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Review Paper

# Sex-linked Neuromodulatory Profiles May Shape Economic Decision-making

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## ABSTRACT

Decision-making (DM) is an important issue in our daily lives. Even the most trivial decisions can have significant long-term impacts. Among the various forms of DM, economic DM is one of the most complex because it requires integrating information about rewards, costs, risks, and future consequences. Studies on economic DM have developed a new branch of research called neuroeconomics, in which economic DM is examined through psychological and neuroscience studies to determine the underlying cognitive processes involved. Since neuroscience can directly investigate brain organization, related biochemical mechanisms, and the causal relationships between these components and behaviors, it can play an important role in this interdisciplinary approach. Due to the structural and biochemical differences in the nervous system of men and women, different strategies may be used in their economic decisions, leading to different results. Economic DM engages distributed neural networks, with distinct brain regions contributing to different stages of the decision-making process. The structural organization of the brain, together with neuromodulatory systems, may influence the evaluation of rewards, risks, and future outcomes. In this review, we synthesize evidence from human and animal studies on sex-related differences in brain organization and major neuromodulatory systems and discuss how these differences may contribute to variability in economic DM. Although current evidence indicates potentially important associations, further well-designed studies in both humans and animals are required to elucidate the underlying mechanisms and determine how these biological differences shape economic DM in humans.

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## Highlights

- Sexually dimorphic brain organization may contribute to sex differences in DM.
- Dopamine and serotonin may contribute to sex differences in the temporal evaluation of rewards.
- Glutamatergic signaling may contribute to sex differences in decision speed and accuracy.
- GABAergic signaling may contribute to sex differences in impulsive DM.
- Gonadal hormones may shape sex-specific neuromodulatory influences on economic DM.

## Plain Language Summary

Every day, people make decisions that affect their health, finances, relationships, and future. Although these choices may appear simple, they depend on complex communication among multiple brain regions. Research also suggests that biological differences between males and females may influence decision-making (DM); however, the underlying neural mechanisms remain incompletely understood. This review synthesizes current evidence on how several brain chemicals—including dopamine, serotonin, glutamate, and gamma-aminobutyric acid (GABA)—may contribute to economic DM, defined as choosing among options involving different costs, benefits, risks, or delays. Rather than reporting new experimental findings, the article reviews evidence from human and animal studies to examine how these chemical signaling systems may interact with biological sex to influence DM. Available evidence suggests that these neurotransmitter systems play important roles in reward evaluation, impulsivity, learning, risk assessment, and cognitive control. The reviewed studies also indicate that sex-related differences in brain structure, hormone levels, and neurotransmitter systems may contribute to variation in certain aspects of DM. However, findings are not always consistent across studies, underscoring the need for further research to clarify these relationships. A clearer understanding of how brain chemistry and biological sex interact to influence DM could advance research in neuroscience, psychology, and behavioral economics. It may also support the development of more personalized approaches to understanding decision-related disorders and designing interventions that account for biological differences among individuals.

## Introduction

Decision-making (DM) is probably the most frequent behavior in our daily lives. Even the most insignificant decisions could have a significant influence on our future. Economic decisions are among the most challenging and intriguing topics to contemplate. One of the primary goals of studies in this field is to assess the feasibility of choosing an optimal option by investigating the elements that influence economic decisions. To predict the outcome of this cognitive process, economists attempted to construct theories based on mathematical models, such as expected utility theory, prospect theory, and game theory (Kahneman & Tversky, 2013). Although these models had predictive values, they were not completely flawless, and in some situations, people might decide in ways that contradicted the predictions. It sparked a new branch of study known as neuroeconomics, in which economists, psychologists, and neuroscientists collaborate to identify the cognitive processes that drive economic DM (Bachman & Huettel, 2020). As it can directly investigate brain circuits, associated biochemical machinery, and the causality relationship between these components and behaviors, neuroscience plays a unique role in this interdisciplinary field. With the identification of the critical elements, some parameters may be modified and adjusted to achieve optimal outcomes (Glimcher & Rustichini, 2004).

Considering the different strategies men and women use during economic DM, resulting in various outcomes, studying the underlying neural changes in the networks and neuromodulator levels is intriguing. In this approach, the secrets of processing preferred economic choices, which may differ between genders, could be revealed. Findings from investigations of various financial decision contexts in men and women suggest that different brain regions may be involved in each gender (Vanutelli et al., 2020). Since neurotransmitters and neuromodulators can operate differently across various brain regions, studying these compounds and how they differ between

sexes could provide important clues for making more successful economic judgments. Interestingly, emerging applied studies support the view that companies, governments, and investors should consider neurotransmitter effects to make better economic decisions (Gautam et al., 2024). In this review, serotonin, dopamine, norepinephrine (NE) (or noradrenaline), acetylcholine (ACh), gamma-aminobutyric acid (GABA), glutamate, oxytocin (OT), and histamine were described as the main neuromodulators that might be implicated in DM. The key point is that sex differences in economic DM do not arise from isolated neuromodulators but from sex-specific configurations and interactions among neuromodulatory systems across valuation, timing, and control processes.

## Economic DM from a neuroscience perspective

The DM strategies applied by decision-makers shape the outcomes of the DM process. Classical fields such as economics, neuroscience, and computer science have proposed various DM strategies. These strategies can be divided into four groups: intuitive, empirical, heuristic, and rational (Wang & Ruhe, 2007). DM is further classified based on strategies and goals into perception-based DM and reinforcement-guided DM (Khani & Rainer, 2016). Perceptual DM involves selecting a possibility or course of action depending on available sensory data (Lepora & Pezzulo, 2015; Khani & Rainer, 2016). Reinforcement (or reward)-guided DM applies economics and reinforcement learning theories to maximize the value obtained over a certain time interval. Value-based DM is a comparable concept, where choices mainly depend on the subjective value assigned to each possibility. While our primary focus is on the role of subjective value in preference behavior, it is important to note that objective perceptual qualities, like the prominence of choice-related stimuli also affect DM (Cohen, 2008; Khani & Rainer, 2016). This study assessed the latter type of DM because it is one of the most relevant types in assessing economic decisions, especially from a neuroscience standpoint.

