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Abstract

Years of research have shown that stress influences cognition. Most of this research has focused on how stress affects memory and the hippocampus. However, stress also affects other regions involved in cognitive and emotional processing, including the prefrontal cortex, striatum, and insula. New research examining the impact of stress on decision processes reveals two consistent findings. First, acute stress enhances selection of previously rewarding outcomes but impairs avoidance of previously negative outcomes, possibly due to stress-induced changes in dopamine in reward-processing brain regions. Second, stress amplifies gender differences in strategies used during risky decisions, as males take more risk and females take less risk under stress. These gender differences in behavior are associated with differences in activity in the insula and dorsal striatum, brain regions involved in computing risk and preparing to take action.

Keywords

choice, decision making, impulsivity, reward learning, risk taking, stress, valuation, ventral and dorsal striatum

The word *stress* describes experiences that are emotionally or physiologically challenging (McEwen, 2007). Stressful experiences elicit sympathetic-nervous-system responses and stimulate the release of stress hormones (e.g., cortisol in humans; Sapolsky, 2004) that mobilize the body's resources to respond to a challenge. The physiological effects of a stressful experience such as making a speech are evident not only during the event, but also in the next hour or so (Dickerson & Kemeny, 2004). When stressors are constantly present or anxiety about potential stressors is high, stress levels may become chronically elevated. Beyond the physiological effects of stress, a substantial literature indicates that both acute and chronic stress affect cognitive function.

Until recently, most studies examining stress and cognition have focused on stress effects on memory; effects on other aspects of cognition, including decision making, have received less attention. However, it is crucial to understand whether and how stress may alter decision making, as important decisions are often made under stress. For example, decisions about finances, health care, and social relationships are frequently accompanied by stress or cause stress. Early work on stress and decision making determined that stressors like time pressure and noise impaired decision making, resulting in decision making that is hurried, unsystematic, and lacking full consideration of options (Janis & Mann, 1977).

More recent work focuses on how stress influences how people respond to the risks and rewards of decisions. Acute stress potentiates dopaminergic reward pathways in the brain (Ungless, Argilli, & Bonci, 2010), which may intensify the allure of potential gains associated with decision options. The

core brain–body feedback loops involved in the stress response also are involved in assessing risk and reward (Bechara & Damasio, 2005). As part of this brain–body feedback system, the insula helps represent somatic states and signals the probability of aversive outcomes during risky decisions (Clark et al., 2008). Both physical and psychological stress activate the insula, but differently for males and females (Naliboff et al., 2003; Wang et al., 2007).

In the following sections, we review recent evidence for two distinct effects of stress. First, stress enhances learning about positive choice outcomes and impairs learning about negative choice outcomes. This effect appears to be similar across gender and age groups. Second, stress affects decision strategies differently for males and females, with behavior diverging under stress when decision making involves immediate risk taking.

Seeing STARS: Stress Can Make Rewards Gleam More Brightly

What makes decisions difficult? Often, it is the challenge of weighing and integrating positive and negative aspects of decision options. Is a higher salary worth a longer commute? Is the pleasure of watching your favorite television show worth the sacrifice of staying up later to meet an assignment

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deadline? In addition to their immediate impact on choice, rewarding and aversive outcomes of a decision can influence future choices through learning. For instance, receiving a poor grade on the assignment might influence future time-allocation decisions. But the pleasure of laughing and relaxing during the show might instead make it even harder to resist watching future episodes.

We propose that stress alters decision value assignments because *stress triggers additional reward salience* (STARS). The STARS model is based on research examining how stress affects dopaminergic reward-processing brain regions. Dopaminergic regions and their target structures—such as the striatum (especially the nucleus accumbens) and orbitofrontal cortex—play key roles in representing reward value (Rangel, Camerer, & Montague, 2008). In rats, acute stress increases extracellular levels of dopamine in the nucleus accumbens (Abercrombie, Keefe, Difrischia, & Zigmond, 1989; Kalivas & Duffy, 1995), an effect that is mediated by cortisol (Rouge-Pont, Deroche, Le Moal, & Piazza, 1998). Stress also increases firing rates in rat midbrain dopamine neurons (Anstrom & Woodward, 2005) and long-term potentiation in dopamine neurons (Saal, Dong, Bonci, & Malenka, 2003).

