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Review

Decision making under stress: A selective review

Katrin Starcke[a,*], Matthias Brand[a,b]

[a] Department of General Psychology: Cognition, University of Duisburg-Essen, 47057 Duisburg, Germany
[b] Erwin L. Hahn Institute for Magnetic Resonance Imaging, Essen, Germany

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ABSTRACT

Many decisions must be made under stress, and many decision situations elicit stress responses themselves. Thus, stress and decision making are intricately connected, not only on the behavioral level, but also on the neural level, i.e., the brain regions that underlie intact decision making are regions that are sensitive to stress-induced changes. The purpose of this review is to summarize the findings from studies that investigated the impact of stress on decision making. The review includes those studies that examined decision making under stress in humans and were published between 1985 and October 2011. The reviewed studies were found using PubMed and PsycInfo searches. The review focuses on studies that have examined the influence of acutely induced laboratory stress on decision making and that measured both decision-making performance and stress responses. Additionally, some studies that investigated decision making under naturally occurring stress levels and decision-making abilities in patients who suffer from stress-related disorders are described. The results from the studies that were included in the review support the assumption that stress affects decision making. If stress confers an advantage or disadvantage in terms of outcome depends on the specific task or situation. The results also emphasize the role of mediating and moderating variables. The results are discussed with respect to underlying psychological and neural mechanisms, implications for everyday decision making and future research directions.

Contents

* Corresponding author at: Department of General Psychology: Cognition, University of Duisburg-Essen, Forsthausweg 2, 47057 Duisburg, Germany. Tel.: +49 203 3792251; fax: +49 203 3791846.
E-mail address: katrin.starcke@uni-due.de (K. Starcke).

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1. Introduction

Many decisions must be made under stress. Examples of decisions that are made under stress include choosing the correct alternatives in an exam or making the best decision in an emergency. Additionally, many decision situations elicit stress responses themselves. The decision about whether to turn off life-saving machines for fatally ill patients or decisions that have extensive financial consequences are stress-eliciting in and of themselves. Thus, stress and decision making are intricately connected, and the influence that stress has on the quality of a decision is of special interest. The purpose of the present review is to summarize findings from studies that have investigated the impact of stress on decision making. The review indicates that stress alters decision making, suggesting that stress may affect how we make everyday decisions and life-altering choices. There is also a connection between stress and decisions on a neural level. The brain regions that are associated with intact decision making are sensitive to stress-induced changes. Nevertheless, studies that have investigated the effect of stress exposure and stress reactions on decision-making performance are rare compared to the wealth of studies that have investigated memory performance under stress (reviews in Lupien et al., 2007; Wolf, 2009). The present review aims to fill this research gap.

The effects of stress on decisions may be relevant to public health. The detrimental effects of stress on health are well documented. Stress is thought to increase the risk for cardiovascular, psychiatric and psychosomatic diseases, and it also encourages unhealthy lifestyle behaviors, such as smoking, drinking or unhealthy diet (Juster et al., 2010; McEwen, 2008; Schneiderman et al., 2005). Thus, stress may have indirect effects on health, and these effects may be mediated by the individual's suboptimal decisions, which offer immediate reward at the cost of long-term negative consequences.

2. Method of review

The present review has summarized studies of stress and decision making in healthy humans that were published between 1985 and October 2011. Due to the limited space of this article, the review omitted the effects of stress on the decision processes that underlie perception and attention, such as signal detection (review in Broadbent, 1971), memory (review in Wolf, 2009), executive functioning, such as set shifting and categorization (e.g., McCormick et al., 2007) or operant conditioning (e.g., Schwabe and Wolf, 2009). The review focused on decisions in a narrower sense including the choice among at least two alternatives that is generally made in complex situations. In daily life, most decisions have to be made among at least two options. Although in some situations, one option may be to act and the other not to act, in most cases, two or more options that provide different outcomes are available (see examples in Brand et al., 2006). As stated by Balleine (2007), decision making refers to the 'ability of humans and other animals to choose between competing courses of action based on their relative value of consequences.' In accordance with this definition, the most popular tasks that assess decision making, for example in patients with neuropsychological impairments, comprise two or more options. Such tasks have also been applied to healthy participants to investigate personality and other individual factors that could potentially influence decision making. These decision-making tasks have also been used to experimentally investigate the effects of stress on decision making. In line with this research, the review focused on stress and decision making as measured by tasks that provide at least two choices, in contrast to more basic tasks in which subjects must simply react or fail to react to specific stimuli (such as Go/No–Go tasks or other, more basic, experimental paradigms that involve reaction times, and so on).