Neuroeconomics is the study of how humans make value-based decisions neurobiologically, cognitively, and behaviorally (Lăzăroiu et al., 2017). Every decision is made in five consecutive steps. First, the brain is presented with all possible choices with internal and external states. Secondly, the brain evaluates these inputs to assess the level of their desirability. The brain selects the most persuasive alternative in the third step. Fourthly, the brain reevaluates the outcome of the decision to compare the desirability level of the chosen alternative before and after DM. The final step is learning from previous DM rounds, which can influence the outcomes of upcoming decisions. Evaluation is the central stage in the neurobiology of DM. The brain can compare all options, even though they are very different. It encodes all the aspects of each option into a common signal, which is perceived as the subjective value for an option. Through this conversion of inputs into single signaling, the brain can compare the desirability of various choices. This theory is known as "common currency" and was supported by compiling empirical evidence (Kable & Glimcher, 2009; Levy & Glimcher, 2012; Pearson et al., 2014). It should be noted that there is mounting evidence that subjective value representations play a key role at the neuronal algorithmic level. These representations are mostly encoded in the striatum and the ventromedial prefrontal cortex (PFC) (Kable & Glimcher, 2009).

In general, two types of variables influence the evaluation of an option. The first type consists of external elements (Bakshi, 2012) that seem to be exclusively relevant to the option itself, such as the intrinsic value of the option (Levy & Glimcher, 2012), related risks (Platt & Huettel, 2008), ambiguities (Oakes et al., 2007), and reward-related delays (Kable & Glimcher, 2007). The second type is the internal factors that are related to the decision-maker (Quirk & Mueller, 2008; Bakshi, 2012), such as positive and negative emotions (Lerner et al., 2015), optimism (Pulford, 2009), the opportunity to behave altruistically (Powell et al., 2018), trust (Axelrod & Hamilton, 1981), and the desire for social conformity (Klucharev et al., 2009). Almost all economic decisions involve some combination of internal and external influences. The significant point is that possible disparities in processing these elements between males and females may generate gender differences in DM. Understanding the neurobiological basis for these disparities might pave the way for a more precise prediction of gender-specific choosing outcomes.

## Neural substrates of reinforcement-guided DM

Although DM has been studied for over a century, the role of functional neural circuits in various types of cost/benefit DM has been recognized only in the last 20 years (Fobbs, 2016). Many efforts have been made to comprehend how the human brain processes information to make decisions. It has been revealed that a substantial part of economic DM takes place in the forebrain and the limbic system, the latter of which is also important for processing emotions (Khan & Mubarik, 2022). During efficient DM, different brain regions, like the PFC, amygdala, and nucleus accumbens (NAc) become activated (Pittaras et al., 2016). Economic DM could be

broken down into two functions: "reward utility calculation" and "loss utility calculation". When a predicted gain or a practical conclusion results in an improvement, reward-related areas are stimulated, leading to a tendency behavior. The ventromedial PFC, orbitofrontal cortex, anterior cingulate, ventral striatum, and mesolimbic system are involved in reward-based DM. The orbitofrontal cortex, in particular, is crucial in this type of DM, especially when the decision-maker has enough information to develop a decision (Guo et al., 2013). Furthermore, both in business and in daily life, uncertainty is common and unavoidable. Most decisions are made in uncertain conditions, and uncertainty influences how decisions are made (Leake, 1998).

We are frequently faced with situations in which we do not have all the required information and must decide despite the uncertainty about the consequences. In recent years, studies have been undertaken on DM in risky settings, which are classified into three levels: certain, ambiguous, and risky conditions. In a study, using fMRI with a novel DM card-matching task involving the three conditions of certain, risky, and ambiguous, more brain regions became activated as the degree of reward uncertainty increased, including regions associated with processing information about loss. They demonstrated that the orbitofrontal cortex, ventrolateral prefrontal lobe, the frontal pole of the PFC, precentral gyrus, inferior temporal gyrus, fusiform gyrus, inferior parietal lobule, supramarginal gyrus, and cerebellar posterior lobe showed considerably more activity in the 'risk' condition in comparison to the'certain' condition (Guo et al., 2013). Using magnetic resonance imaging (fMRI), Farrar et al. investigated brain activity during a task involving certain and uncertain states. They reported the involvement of the dorsolateral PFC, anterior cingulate cortex (ACC), posterior parietal lobule, striatum, thalamus, amygdala, and hippocampus in the 'uncertain' condition. All these areas were expected, as they are regions involved in resolving ambiguity and rule updating. Occipital and midbrain engagement is also reported in studies, which may be associated with more required visual attention and motor control activities, respectively (Farrar et al., 2018). Prior studies have reported activation of the orbitofrontal cortex, prefrontal, parietal, temporal, and occipital lobes, ACC, amygdala, hippocampus, cerebellum, and midbrain during the risk-taking DM process (Guo et al., 2013). Also, the dorsolateral PFC and the cerebellar posterior lobe showed substantially larger activity in the 'ambiguity' condition than in the 'risk' condition. The frontal pole of the PFC displayed considerably more activity in the 'ambiguity' condition compared to the 'certain' condition (Guo et al., 2013). However, the variability in tasks used to investigate the same concept of risky/uncertain DM makes comparisons difficult. It has been suggested that evidence about proper choices is stored in the ventral temporal cortex and posterior parietal cortex (Philiastides et al., 2010). It has also been suggested that calculating expected value and reward outcomes involves the ventromedial PFC. Additionally, the hippocampus and ventromedial PFC work together to detect mismatches in the data (Garrido et al., 2015). Also, the basal ganglia contribute to DM as rules are learned. The striatum is engaged in habit formation and reward learning, and its activity may correlate with the prediction of punishment (Samejima et al., 2005; Daw & Doya, 2006). The ACC interacts with the PFC, and its involvement has been reported in conflict monitoring and evaluation of final results (Botvinick, 2007).