In positron emission tomography (PET) studies, people are injected with a radiotracer that allows researchers to track the activity of specific neurotransmitters, such as dopamine. Experiencing painful stressors increases PET measures of striatal dopamine among healthy young adults (Scott, Heitzeg, Koeppe, Stohler, & Zubieta, 2006; Wood et al., 2007). In addition, how much cortisol levels increase when exposed to a psychological stressor (mental arithmetic) correlates with PET measures of striatal dopamine (Pruessner, Champagne, Meaney, & Dagher, 2004). It appears that, similar to findings observed in rats, stress enhances striatal dopamine in humans. Consistent with this idea, stress appears to increase drug craving and often induces relapse in drug addicts (Sinha, 2009). Importantly, dopamine plays a role in desire for drugs, suggesting that stress may increase dopamine levels in drug addicts and thereby amplify the reward value attached to their drug of choice—an example of how the STARS effect can have negative consequences.

We propose that stress enhances reward salience via modulation of the dopamine system, resulting in reward-biased learning and decision making under stress, a pattern that may benefit or impair decisions, depending on the context. The following studies support a STARS account of stress effects on option valuation in humans.

Influence of Stress on Learning About Decision Values

We often use past experiences in decision making, as previous choices may carry positive or negative associations. For this reason, it is important to consider the impact of stress on learning associations between decisions and their outcomes. Recent behavioral studies with humans suggest that stress enhances learning about positive outcomes while diminishing learning

about negative outcomes (Fig. 1; Lighthall, Gorlick, Schoeke, Frank, & Mather, 2011; Petzold, Plessow, Goschke, & Kirschbaum, 2010). In these studies, participants completed a probabilistic reinforcement-learning task after either experiencing an acute stressor or performing a no-stress control task. The reinforcement task involved learning probabilistic associations between visual cues and different types of feedback. Using trial and error, participants learned which cues were most likely to result in correct or incorrect feedback and were asked to select the cues that gave positive feedback most often. In both studies, stress led to relatively better learning from positive feedback and worse learning from negative feedback.¹ The similar pattern in the two studies occurred despite different types of stress inductions. Lighthall, Gorlick, et al., 2011 induced stress before the start of the reinforcement-learning task by having participants hold their hands in ice water (cold pressor stress), whereas Petzold et al. (2010) induced psychosocial stress by making participants anticipate, then give, a speech and also do difficult mental arithmetic in front of an audience. Of additional interest, both studies found that the effects of stress on reinforcement learning were similar for males and females. Lighthall et al. also found similar effects among older adults.

The increased learning from positive outcomes under stress seen in these studies is consistent with the STARS model proposal that increased dopamine from stress should facilitate learning reward-associated behaviors but not punishment-associated behaviors. Cortisol levels also appear to be associated with impaired avoidance learning, as Lighthall and colleagues found that cortisol was related to higher rates of erroneously selecting



Fig. 1. Proportion of correct choices (choosing positive outcomes versus avoiding negative outcomes) made under stress. Participants were asked to make repeated choices among options that probabilistically delivered positive or negative feedback (Lighthall, Gorlick, Schoeke, Frank, & Mather, 2011). If they did this learning task after experiencing an acute stressor, they were better able to later select the option that delivered the most positive feedback but were less effective at avoiding the option that delivered the most negative feedback.

negative feedback cues. So stress responses may result in a bias toward potentially rewarding options while diminishing avoidance of negative options. Stress can also impair avoidance of previously rewarding but no-longer-rewarding stimuli. For example, in one study, participants learned actions to obtain two food rewards; after becoming satiated for one of the foods, only the nonstressed participants stopped performing the action to obtain that food (Schwabe & Wolf, 2009), even when the stress occurred after satiation (Schwabe & Wolf, 2010). Another study also suggests that stress affects learning about rewards or losses, as participants who were anticipating giving a speech performed worse than control participants on a gambling task when feedback was given but not when no feedback was given (Starcke, Wolf, Markowitsch, & Brand, 2008). Unfortunately, the task used did not distinguish between learning about rewards and learning about losses.