The present review begins with a short overview of decision-making research and stress research before their reciprocal relationship is elucidated. The review focuses on studies that have examined the influence of acutely induced laboratory stress on decision making. This section focuses on two databases that were searched for suitable articles. In PubMed, a search was conducted using the search terms 'decision making,' 'risk taking' and 'selection,' each of which was combined with each of the terms 'stress,' or 'social evaluation' using the conjunction 'AND.' Each term was required to be present in the 'Title/Abstract' of the paper. In PsycInfo, a search was conducted using the same search terms as in the PubMed search. Each term was required to be present in the 'Title.' Both searches were further limited by 'English' as the publication language and 'Publication Date from 1985 to October 2011.' The only studies that were selected for the review were original research papers that were published in peer-reviewed journals. All of the studies included healthy human participants and examined the acute induction of laboratory stress and its relationship with decision-making performance in a laboratory decision-making situation. Both variables, i.e., decision-making performance and stress responses, must have been quantified by the authors. The inclusion criteria were chosen to focus on neuroscientific studies about stress and decision making rather than on the wealth of existing studies and reviews concerning time pressure and decisions (e.g., Svenson and Maule, 1993). The following hits were retrieved from the search of PubMed: 'decision making' and 'stress' (884); 'risk taking' and 'stress' (132); 'selection' and 'stress' (3649); 'decision making' and 'social evaluation' (2); 'risk taking' and 'social evaluation' (1); 'selection' and 'social evaluation' (1). The following hits were retrieved from the search of PsycInfo: 'decision making' and 'stress' (362); 'risk taking' and 'stress' (156); 'selection' and 'stress' (26). A total of 17 studies fulfilled the above mentioned criteria and were included in this main section of the review.

After this main section, some studies that examined the relationship between naturally occurring stress levels and decision making and decision making in patients who suffered from stress-related disorders are described. Each section ends with a discussion of the summarized findings. The review concludes with a general discussion that focuses on the psychological and neural mechanisms that underlie the phenomena, implications for everyday decision making and future research directions.

3. Mechanisms of stress and decision making

3.1. Theoretical approaches to decision making

Decisions play a prominent role in many areas of psychological research. Decision processes cover a wide array of complex decisions, such as making inferences, selecting an alternative with the highest benefit or making social or moral decisions. On a conceptual level, decisions can be differentiated by their relative degree of uncertainty because some decision situations offer more information about the expected outcome than others (see Weber and Johnson, 2009). Each decision can be placed on a continuum from 'complete ignorance' (not even the possible outcomes are known) through 'uncertainty' or 'ambiguity' (the outcomes are known but their probabilities are not known) to 'risk' (the outcome probabilities are specified) and, finally, to 'certainty' (only a single outcome is known to result). A broad line of decision-making investigations conducted from a neuroscientific perspective includes situations that range from risk to uncertainty/ambiguity. This range is reflected in the studies that are included in the current review.

The theories that address decisions made under risk propose that humans follow the rules of probability. Mathematical models have been proposed to explain and predict decision-making outcomes (Kunz, 2004; Simon, 1993). For modeling purposes, all of the alternatives are compared and ranked in order of preference. Preference is determined by a personal utility system (Neumann and Morgenstern, 1944). The cognitive ability of the individual and the time to balance alternative actions has been regarded as unbounded. Recent neuropsychological decision-making research has also investigated decisions that are based on explicit rules for gains and losses. In these situations, individuals can generally calculate the risk associated with each choice. These decisions are considered to depend upon executive functioning, such as categorization, set shifting, planning and working memory (Brand et al., 2006). Thus, if outcome probabilities are specified, decisions can be made strategically.

A wealth of research has demonstrated that humans do not always make strategic decisions that are well calculated. Instead, humans have been shown to make decisions based on heuristics, biases and other 'non-rational' or intuitive tendencies (e.g., Gigerenzer and Todd, 1999). Framing effects are prominent demonstrations of intuitive responses overcoming mathematical considerations (Kahneman and Frederick, 2007). For example, the wording of a decision problem strongly influences the answer (Tversky and Kahneman, 1981). Other biases include the use of prototypes and the neglect of probabilities (Kahneman and Frederick, 2002). The dual process theory is an integrative approach. The theory proposes that humans make both strategic and intuitive decisions (Epstein et al., 1996). Humans are generally supposed to be able to make rational choices. The so called rational–analytical system (Epstein et al., 1996), which is linked to slow and serial but controlled, flexible, neutral, rule-governed and effortful information processing, is involved in these kinds of decisions (see also Kahneman, 2003). However, the theory also asserts that the ability to make rational choices does not guarantee its application. Decisions can also be made based on the so-called intuitive–experiential system (Epstein et al., 1996), which is a fast, parallel, associative, and emotional type of processing. The intuitive–experiential system is also referred to as either natural or heuristic (Tversky and Kahneman, 1974). If the decision is associated with uncertainty, either because consequences of a decision are only given implicit or because the totality of the information cannot be processed by the individual, then a strategic choice following the rules of mathematical calculation is not possible. If uncertainty exists to a moderate degree by offering only some indicators of possible outcomes, then both systems of the dual process theory may act in concert. Thus, a temporary first automatic response, which occurs prior to the slower reacting deliberate system, can be adjusted by deliberative thought. This concept has been applied to different kinds of decisions, such as anchoring and adjustment when making inferences (e.g., Gilbert, 1999), or to intertemporal choice when small immediate gains must be weighted against larger long-term gains (e.g., Chabris et al., 2007). A struggle between the intuitive and deliberative responses does not necessarily presuppose that the decision presents uncertainty. Some moral decisions offer certain outcomes, but are a dilemma for the decision maker and can elicit a conflict between 'gut feelings' and cognition (Greene and Haidt, 2002; Haidt, 2007). The same conflict may arise in social decisions that are profitable for the individual but are nevertheless perceived as unfair (Yamagishi et al., 2009). In this case, the intuitive system can also override a rational decision despite the knowledge that the outcome is disadvantageous. Thus, in situations that present some degree of uncertainty or that offer a conflict between emotional–intuitive and deliberate–strategic decisions both decision systems may act in concert.