## Brain lateralization and economic DM

Economics is not really about money; it is about choices. In neuroeconomics, we study economic DM and how cognitive abilities influence preferences in economic settings (Glimcher & Rustichini, 2004). However, humans differ in the valuation of costs and benefits, which is a common aspect of their economic DM (Seymour & McClure, 2008). Individual differences, such as the level of intrinsic connectivity of brain networks, have been cited as an influential factor in DM (Fuentes-Claramonte et al., 2016). Aside from individual variations, there is a disparity in the economic DM process between men and women. Recent work in economic psychology highlights that gender differences in economic behavior, particularly in risk attitudes, competitiveness, and bargaining, have substantial real-world economic consequences; however, the neurobiological mechanisms underlying these differences remain largely unexplored (García-Segarra et al., 2025). Women process integrated information, applying all available environmental information, even if it leads them to make undesirable decisions. On the other hand, men selectively utilize data, relying on the details that support their choices (Lim et al., 2021). According to behavioral economic studies, women seem to be more risk-averse than men in economic DM under risk and ambiguity, as they invest less in risky investments (Charness & Gneezy, 2012). Conclusively, in value-based DM, women and men show behavioral differences (Villanueva-Moya & Expósito, 2021).

An intriguing description that can explain why men and women perform differently in DM is called "neural sexual mosaicism". According to neural sexual mosaicism, while men and women may have extremely similar neural organization in some features, they may

be distinct in others. Sex hormones in embryonic or perinatal sexual differentiation, discussed in the following sections, can be one potential reason for these disparities (Cahill, 2006).

Several theories, including the functional lateralization of the neural organization, the role of neurotransmitters, and sex hormones, have been proposed to explain the differences between sexes in DM (Zaidi, 2010; Ambrase et al., 2021). These disparities may be due to sex differences in the functional lateralization of neural organizations associated with DM circuits, such as ventromedial PFC and amygdala (Tranel & Bechara, 2020). The unique roles and different social goals may be due to gender-related hemispheric asymmetry (Koscik et al., 2010). This functional asymmetry is not an emergent process and may be a way to enhance brain capacity without increasing individual brain size (Gupta et al., 2011). There is a wealth of data demonstrating that gender influences the functional lateralization of DM and emotion in areas, like the ventromedial PFC and amygdala, with left-sided lesions in women and right-sided lesions in men causing the most disturbance (Reber & Tranel, 2017). For instance, fMRI experiments demonstrate that men and women with injured ventromedial PFC on the right and left sides, respectively, exhibit lower risk and ambiguity aversion in their decisions, which may reflect the deployment of different processes between sexes (Sutterer et al., 2015).

Recent human research has studied the role of the amygdala in more intricate patterns, including social contact, social judgment (e.g. reliability, stereotyping), and DM (Brand et al., 2007; Gupta et al., 2011). The amygdala is involved in involuntary DM based on emotional inputs, such as rewards and punishments in money (Bechara et al., 1999). Structurally, the amygdala is larger in men than in women (Orsini & Setlow, 2017). Moreover, evidence suggests that the injured right amygdala leads to more defects in DM in men, whereas the injured left amygdala appears to be more harmful to women (Gupta et al., 2011). fMRI studies also show a consistent pattern of amygdala activity, including gender differences, in brain responses to social and emotional inputs (Hamann, 2005).

The ventromedial PFC is another important region involved in DM, emotion regulation, and social functioning. Injured right ventromedial PFC is likely related to impaired social behavior, emotional functioning, and DM in men, whereas in women, damage to the left ventromedial PFC is more likely to lead to these impairments (Tranel et al., 2005; Tranel & Bechara, 2020). The dorsolateral PFC in women is more active than in men in both hemispheres when they lose monetary rewards (Cazzell et al., 2012). These findings are also noteworthy given the strong anatomical association between the amygdala and ventromedial PFC in different aspects of emotion and DM. Generally, although men's and women's brains appear relatively similar, they exhibit considerable structural and functional differences. More significantly, sexually dimorphic brain regions play diverse roles in different types of DM (Valentine & Rittenburg, 2007).

## Neuromodulator systems involved in DM

Several brain regions create complicated networks for data processing and cognitive evaluation to make optimized decisions. Neuromodulators and neurotransmitters play critical roles in these neural processes. In the following sections, we will focus on the role of neurotransmitters and neuromodulators in DM in different contexts.

### Serotonin (5-hydroxytryptamine; 5-HT)

Serotonin is an essential neurotransmitter for risk-taking in DM (Ishii et al., 2015), loss aversion (Takahashi, 2013), decreased delay discounting, emotional/reversal learning, and social behavior (Crişan, et al., 2009; Homberg, 2012). The activity of 5-HT neurons in the dorsal raphe, projecting directly into the basolateral amygdala and orbitofrontal cortex, is necessary for goal-directed and purposeful behaviors (Pickens et al., 2003; West et al., 2013; Ohmura et al., 2021). Updating plans and goals based on new information during the day is done by dorsal raphe 5-HT neurons (McDannald, 2021). 5-HT also regulates reward-related behavior, and almost all of its receptor subtypes are certainly implicated (Hayes & Greenshaw, 2011). Moreover, decreasing tryptophan can disrupt financial decisions (Blair et al., 2008). Some serotonin receptors, such as 5-HT1B and 5-HT2C, have also been reported to be associated with DM (Faulkner et al., 2016; Adams et al., 2017). Affective, cognitive, and response-based aspects of DM are mediated by 5-HT (Rogers, 2011). 5-HT influences unfair DM by affecting cognition and emotion. A study using the ultimatum game, an experimental economics game, showed that emotion can overshadow the logic of making a financial profit through serotonergic transmission (Emanuele et al., 2008). Specifically, low levels of 5-HT promote the refusal of unfair options—not only in offering but also in accepting—which is related to impulsivity (Nishina et al., 2022). Serotonin levels differ in the various brain regions (Crişan et al., 2009). The mean rate of 5-HT synthesis is higher in males (Nishizawa et al., 1997).