Gender-Divergence Effect: Stress Can Amplify Gender Differences in Risk Taking

Although stress affects learning about positive versus negative outcomes similarly for men and women, research indicates a gender divergence under stress in decision strategies (Fig. 2) when people must choose between safer options (that offer lower potential gains but also lower losses) and riskier options (higher potential gains but also higher losses). In one study, participants received points for inflating a series of balloons shown on the computer screen (Lighthall, Mather, & Gorlick, 2009). The larger a balloon got, the more it was worth; but with each additional pump, there was increased risk of an explosion and loss of earnings for that balloon. To earn points, participants had to choose when to “cash out” each balloon. Half of the participants completed the cold pressor stress task about 20 minutes before playing the balloon game. Experiencing cold pressor stress before the game led males to increase

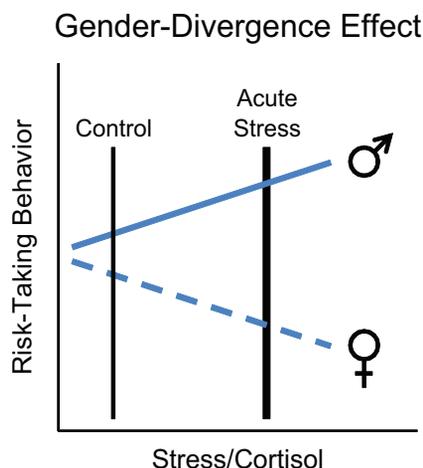


Fig. 2. Gender-divergence effect for risk taking under stress. When stress or cortisol is low, risk taking is similar for males and females, but when stress or cortisol increases, risk taking diverges by gender—increasing for males and decreasing for females.

risk taking (more pumps per balloon) in pursuit of greater reward, whereas stress effects were opposite for females (Fig. 3). As risk taking in stressed males did not reach a level of diminishing returns, they were able to earn more reward than their female counterparts. Similarly, gender differences in stress effects were observed by others using the Iowa Gambling Task (Preston, Buchanan, Stansfield, & Bechara, 2007; van den Bos, Harteveld, & Stoop, 2009), such that men exposed to a psychological stressor prior to the task selected card decks that offered greater reward at the cost of higher risk of losses. Selecting cards from these risky decks resulted in lower earnings overall. In a study with only males, administering cortisol increased choices of risky gambles, especially for gambles with a large probability of losing and a large possible gain (Putman, Antypa, Crysovergi, & van der Does, 2010). Similarly, formerly heroin-addicted male patients made more disadvantageous risky choices after stress than they did before stress, an effect that was blocked by the β -adrenoceptor antagonist propranolol (Zhang et al., 2011). Across the various laboratory decision studies, stress enhanced males' performance when increased risk taking was beneficial but impaired males' performance when increased risk taking was detrimental, and vice versa for females. In addition, unlike the STARS effects outlined earlier, these gender-divergence effects on decision strategies seem unrelated to learning processes. For instance, for studies conducted in our lab, gender-by-stress interactions were similar in initial and final blocks of the games.

In a follow-up to Lighthall et al.'s (2009) balloon game study, participants completed either the cold pressor stress task or a warm-water control task before entering a functional magnetic resonance imaging (fMRI) scanner and playing an fMRI-adapted version of the balloon game (Lighthall, Sakaki, et al., 2011). In this adapted version, participants each played for the

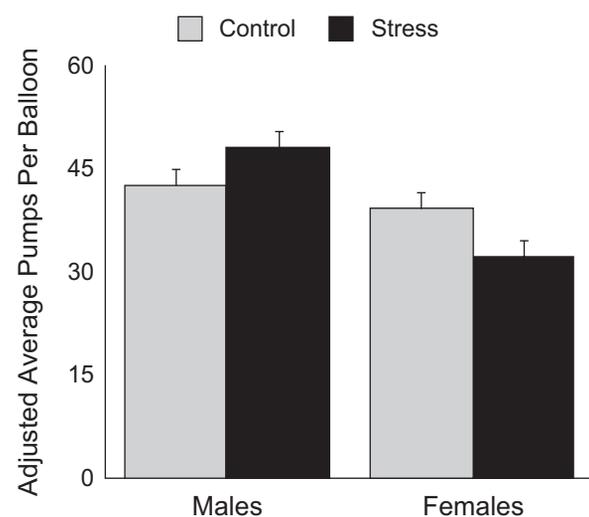


Fig. 3. Risk taking by males and females after a stressor versus a control task. Experiencing an acute stressor before playing a balloon-pumping game (reward increased as simulated balloons were inflated, but so did risk of a balloon bursting) increased males' risk-seeking behavior but decreased females' risk-seeking behavior (Lighthall, Mather, & Gorlick, 2009).

