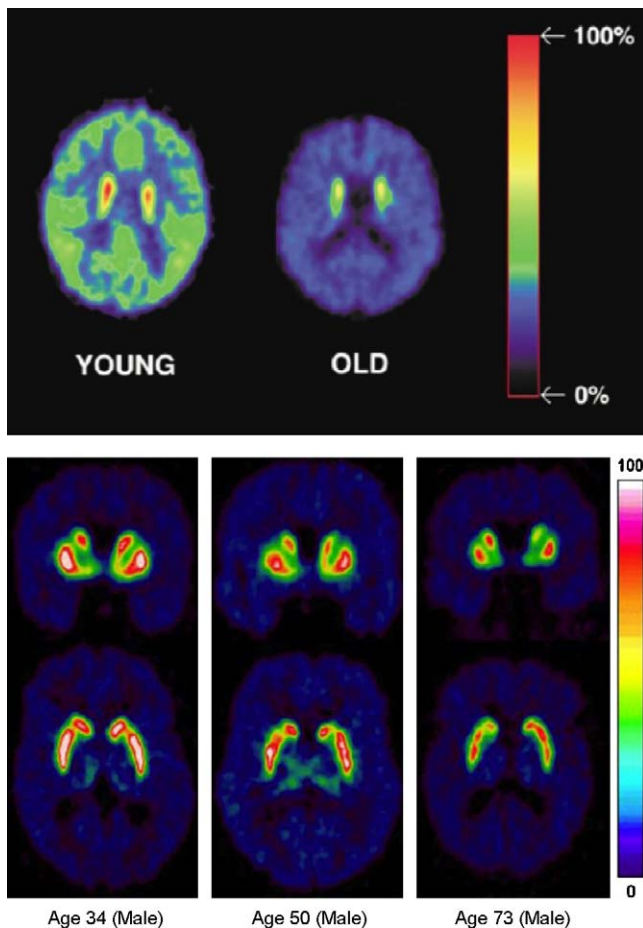


Fig. 4. Age-related reduction in D2 receptors and dopamine transporters during aging. (A) Difference in D2 binding between a young (25 years) and an old (70 years) healthy woman as seen in PET (adapted with permission from Kaasinen and Rinne, 2002, Copyright Elsevier). (B) Declines of dopamine transporter density in caudate and putamen as a function of age (adapted with permission from Erixon-Lindroth et al., 2005, Copyright Elsevier).

dopamine transporter and postsynaptic markers suggests that the expression of transporters and receptors may reflect adaptation of major components of the dopaminergic pathways. One possibility derived from work on knockout mice is that loss of the dopamine transporter initially results in increased dopamine concentrations; increased dopamine levels may subsequently lead to down regulation of neurotransmission in postsynaptic neurons (Shinkai et al., 1997; Zhang et al., 1995).

Various neurocomputational models have been proposed to link aging-related decline in dopaminergic neuromodulation to behaviorally observed cognitive deficits. One of these models relates weakened phasic activity of the mesencephalic dopamine system with aging-related deficits in detecting performance error (Nieuwenhuis et al., 2002). Another model focuses on capturing the effect of deficient dopaminergic neuromodulation on compromised prefrontal cortex functions, such as cognitive control (Braver et al., 2001). A third model captures the effects of deficient neuromodulation on processing variability and the distinctiveness of memory and goal representations in more general terms (Li et al., 2001).

Compared to dopamine there is limited data in the literature regarding changes in the serotonin system during normal aging. Several post-mortem studies have reported a reduction in the number of serotonin binding sites with age in the frontal lobe, occipital lobe, and hippocampus (Arranz et al., 1993; Cheetham

et al., 1988; Gross-Isseroff et al., 1990; Marcusson et al., 1984a,b; Sparks, 1989). A PET study provided in vivo evidence for an age-related decline in cortical serotonin binding sites (Wong et al., 1984). Further, abnormalities of the serotonergic nervous system are well documented in studies of Alzheimer's disease, and there is evidence suggesting that changes in this system occur in association with non-disease aging (McEntee and Crook, 1991).

In summary, separate lines of research have found evidence for the implication of dopamine and serotonin in economic decision making in younger adults, and substantial declines in both the dopaminergic and serotonergic brain systems over the adult lifespan. Together these findings suggest that the alterations of dopaminergic and serotonergic brain systems may contribute to changes in economic behavior over the adult lifespan. In the following section we will review evidence from experimental and survey studies that support the idea of altered economic behavior in older adults.