5-HT plays a significant role in cognitive and socioemotional processes associated with economic DM. Interestingly, 5-HT interacts with dopamine, another major neurotransmitter involved in goal-oriented learning and behaviors (McDannald, 2021). The interplay between these neurotransmitters is further clarified in the dopamine section.

## Dopamine

Nowadays, dopamine is mentioned as one of the neurotransmitters with a direct impact on the cost/benefit of DM (Treadway et al., 2012). According to Mohr and Heekeren's study, dopamine has a prominent role in risk-taking during the investing process (Mohr & Heekeren, 2012). In 2015, Rutledge et al. demonstrated that increasing dopamine levels led to enhanced numbers of risky economic decisions in trials with possible rewards and not in those with potential losses (Rutledge et al., 2015). However, it was reported that the amount of work needed to obtain those rewards modifies dopamine density in the striatum. As a result, it appears that dopamine involves two different aspects: following the reward and considering the effort required to obtain it (Shadmehr & Ahmed, 2021). Dopamine is also involved in enhancing the enjoyment brought on by rewards following the ingestion of L-DOPA (Rutledge et al., 2015). The dopaminergic system is a neural substrate for improving learning mechanisms, which are vital in DM (Schultz, 2015). Dopamine plays a role in representing reinforcement prediction errors, which measure the gap between experienced and expected outcomes. These prediction errors are heavily weighted in learning (Rutledge et al., 2015). Dopamine is synthesized from the amino acid tyrosine in the substantia nigra, ventral tegmental area (VTA), and hypothalamus (Juárez Olguín et al., 2016) and is involved in DM via projecting to the cortical, striatal, and mesolimbic areas (Everitt & Robbins, 2005). Moreover, dopamine receptor subtypes in the brain influence functions, including affect, attention, impulse control, and DM. D1 and D2 receptors are engaged in reward learning (Roughley et al., 2021), and D1 receptors in the ACC govern effort-based DM (Schweimer & Hauber, 2006). According to an animal study that demonstrated the positive effect of a D2 antagonist on optimizing gambling-related choices, this antagonistic effect appears to influence choices only when both the probability and temporal length of punishment differ across alternatives (Zeeb et al., 2009).

Interactionally, 5-HT modulates dopamine activity and release in the VTA, substantia nigra, NAc, and striatum (Rogers, 2011). There is an association between how the brain values objects and how it controls the vigor to move toward them (Shadmehr & Ahmed, 2021). Dopamine and 5-HT affect the vigor in the process of DM (Beierholm et al., 2013). Unlike dopamine, it appears that 5-HT is influenced by the effort/reward history, which is fundamental in vigor-related behaviors (Cohen et al., 2015; Shadmehr & Ahmed, 2021). Whenever 5-HT levels are raised in the brain, it is accompanied by decreased vigor to expend effort to get a reward and an increased propensity to linger and harvest for a longer duration (Bailey et al., 2018; Shadmehr & Ahmed, 2021). Dopamine modulates glutamate/GABA-mediated neurotransmission slowly in neural circuitries to influence various activities in the brain (Beaulieu & Gainetdinov, 2011). The effect of dopamine on the DM process is probably mediated through intricate interactions among several neuromodulators. According to animal research, whereas male rats are entirely focused on profitability and prefer longer-delayed rewards, females typically prefer outcomes that are both profitable and less delayed (van den Bos et al., 2009). This difference between males and females is attributed to estrogens via two potential mechanisms: enhancing dopamine release in female rats by inhibiting GABAergic neurons and directly modifying dopamine terminals in the striatum and NAc (Becker, 1999). As previously stated, the average rate of 5-HT synthesis in females' brains is lower than in males. Therefore, higher dopamine and lower serotonin levels in females may explain why women prefer rewards that arrive faster than men. Despite the studies conducted in this field so far, it is still not completely clear how natural changes in dopamine systems can cause gender differences in economic behavior.

## NE

Studies show that monoaminergic systems, including dopamine, 5-HT, and NE, modulate risky DM. Catecholamine transmission, as a crucial player in various cognitive and reward-related mechanisms, could facilitate intricate processes, like perceptual and value-based or cost/benefit DM (Montes et al., 2015; Pfeffer et al., 2020). Although the roles of dopamine and 5-HT as monoamine neurotransmitters in DM have been investigated, the role of NE and possible interactions between the three monoamines are less studied. NE is synthesized from tyrosine in the noradrenergic neurons in the locus coeruleus (LC). These neurons project terminals throughout the brain, such as the thalamus, hippocampus, dorsal hypothalamus, cortex, and cerebellum, in addition to the limbic structures of the basal forebrain, including the amygdala and dorsal bed nucleus of the stria terminalis (BNST). NE modulates behavioral func-

tion by regulating neural excitability, synaptic activity, and the release of NE throughout the cortex (Terbeck et al., 2016; Vazey et al., 2018). Research on animals indicates that NE, which is associated with the reward response in neural interruption or resetting, is critical for some aspects of learning, vigilance, and attention (Dayan & Yu, 2006). One of the important roles of NE is to detect environmental changes to facilitate learning (Lawson et al., 2021). According to theories, the activity of LC encourages rapid adjustments in cortical attentional networks in response to external changes, and it is central for organizing resources to handle challenges (Xiang et al., 2019). LC is involved in mobilizing the required energy for effort-related behaviors and is critical in eliciting motivational responses to challenges (Varazzani et al., 2015).

In addition, a clinical study revealed that NE inhibition lowered learning rate and flexibility in learning and memory (Ridley et al., 1981; Janitzky et al., 2015; Lawson et al., 2021). These findings indicate that NE neurotransmission boosts behavioral and computational responses to uncertainty and participates in the influence of uncertainty on cognitive activities (Lawson et al., 2021). Similar to 5-HT, NE is associated with loss aversion. People with lower amounts of NE transporters in thalamic circuits exhibit a heightened aversion to financial loss, reacting more emotionally or with greater arousal to losses than to gains (Takahashi et al., 2013).