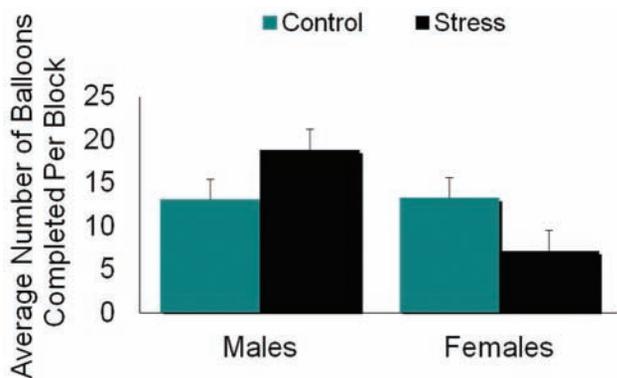


Fig. 4. Number of balloons “cashed out” under stress versus a control condition. In this risk task, pumping up simulated balloons yielded rewards but also increased risk of the balloon bursting, and participants could work through more balloons by pumping them faster. In the control condition, males and females completed a similar number of balloons, whereas under stress their strategies diverged.

same total time, resulting in a variable number of balloons played. This change meant that playing more balloons more quickly was an alternate strategy to earn more money. In this version of the game, stress did not affect the number of pumps per balloon that participants made (risk taking) but instead affected their decision speed and number of balloons “cashed out.” The frequency of reward collections (cash outs) during the risky-decision task was altered by stress in a gender-dependent manner (Fig. 4). Gender-by-stress interactions were also seen in brain activation in the insula, a brain region implicated in signaling the probability of aversive outcomes and learning about risky outcomes (Clark et al., 2008), and in the putamen (in the dorsal striatum), a brain region thought to integrate sensorimotor, cognitive, motivational, and emotional signals to help select and initiate actions and to help control habit-based behaviors (Balleine, Delgado, & Hikosaka, 2007; Balleine & O’Doherty, 2010). Stress increased activity in both the insula and putamen during the task (compared with a