6. Age-related changes in economic behavior

Economic preferences are quite stable in the short term, but it is assumed that value (utility) functions change over the long run, that is, over the adult lifespan (Rogers, 1994; Trostel and Taylor, 2001). Economic preferences are influenced by situational, environmental, and biological factors. A woman, for example, who has just become a mother will likely have different economic preferences than she did a few years earlier. Similarly, a newly retired man may also have different financial considerations than before the retirement. Age is a descriptive variable for many changes that might cause changes in economic behavior over the adult lifespan.

One study that used data from a large representative sample found that age has a significant effect on the willingness to take risks (Dohmen et al., 2005). The applied scale was validated in a sub-sample by showing that it predicts actual risk-taking behavior in a lottery game where subjects repeatedly had to choose between safe gains and risky lotteries. Thus, the authors conclude that risk-taking behavior decreases over the adult lifespan. An experimental study using a gambling task supported this finding (Deakin et al., 2004). In each trial of the gambling task, subjects received a certain amount of points, which were free to distribute between two options. In one option, points were kept safe, whereas they were exposed to lottery risk in the other. The authors observed that the mean proportion of available points that a subject staked on each trial was significantly lower in older adults than in younger adults, that is, older adults showed less risky behavior.

Further support for the hypothesis that economic behavior changes over the adult lifespan comes from experimental studies that used the Iowa Gambling Task (IGT) (Bechara et al., 1997), which has been used in numerous studies to investigate individuals' ability to make favorable choices (Bechara et al., 2000; Maia and McClelland, 2004). In the IGT subjects have to choose repeatedly between four decks of cards without any knowledge about possible outcomes (i.e., reward magnitude and probability). Two of these card decks are "bad decks" in the sense that they result on average in a loss. The other two decks ("good decks") have a positive expected reward. Usually individuals start with preferring the bad decks, which have higher gains but also much higher losses compared to the good decks, and then switch to the good decks.

In one study, both younger and older subjects started with the usual pattern to choose the bad card decks (Denburg et al., 2005). Whereas the younger subjects then gradually shifted towards the good card decks as the game progressed, the older subjects did not demonstrate this shift, staying with the bad card decks, indicating an impaired ability to identify favorable options in the long run. Two other studies also found that older adults perform less

advantageously in the IGT compared to younger adults (Fein et al., 2007; Zamarian et al., 2008). Zamarian et al. (2008) compared the performance of younger and older adults in the IGT with their performance in another task that provides the subjects, in contrast to the IGT, with full information about the lotteries (probabilities and magnitudes of associated gains and losses). Older adults showed poor performance in the IGT relative to younger adults, indicating difficulty in making advantageous decisions under ambiguous conditions. In contrast, older adults performed as well as younger adults in the other task, demonstrating their ability to make decisions in situations where they are given full information about the problem. However, despite substantial evidence for age-related differences in the performance of the IGT, it should be noted that there is also one study using a variant of the IGT (only two card decks) to compare the economic behavior of younger and older adults that did not find any significant differences between the age groups (Kovalchik et al., 2005).

There is also substantial evidence for a relationship between age and changes in delay discounting. Green et al. (1994) tested three groups of 12 participants (pre-teens, young adults, and older adults) in a delay discounting task. They used a choice procedure to elicit discount rates for eight delays and two amounts of money. One of their observations was that the discount rate increases with age, which means that older adults have a higher preference for immediate rewards. This result was supported by a study investigating 268 individuals aged between 19 and 75 years (Harrison et al., 2002). They found, consistent with Green et al. (1994), that the discount rate was greatest in the 'old' group (defined as people aged 50 or older). Another study (Read and Read, 2004) that investigated delay discounting in 123 individuals (age 19–89), suggested an inverted u-shaped relationship between age and delay discounting. Their results showed that older adults discount more than younger ones, and that middle-aged people discount less than either group.

Indirect support for the hypothesis that economic behavior changes over the adult lifespan can be derived from age-comparative studies related to second-order factors influencing economic decision making. Working memory capacity and processing speed both decline during the course of usual aging (e.g., Bäckman et al., 1999; Baltes and Lindenberger, 1997; Dobbs and Rule, 1989; Li et al., 2008; Salthouse and Babcock, 1991; Schmiedek et al., 2009) and thus likely influence economic behavior and decision making in general. In one study that investigated the effect of aging on the adaptive selection of decision strategies older adults with lower working memory capacity and lower processing speed tended to look up less information, took longer to process it and use simpler, less cognitively demanding strategies (Mata et al., 2007).

Thus far many studies have identified age-related differences in economic behavior, specifically in risk-taking behavior, delay discounting, and the ability to make advantageous decisions in the IGT. These studies, however, provide no evidence for the underlying mechanisms that drive age-related changes in economic decision making. Neuroeconomics provides the tools to investigate this question in more detail. In the following section we will review studies that attempted to ground age-related differences in economic behavior in neurocognitive mechanisms.