Pupil dilation in response to NE is a cue in social interactions and cognitive functions and can be considered a physiological indicator of decision variables (Preuschoff et al., 2011). Since the 1960s, studies have highlighted that DM influences pupil dilation (Bradshaw, 1967; Simpson & Hale, 1969). Subsequent studies suggested a connection between the duration of pupil dilation and the duration of DM (Einhauser et al., 2010). In 2011, Preuschoff et al. revealed that pupil dilation indicates surprise (errors in evaluating uncertainty) and is highly correlated with risk prediction error, but not with expected reward or uncertainty. They hypothesized that NE is involved in uncertainty learning and encoding of error signals, in the same way that dopamine serves in reward learning (Preuschoff et al., 2011). Dopamine and NE are associated with effort/cost-related motivation (Varazzani et al., 2015). Motivation directs DM by affecting subsequent behavioral and physiological expression (Torrealba et al., 2012). Dopaminergic neurons in the substantia nigra pars compacta calculate the value of outcomes, guiding behavior toward options requiring minimal effort. Conversely, NE neurons in the LC respond to data about current obstacles rather than future predictions (Varazzani et al., 2015). The size of the LC differs between males and females. Female rats have a larger LC than males, presumably due to neurogenesis, which continues in females but not males during puberty (Pinos et al., 2001; Bangasser et al., 2016). Interestingly, LC neurons in females receive more projections from the limbic system (Valentino et al., 2012). Further research is required to fully understand the significance of the LC nucleus in the various cognitive processes, particularly DM, between the genders. However, it can be hypothesized that greater dopamine release and a larger LC in females may result in financial decisions that respond better to existing challenges and require less effort to attain.

## ACh

The cholinergic system is largely involved in the processing of impulse control and perceptual/reward-guided DM, especially under conditions uncertainty or risk (Angela & Dayan, 2005; Guillem et al., 2011; Betts et al., 2021). The sources of ACh in the CNS are the basal nucleus of Meynert, the mesopontine tegmentum area, and the medial septal nucleus (Oda & Nakanishi, 2000). The brain's cholinergic system projects widely into different parts, including intertemporal structures and circuits involved in risk-based decisions. In particular, two classes of ACh receptors are engaged in this process: muscarinic and nicotinic receptors (Picciotto et al., 2012). Muscarinic cholinergic receptors play a key role in learning enhancement, reward-seeking, and DM (Mendez et al., 2012); however, studies have shown that nicotinic ACh receptors in the VTA participate in translating expected uncertainty into motivational value (Naudé et al., 2016).

ACh modulates neuronal excitability, synaptic transmission, and synaptic plasticity, and synchronizes the firing of the neurons (Picciotto et al., 2012); therefore, cholinergic modulation is crucial for complex behaviors, such as arousal, attention, cue detection, learning (Guillem et al., 2011; Picciotto et al., 2012; Fobbs, 2016), and cost-effective DM (Fobbs, 2016). It has been shown that atropine, an antagonist of muscarinic ACh receptors, can lead to unsatisfactory decisions under impulsive and risky conditions. Muscarinic cholinergic transmission in the NAc is necessary to prevent decisions favoring delayed rewards independently of dopamine (Fobbs, 2016). ACh also acts as a stimulator of dopaminergic circuits to induce reinforcement and smoking (Faure et al., 2014; Dongelmans et al., 2021). Chronic nicotine consumption decreases exploration by altering the dopaminergic system (Dongelmans et al., 2021). Failure of impulse control seems to be also central to nicotine addiction (Soutschek et al., 2022). Short-term nicotine abstinence increases

impulsive drug-related DM and time discounting during DM (Mitchell, 2004; Barlow et al., 2017). However, long-term abstinence decreases discounting (Barlow, McKee et al., 2017). In 2022, Soutschek et al. demonstrated that smokers could describe choice uncertainty less accurately than non-smokers, using a monetary intertemporal choice task to assess subjects' metacognitive awareness of their temporal preferences (Soutschek et al., 2022). It has also been indicated that short-term nicotine deprivation can increase impulsive DM in smokers; however, this effect pertains to substance-related options and does not affect financial choices (Mitchell, 2004). In 2021, Modak et al. confirmed considerable differences in the neural process behind risky decisions concerning finances versus substance rewards (Modak et al., 2021).

There is a local circuit through which striatal dopamine and ACh directly influence the release of each other and, therefore, affect DM. In 2022, Chantranupong et al., using a reward-based DM task, demonstrated that decision history and reward outcome influence multiphasic and anticorrelated activities of dopamine and ACh. They reported that dopamine reduces ACh levels in the basal ganglia via dopamine D2 receptors and that failure of this modulation affects DM. Chantranupong et al. also found that glutamatergic inputs from the cortex and thalamus are required for ACh release in this circuit. Consequently, the regulation of cholinergic interneurons by local dopamine neurotransmission and cortical and thalamic glutamatergic inputs is fundamental for DM (Chantranupong et al., 2022). In addition, psychological disorders, such as schizophrenia or addiction are accompanied by changes in both DM and interactions between ACh and dopamine (Dani & Bertrand, 2007). Thus, the interaction between these neuromodulators is undeniably important in DM.