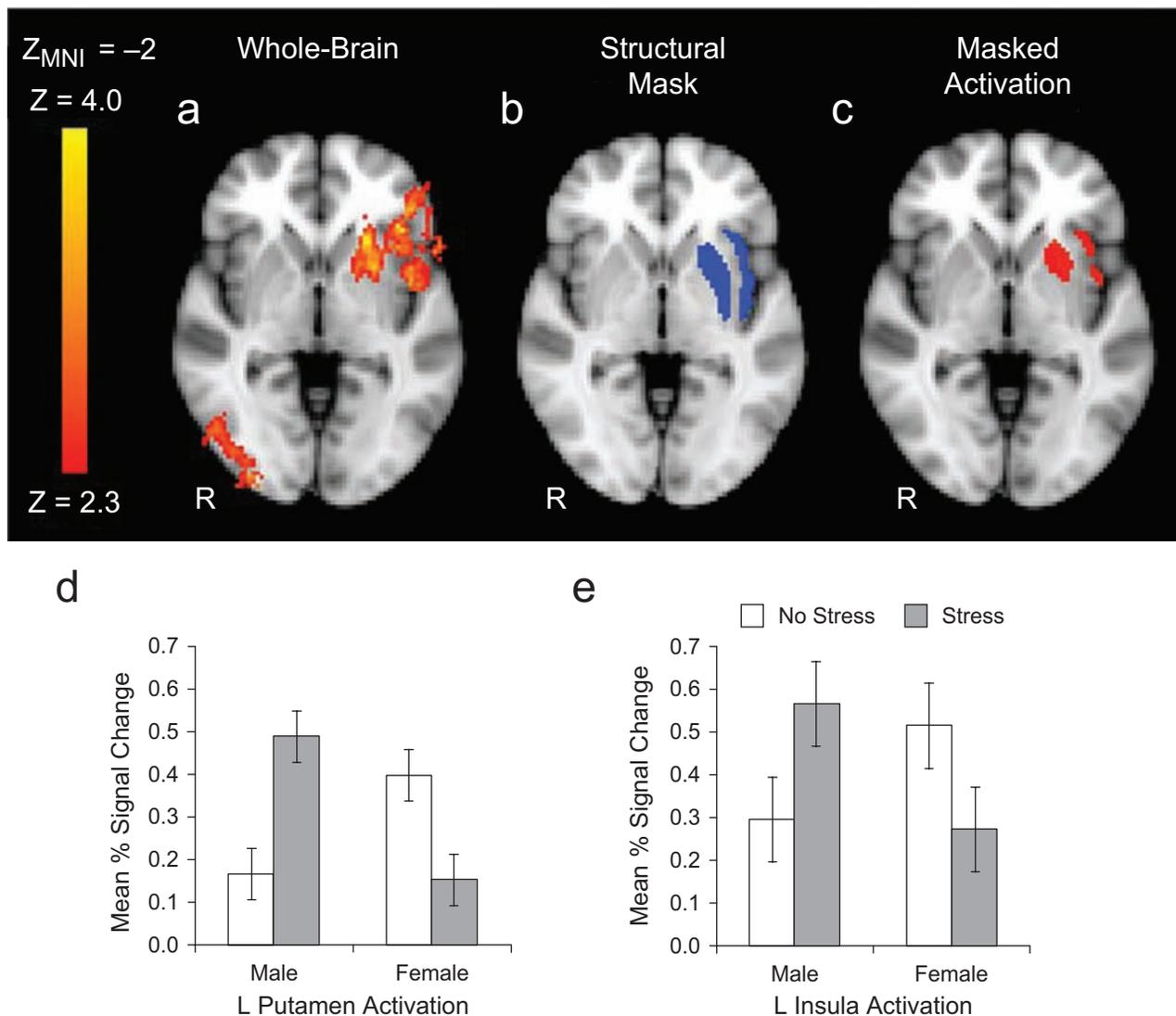


Fig. 5. Interaction between stress, gender, and brain activation. Under stress, the putamen and insula (a) showed significant gender-by-stress interactions (as indicated by regions colored orange) while participants played a decision game to earn money (Lighthall, Sakaki, et al., 2011). Outlines (“masks”) of the structurally defined putamen and insula (regions in blue; b) were overlaid on the activation maps to distinguish the activity in these two regions (c). Average brain activation from these two clusters revealed that, under stress, males showed greater activity in the putamen (d) and insula (e) while playing the decision game while females showed the opposite pattern.

no-decision control) for males but decreased that activity for females (Fig. 5). Also, activation of the dorsal striatum was associated with increased reward-collection rate under stress in males but not females.

Conclusions

Making decisions involves interacting brain mechanisms that compute the potential value of options and adjust that value to account for uncertainty and risk. Such calculations need to be translated into action, often under time pressure. The effects of stress on these processes are beginning to be examined, and initial research reveals some consistent patterns.

First, stress enhances learning about positive outcomes but impairs learning about negative outcomes of choices (Lighthall, Gorlick, et al., 2011; Petzold et al., 2010), effects that may help explain how stress increases the likelihood of acquiring and maintaining drug addiction (Saal et al., 2003; Sinha, 2009). In the laboratory, these STARS effects are similar across gender and age groups, but when it comes to drug addiction, gender differences in how stress influences learning about rewards and losses may be more likely, as drugs affect the stress system differently for men and women (Fox & Sinha, 2009). Second, when decisions must be made under risk and uncertainty, stress alters decision strategies—but in opposite ways for men versus women (Lighthall et al., 2009; Lighthall, Sakaki, et al., 2011; Preston et al., 2007; van den Bos et al., 2009). In this review, we focused on the effects of acute stress on decision processes; however, initial findings also suggest that chronic stress or anxiety also predict individual differences in risky decision making (de Visser et al., 2010; Salo & Allwood, 2011) and that baseline cortisol levels predict decision impulsivity differently for males and females (Takahashi et al., 2010).

Decisions often are made under stress. For instance, anticipating a hectic day at work may influence one's willingness to risk speeding through a yellow light on the way to the office. Feeling stressed may also induce a bias in weighing positive over negative aspects of a job offer more heavily. The laboratory studies reviewed here provide evidence that stress affects decision making, highlighting the need for additional work to better understand the nature of these effects and their brain mechanisms.

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Declaration of Conflicting Interests

The authors declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Note

1. In one study the enhancement but not the impairment was significant, and in the other study the impairment but not the enhancement was significant. Due to the way the learning phase of the task was set up, attention to cues yielding positive outcomes could detract from learning about cues yielding negative outcomes; future work is needed to independently examine learning about positive versus negative outcomes.

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