7. Age-related differences in neural systems underlying economic behavior

The strongest link to date between age-related changes in cognitive functions important for economic behavior and underlying neurobiological changes lies in the domain of reward-based learning and decision making. Schott et al. (2007) compared the ability to learn stimulus-reward associations between younger and

older adults. Young adults showed the well-replicated pattern of midbrain and ventral striatal activation for stimuli that predicted monetary reward when compared with stimuli that predicted neutral feedback. Healthy elderly subjects showed the opposite pattern, with an absent reward prediction response, but with mesolimbic activation to reward feedback itself. The authors speculate that this result could reflect a reduced ability of older participants to accurately estimate expected rewards due to a dopamine-dependent decrease of the signal-to-noise ratio in the mesolimbic system. These results underpin behavioral results that indicate that older adults have deficits in learning from positive feedback (Mell et al., 2005).

Further support for this interpretation is given by two studies that investigated stimulus-reward association learning and outcome processing (Cox et al., 2008; Marschner et al., 2005). Marschner et al. (2005) used a probabilistic object reversal task, where stimulus-reward associations change after they have been properly learned. Younger participants in their study showed greater responses in the VST to reward cues after stimulus reward associations had been learned than older adults, indicating that younger adults have a clearer representation of the expected reward. Cox et al. (2008) focused on the delivery of reward. Older adults retained most of the typical features of a striatal response, so that activity in the caudate head showed reliable differentiation between rewards and punishments after the outcomes were presented. Although the authors found small age-related differences in the magnitude and extent of striatal activation, this indicates that outcome processing is more robust to age-related decline than the processing of reward expectation.

In a different study, Samanez-Larkin et al. (2007) investigated the effect of age on reward expectation. In contrast to learning studies where reward anticipation is generated through the repeated experience of reward, the authors used the monetary incentive delay task (Knutson et al., 2000), where reward anticipation is induced by variations of the stimulus. The authors found evidence for intact striatal activation during gain anticipation with age, but report a relative reduction in activation during loss anticipation (compare Fig. 5). This supports the finding from behavioral studies that report a reduced experience of negative emotions in older adults (Mather and Carstensen, 2005).

There is not only evidence for age-related changes in reward processing but also provides the first evidence for changes in brain systems related to risk perception and risk-taking behavior. Lee et al. (2008) found that older subjects chose significantly less often the risky out of two options (risky vs. safe); however, when they chose the riskier option, they had a stronger activation in the right insula compared to younger adults. This stronger insula activity in older adults was interpreted as indicating that the risky option is perceived as more risky by elderly than by young adults, resulting in an increased avoidance of risky situations.

8. Outlook

The dopaminergic system and the serotonergic system interact in value-based decision making as well as in reward-based learning. Both are known to influence reward, risk, and delay of reward, and undergo significant changes during the adult lifespan. These changes are paralleled by changes in economic behavior, specifically in risk-taking, delay discounting and reward-based learning. The neuroeconomics approach has already helped to identify age differences in activation patterns associated with reward processing, indicating that older adults have problems forming correct stimulus reward associations. They also fail to activate reward-related brain regions like the VST or VMPFC during the presentation of a reward-predicting stimulus, thereby lacking a basis to make profitable decisions.

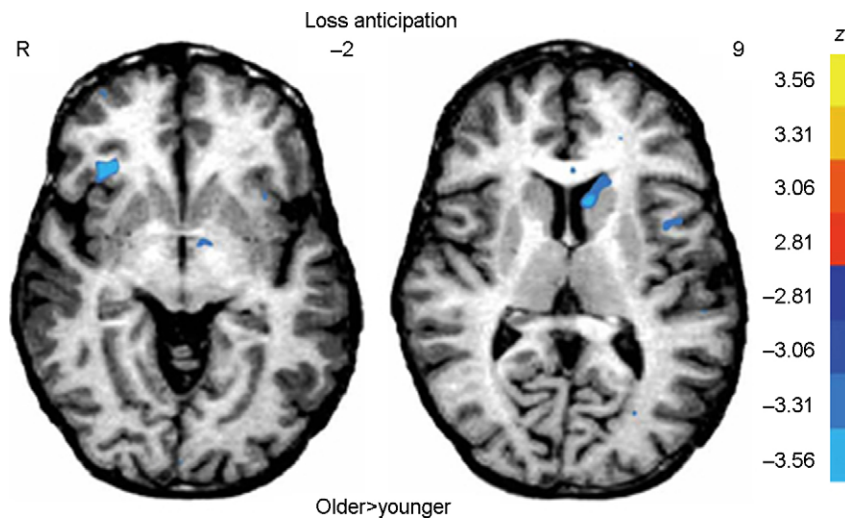


Fig. 5. Between-group *t*-tests of loss vs. non-loss anticipation contrast maps (older adults > younger adults; SVC, $z > 2.81$; $P < 0.005$ uncorrected). Negative *z*-scores showed less activation for older adults in both the anterior insula and medial caudate (adapted with permission from Samanez-Larkin et al., 2007, Copyright Nature).