The basal forebrain and medial PFC cholinergic systems differ between males and females. Although ACh release follows a circadian rhythm in both genders, females release more ACh in cortical regions such as the medial PFC (Takase et al., 2007; Takase et al., 2009; Bangasser et al., 2019). This difference was found to be greater at maximal release in the dark period (Takase et al., 2007). Higher ACh release in females' cortical regions may be attributed to greater ACh synthesis capability or a larger number of neurons with choline acetyltransferase in females' basal nucleus of Meynert (Takase et al., 2007; Takase et al., 2009; Bangasser et al., 2019). Findings also highlight the role of estradiol in regulating cholinergic neurons, which may explain the observed sex difference (Bangasser et al., 2019). On the other hand, although there are no sex differences in the number of medial septum cholinergic neurons—the primary sources of cholinergic inputs to the hippocampus—or in the amount of hippocampal ACh release during the light period, ACh release is much lower in females during the dark period (Schaevitz & Berger-Sweeney, 2005; Mitsushima, 2011). Animal studies have indicated that males, under chronic stress conditions, are more likely to experience interruptions in "sustained attention" and the ability to recognize sporadic and unexpected occurrences. It appears that females' ovarian hormones protect against the detrimental effects of corticotropin-releasing factors on sustained attention, which heavily relies on the cholinergic system (Albeck et al., 1997; Bangasser et al., 2016; Bangasser et al., 2019).

The discovery that women seem to depend more on the frontal cortex for cognitive functions, whereas men tend to rely more on the hippocampus and perform better on spatial tasks, is consistent with findings that female and male rats have higher frontal and hippocampal cholinergic activity, respectively (Gur et al., 2002; Giacobini & Pepeu, 2018; Gur & Gur, 2022). Overall, these findings suggest that both nicotinic and muscarinic cholinergic systems can affect the cost/benefit analysis of DM (Hosking et al., 2014). Therefore, considering the importance of ACh in this type of DM, as well as the mentioned gender differences, it can be suggested that ACh is one of the promising neuromodulators for understanding distinct reinforcement-guided DM in males and females.

## Glutamate

Glutamate is the main excitatory neurotransmitter in the brain and plays key roles in physical, cognitive, and emotional processes, such as memory consolidation and learning (Hädel et al., 2013; Zhou & Danbolt, 2014). N-methyl-D-aspartate (NMDA) receptors, one type of ionotropic glutamate receptor, play critical roles in many forms of plasticity, learning, and DM (Scholl et al., 2014; Scholl, 2015). These receptors have been proposed to be essential for the slow temporal integration of noisy input to enable accurate judgments (Wong & Wang, 2006; Salvador et al., 2022). NMDA receptor dysfunction is associated with erroneous inference, which can result in choice biases, leading to flawed conclusions as well as deficiencies in confidence (Salvador et al., 2022).

The medial PFC, a fundamentally important region for selection and goal-directed activities, expresses NMDA receptors and receives glutamatergic projections (Del Arco & Mora, 2008; Davis-Reyes et al., 2019). The frontal cortex is significantly involved in striatal glutamater-

gic inputs (Lapper & Bolam, 1992). Through NMDA receptors, medial PFC-related glutamatergic neurotransmission significantly contributes to motor impulsivity (Davis-Reyes et al., 2019). It is hypothesized that greater unpredictability in DM arises when glutamate receptor-dependent plasticity is impaired at corticostriatal synapses in the dorsal striatum compared to the ventral striatum (Cieślak et al., 2018).

Interactionally, dopamine activity is highly dependent on glutamate transmission (Surmeier et al., 2007; Cieślak et al., 2018). NMDA receptors activate burst firing in dopaminergic neurons, phasic dopamine release, and long-term potentiation in dopaminergic neurons, which forms the basis for learning (Cieślak et al., 2018). In addition, NMDA receptors and metabotropic glutamate receptor 5 (mGluR5) are important for inducing synaptic and structural plasticity in dopamine-sensitive striatal medium spiny neurons (Surmeier et al., 2009; Yagishita et al., 2014). When the glutamate-dependent dopaminergic signaling is interrupted, it raises the number of exploratory and random decisions, slows DM, and impairs reward-based learning, causing DM to be disrupted (James et al., 2015; Cieślak et al., 2018). In 2016, Locklear et al. measured dopamine levels in the PFC in response to intracortical injection of NMDA receptor antagonists in adult male and female rats. They concluded that NMDA antagonists increase dopamine levels in the PFC in males but decrease its levels in females (Locklear et al., 2016). Also, Grachev and Apkarian reported that women have higher levels of glutamate than men in the cingulate, sensorimotor, dorsolateral prefrontal, and orbital frontal cortices in the left hemisphere, but not in the thalamus and insula (Grachev & Apkarian, 2000). Women also have higher glutamate levels in the hippocampus (Hädel et al., 2013), striatum, and cerebellum (Zahr et al., 2013), whereas men have higher dorsolateral PFC glutamate levels (Hädel et al., 2013). All these results may be explained by the influence of female steroidal sex hormones. It seems that glutamate could be a possible explanation for the disparities in DM between the sexes, particularly in terms of decision speed and accuracy, due to differences in the levels and functions of its receptors.

## GABA

GABA, a central nervous system (CNS) inhibitory neurotransmitter, may be implicated in the neuromodulation of action control mechanisms (Steenbergen et al., 2015). GABA also plays a role in memory coding (Szodorai et al., 2018). Due to structural and functional changes in the brain during adolescence, cognitive control and DM become more advanced, while impulsivity and risk-taking diminish (Luna & Sweeney, 2004; Silveri et al., 2013). These behavioral components are associated with the frontal lobe, the last area of the brain to mature in humans, with GABA receptors in the frontal lobe reaching adult levels late in adolescence (Silveri et al., 2013). In rats, the concentration of GABA at birth is about half that of adult levels (Silveri et al., 2013). According to these findings, GABA depletion appears to be fundamental in the neurobiological processes of the adolescent brain, potentially jeopardizing safety by directing adolescents to make poor decisions (Silveri et al., 2013). GABA transmission in medial PFC is implicated in efficient DM when selecting among rewards that differ in terms of value and cost (Piantadosi et al., 2016). Reduced GABA activity in the PFC has been shown to cause selective delays, even in basic decisions (Auger & Floresco, 2014). GABA synthesis is reduced in schizophrenic patients in parts of the cortex that are functionally essential for executive functions, such as DM (Lewis et al., 2012; Paine et al., 2015). Adolescents with major depressive disorder also have lower levels of GABA in the ACC than healthy individuals (Gabbay et al., 2012). It is important to note that increased impulsivity and reduced motor control can result in higher risk-taking and poor DM during life-critical periods (Silveri et al., 2013). Functional and anatomical evidence suggests that the ACC is composed of two main components: the pregenual ACC (pgACC) and mid-ACC in humans. The pgACC is anatomically linked to the amygdala, hippocampus, hypothalamus, NAc, insula, and orbitofrontal cortex, and plays a major role in affective control (Fujihara et al., 2015). However, neuroimaging studies using magnetic resonance spectroscopy (MRS) have shown that the concentration of GABA in pgACC is associated with DM or impulsivity (Jocham et al., 2012; Silveri et al., 2013). The NAc is also involved in mediating various types of DM in both humans and animals. Inactivating the NAc by injecting GABA agonists in rats reduces the preference for large/risky choices and increases response delays in a probabilistic discounting task (Stopper & Floresco, 2011; Sugam et al., 2012). Moreover, GABAergic dysfunction in the insular cortex, a vital region for DM, leads to risky behaviors (Mizoguchi et al., 2019). In light of GABA-related sex differences in different brain areas, GABA levels in the dorsolateral PFC (O'Gorman et al., 2011) and ACC (Sheffield & Noseworthy, 2010) are considerably greater in men. Interestingly, in 2022, Spurny-Dworak et al. found that cisgender women had higher insula GABA concentrations than cisgender men (Spurny-Dworak et al., 2022). According to studies, women generally display greater impulsivity

for hypothetical offers, whereas men may display more impulsivity for real benefits (Weafer & de Wit, 2014). However, a study in 1995 revealed no gender differences in choice impulsivity on tasks involving either actual money or hypothetical discounts (Kirby & Maraković, 1995). In 2002, another study found non-significantly higher impulsivity in women for money (Kirby et al., 2002). In general, GABA appears to play a fundamental role in gender differences in impulsive choices. However, gender differences in impulsive financial decisions must be investigated more widely across varied tasks and settings.

## OT

Humans rely on social relationships to survive in complicated social circumstances. Decisions are an integral part of social behavior patterns. Many key decisions in our lives are made in the social context, and the costs and benefits of these decisions must be evaluated as well (Rilling & Sanfey, 2011). It is reported that OT facilitates accurate perception of social interactions (Fischer-Shofty et al., 2013). Some studies have also demonstrated the role of OT in social attachment by modulating areas that are primarily reward-related, like the NAc and ventral pallidum (Baumgartner et al., 2008).

Due to its innervation and high expression levels in the PFC, it has been shown that OT plays a crucial role in cognitive processing, executive function, working memory, and DM (Zebhauser et al., 2022). Numerous studies have confirmed that OT impacts both social and non-social decisions (Rimmele et al., 2009). Furthermore, OT receptors are also found in the PFC and the striatum, and DM seems to be influenced by a balance between the networks of these areas (Kapetaniou et al., 2021). Additionally, OT receptors in the insula participate in social DM (Rogers-Carter et al., 2018). OT also seems to have other effects, such as increasing generosity (Serra, 2020).

In nonhuman primates, differences in social preferences have been reported to be associated with oxytocinergic regulation of amygdala-related neural circuits (Chang et al., 2015). Studies have shown that in nonhuman primates, intranasal OT increases social donation behavior, and intra-amygdala injection of OT significantly increases prosocial DM (Chang et al., 2012; Chang et al., 2015). In a double-blind study, participants who received OT administration demonstrated no alteration in their trusting behavioral patterns, but subjects in the placebo group showed a decline in trust. This difference was linked to a particular decrease in the activity of some fear-related brain areas in the OT group. This suggests that the influence of OT on trust adaptation is mediated by neural systems that regulate fear processing and adaptive responses to feedback information (Baumgartner et al., 2008).

Interestingly, Zebhauser et al. reported that intranasal OT treatment enhanced risk-taking in healthy subjects under conditions of low outcome predictability/high ambiguity, but lowered risk-taking in a risk assessment task with known outcome probability/low ambiguity (Zebhauser et al., 2022).

Along with its function in social recognition, OT can also result in more social information-gathering by promoting behaviors, like directing attention to faces, specifically the area around the eyes. This can help individuals become more aware of social intent and critical information that may be fundamental in DM when the social context matters (Love, 2014). It has been reported that OT increases eye gazing with neutral and happy expressions, but reduces gazing with angry ones (Domes et al., 2013). These findings illustrate the effects of OT on individuals' recognition and the information that can influence the outcomes of a decision. According to Caldwell's comprehensive review, OT and the distribution of its receptors are not dramatically different across the sexes (Caldwell, 2018). However, OT also exhibits sex-specific effects. These include enhanced kinship recognition in women and enhanced competition recognition in men following OT administration (Fischer-Shofty et al., 2013). Thus, OT can play different functional roles in men and women. It should be noted that the effects of OT should always be considered within context.

## Histamine

The brain's histaminergic system is one of the main regulators of the sleep-wake cycle. Although it was long unknown, it is now recognized as a key coordinator of attention, learning, memory, and DM (Passani et al., 2007). Histaminergic neurons originate in the tuberomammillary nucleus of the ventral posterior hypothalamus, which projects to different areas of the CNS (Yuan & Silberstein, 2018). Also, mast cells, microglia, and microvascular endothelial cells can be considered non-neuronal sources of brain histamine (Yamakami et al., 2000; Katoh et al., 2001; Lenz et al., 2018).

The histaminergic system affects learning and memory by modulating ACh release, although it should be noted that the cognitive effects of histamine and histaminergic factors are independent of ACh (Bacciottini et al., 2001). Histamine in the brain is essential for both

the appetitive and aversive stages of motivation. During goal-directed behaviors, histamine leads to increased arousal and reduced desire to consume, enabling a motivated behavior to advance to its maximum potential (Torrealba et al., 2012).