Given the known relationships between reward and dopamine on the one hand and dopamine and aging on the other hand, it can be hypothesized that the observed age-related changes in reward processing are caused by declines in the dopaminergic system. For instance, derived from the temporal difference model of reward prediction (Seymour et al., 2004) and the stochastic gain tuning model of neuromodulation of cognitive aging, it could be expected that both the reward prediction signal and the mapping between reward predictions and choice actions are noisier in older adults due to deficient dopaminergic modulation. The noisier processing at each step of the reward learning history could accumulate results that are less distinctive representations of reward between options, consequently affecting goal-directed reward selection (Li et al., 2007). These general principles can be applied to account for aging differences in other, more specific aspects of decision making, for instance, risk perception and temporal discounting. To investigate these expectations empirically, future research could apply paradigms that include age differences as well as other individual differences that affect the functionality of the relevant transmitter systems.

Currently, there are two complementary approaches to investigate effects of neuromodulation on cognition in general and on decision making in particular: pharmacological intervention and genetics. In the case of a pharmacological intervention, one group of subjects is given a drug that increases or decreases dopamine availability whereas another group receives a placebo, leaving the dopamine level unchanged. In case of genetics studies, subjects are chosen according to a genetic polymorphism that is known to influence the level of dopamine in reward-related brain regions (e.g., the catechol-O-methyltransferase Val¹⁵⁸Met polymorphism). But one should note that the effects are much stronger for pharmacological interventions, and that individuals that have lower levels of dopamine due to a genetic polymorphism might already have compensated for this difference (e.g., by recruiting additional brain resources). The same holds true for serotonin, which also likely affects reward processing. A pharmacological intervention with tryptophan and a polymorphism in the serotonin transporter gene (5-HTTLPR) are candidates to vary the levels of serotonin in an age-comparative study.

Most studies have, thus, only included one of these two approaches. A few exceptions took either a pharmacoinaging approach (Mattay et al., 2003) or a behavioral genetic age-comparative approach (Nagel et al., 2008), which allowed direct investigations of the effects of genetic-based and age-related

differences in neuromodulation and their interactions on cognitive and brain functions (Lindenberger et al., 2008). Along these lines, future combined age-comparative pharmacoinaging studies could shed lights on the triadic relationship between (a) economic decision making, (b) dopaminergic and serotonergic neuromodulation, and (c) aging.

Furthermore, as described above, reward processing is not the only factor influencing economic decision making. Risk and delay significantly affect the values of choice options. Both are strongly related with dopamine and serotonin release, but recruit partly different networks of brain regions. Neuroeconomics should investigate how different age groups differ in the brain regions they recruit to process risk and delay and how these differences are accompanied by differences in dopaminergic and serotonergic neuromodulation. Here again, pharmacological intervention or genetics, combined with studies of different age groups, offers the possibility to shed light on the cause of age-related changes.

Although reward, risk, and delay of reward are likely influenced by both dopamine and serotonin, to date, little attention was put on potential interactions between these factors. This lack of research was mainly based on the fact that reward, risk, and delay of reward were regarded as object-related, independent variables that cannot interact by definition. Changing the perspective to subject-related factors (e.g., perceived risk) allows the investigation of potential interactions. Research on the perception of risk already indicated that the coefficient of variation, a measure of variability per unit of reward, might be a better predictor of perceived risk than the variance of rewards (Weber et al., 2004). Future studies should follow this line of research, shifting to a subject-related view of reward, risk, and delay of reward and investigate possible interactions that might be grounded in the shared influence of serotonin and dopamine. Similarly, it should be a main goal of neuroeconomics to identify experiments that allow investigation of how reward, risk, and delay of reward are integrated into a single value signal. These experiments would allow the investigation of another potential source of age-related differences in economic decision making, namely the way in which reward, risk, and delay interact and are integrated. To arrive at a complete and realistic picture of age-related changes in economic decision making, however, such studies will have to also include social and contextual factors. Goals change as individuals age, especially when the social environment changes (e.g., after retirement) (Ebner et al., 2006). Similarly, the time horizon of economic activities (e.g., investing money) changes due to a

decreasing time to death. Accordingly, the goal of research on neuroeconomics and aging must be to include biological, social, and contextual factors in a comprehensive model of economic decision making across the lifespan.

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