The histamine system is activated in stressful conditions and can lead to anxiety and an inhibitory response, such as focus changes and enhanced exploratory activities (Westerink et al., 2002; Gray & McNaughton, 2003; Miklós & Kovács, 2003; Torrealba et al., 2012). By comparing baseline hypothalamic histamine release in rats of both sexes and different ages, Ferretti et al. reported that baseline release in female rodents was stable and lower than that in male rats throughout all studied ages (Ferretti et al., 1998). On the other hand, there is evidence that histamine levels in this area can be raised in response to 15 minutes of stress (Mazurkiewicz-Kwilecki & Taub, 1978). Moreover, mast cells, as a non-neuronal source of brain histamine, appear to be one of estradiol's main targets and play a key role in sex differences in the brain. In the preoptic region of newborn male rats, mast cells were reported to be more numerous and activated compared to those in females (Lenz et al., 2018).

Overall, it appears that, in addition to gender differences in histamine levels and the number of associated cells in the brain, females have a reduced histamine response to stress, which may be related to females' gradual inability to coordinate biochemical changes (Ferretti et al., 1998; Lenz et al., 2018). This can result in enhanced histamine release in fundamental regions, like the hypothalamus (Ferretti et al., 1998). Perhaps this distinction is a significant factor in the emergence of DM-related differences between the two sexes, especially regarding their inhibitory responses and exploratory activities under stressful conditions.

## Gonadal hormones and DM

As previously stated, males and females can present different outcomes while making decisions in the same context. In men, the social environment is a more significant determinant of risk-taking than in women. For example, men are more likely than women to express a desire to take risks in front of bystanders and when shown photographs of the other gender's charms. In a risky DM task (choosing between a small reward and a larger one with greater possible risk), females tend to value safety over reward magnitude (Stanton, 2017; Hampson, 2018). Hormonal differences may, to some extent, lead to sex differences in the functional lateralization of the brain (Kret & De Gelder, 2012). Gonadal hormones can influence the process of DM by modulating risk-related information and controlling neurobiological mechanisms in brain regions, such as the PFC, amygdala, and NAc (Orsini et al., 2022). A more comprehensive review of the effects of gonadal hormone regulation on risky DM was conducted by Orsini et al. (2022). Gonadal hormones are fundamental to sex-typical risk-taking behavior profiles.

It is essential to thoroughly investigate the role of sex hormones and their interactions with neurotransmitters in DM-related contexts among men and women. Interestingly, changes in ovarian hormones during a woman's reproductive years and throughout each menstrual cycle may also have a notable influence on DM in women (Ambrase et al., 2021). Ovarian hormones can be said to modulate women's DM, but their roles differ depending on the type of DM costs involved (Orsini et al., 2021). According to an fMRI study, the reason why the reward system responds more strongly during the follicular phase than the luteal phase might be due to the relative predominance of estradiol and progesterone throughout these periods, respectively (Dreher et al., 2007; van den Bos et al., 2013). It has also been demonstrated that women experience more pronounced amygdala activation and noticeably enhanced emotion recognition during their follicular phase (Derntl et al., 2008). Elevated levels of estradiol in the follicular phase cause women to perform worse in recognizing emotional facial expressions of sadness and disgust (Gasbarri et al., 2008).

Studies show that, independent of biological sex and the presence of testosterone, estradiol plays a key role in directing DM away from riskier options (Islas-Preciado et al., 2020; Orsini et al., 2021; Orsini et al., 2022). Estradiol may increase risk aversion in both men and women through modulation of dopamine signaling (Yoest et al., 2014). In women, estradiol increases sensitivity to dopamine-induced changes in behavior (Becker, 1990). Therefore, these results suggest that estradiol is a key player in regulating DM behavior in women.

Testosterone, the main sex hormone in men, plays a major role in masculinity and sexual function (Schultheiss & Mehta, 2019). It reduces generosity in economic DM (Wu et al., 2019). Testosterone and 17β-estradiol may also affect the mesocorticolimbic dopaminergic pathway and modulate DM (Hampson, 2018). High testosterone levels in men and women may increase risky behaviors (Stanton, 2017). Taken together, gonadal hormones in men and women play important roles in DM; thus, they can reinforce distinct sex-typical DM phenotypes (Orsini et al., 2021).

## Conclusion

This study examined the potential involvement of neuromodulators in economic DM between the sexes to provide researchers with a broader perspective for designing more comprehensive experimental settings to investigate these differences. Differences in neuromodulators across various brain regions between the two sexes can lead to different DM outcomes. As mentioned, sex-specific configurations and interactions across neuromodulatory systems spanning valuation, timing, and control processes are responsible for sex differences in economic DM, rather than the effects of individual neuromodulators alone. The combined effects of dopamine and 5-HT may explain, at least in part, why women prefer rewards that arrive sooner than men. Differences in glutamate levels and its receptors may account for the variations in decision speed and accuracy between the sexes. GABA appears to play a fundamental role in gender differences in impulsive choices. Generally, neuromodulators play essential roles in economic DM and should be considered potential variables explaining disparities between the sexes in future experiments. Ignoring sex-linked neuromodulatory configurations may obscure key mechanisms underlying economic preferences and contribute to inconsistent findings across studies. However, it should be emphasized that all of these neuromodulators, along with other variables not addressed in this study, affect economic DM in real-world settings in a complex and overlapping manner.

## Ethical Considerations

### Compliance with ethical guidelines

There were no ethical considerations to be considered in this research.

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### Authors' contributions

Conceptualization: Maryam Alsadat Mousavi, Fariba Khodagholi, and Neda Valian; Investigation: All authors; Data curation: Maryam Alsadat Mousavi, Fariba Khodagholi, Mitra Ansari Dezfouli, and Neda Valian; Writing the original draft: Maryam Alsadat Mousavi and Nahid Sarahian; Review and editing: Fariba Khodagholi, Mitra Ansari Dezfouli, and Neda Valian; Supervision and project administration: Fariba Khodagholi and Neda Valian.

### Conflict of interest

The authors declared no conflict of interest.

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