If uncertainty is high, i.e., the decision situation does not offer appropriate cues to make a strategic decision, then the intuitive–experiential system may play a more prominent role compared to the rational–analytical system. Pham (2004) argues that feelings are incorporated into decisions in different ways. On the one hand, they can serve as proxies for values, meaning that they are used as information source concerning an alternative; on the other hand, they prime thoughts, meaning that they trigger what type of content comes to mind. In line with these assumptions, neuropsychological decision-making research focuses on the genesis of emotions that are associated with an alternative and that subsequently influence the decisions (e.g., Bechara, 2004). The somatic marker hypothesis (Damasio, 1996) highlights the connection between feedback processing and decision making. In this hypothesis, it is proposed that decisions that are made in uncertain situations are guided by so-called somatic markers. It is suggested that the experience of a reward or punishment after a decision evokes emotional responses that correspond with certain somatic states. These somatic states are re-experienced during a current decision and 'mark' the available alternatives. These markers are supposed to act as starting or warning signals that guide the current decision in an advantageous direction. A critical evaluation of the somatic marker hypothesis can be found in Dunn et al. (2006). For example, it is debatable whether working memory has a strong influence on decisions that are made under uncertain conditions (Hinson et al., 2002; Jameson et al., 2004; Turnbull et al., 2005). However, Damasio states that somatic markers indicate which alternative should have working memory resources allocated to it. Thus, somatic markers may precede the selection of options that are processed via cognitive resources. Sensitivity to reward and punishment plays a central role in the generation of somatic markers. This is particularly important in decisions that are made under high uncertainty in which no other clues besides feedback are present, but reward and punishment sensitivity should also play a role in other situations. All decisions that have consequences for an individual rely on reward and punishment sensitivity. This sensitivity is of particular interest if an option offers high potential rewards on the one hand, but high potential punishments on the other hand too (e.g., gambling), or high immediate reward, but even larger long-term reward if the reward is delayed (e.g., intertemporal choice).

In summary, decision situations can be described on a continuum from high to low degrees of uncertainty. The placement on this continuum likely triggers specific decision-making mechanisms, such as strategy application, adjustment from automated responses, feedback processing and reliance on reward and punishment. However, these mechanisms most likely interact in many situations. If uncertainty is low and a strategic decision can be made, then the feedback that follows the outcome can nevertheless lead to a modulation of future decisions (see Brand et al., 2006).

3.2. Neurobiological correlates of decision making

In recent years, the neurobiological correlates of decision making have been studied extensively in patients who suffer from neurological or psychiatric diseases and in healthy participants. Behavioral examinations were used in combination with physiological measurements and functional brain imaging techniques (functional magnetic resonance imaging, fMRI, and positron emission tomography, PET) to pinpoint these correlates.

Executive functioning and working memory are supposed to be involved in decisions that are made under risk (Brand et al., 2006). A prominent neural correlate of these functions is the dorsolateral prefrontal cortex (Jonides et al., 1997; Lie et al., 2006). This part of the prefrontal cortex is thought to be involved in making decisions during situations that require the individuals to compare the contingencies of alternatives or to monitor goal-directed behavior. Empirical evidence demonstrates that patients who possess lesions or dysfunctions of the dorsolateral prefrontal and the ventromedial prefrontal cortex frequently show impairments in decisions made under explicit risk conditions (e.g., Brand et al., 2004a,b, 2005a; Manes et al., 2002; Mavaddat et al., 2000; Rahman et al., 1999). This means that the patients prefer the risky and therefore disadvantageous options, particularly if they also have impaired executive functions. In healthy participants, decisions that are made under risk conditions evoke activities in the dorsolateral prefrontal cortex, the ventral prefrontal cortex, the anterior cingulate gyrus and the anterior cingular cortex, the orbitofrontal cortex, and the parietal cortex (Hsu et al., 2005; Labudda et al., 2008, 2010; Rogers et al., 1999, 2004b). The parietal cortex is considered to be involved in the estimation and integration of gain/loss magnitudes (Labudda et al., 2008) and therefore also could play a role when decisions must be made under risk.

If situations present some degree of uncertainty or offer a conflict between the first automatic response and a deliberate adjustment from this response, then the brain regions that are involved in rational–analytical and emotional–intuitive decision making should be involved in these situations, depending on the specific decision that is made or the strength of the conflict. The emotional–intuitive system is thought to rely on the limbic and basal ganglia regions; editing operations and inhibition of fast automatic responses should rely on the prefrontal regions (see Vorhold, 2008). A prefrontal region that is involved in the integration of information from the limbic system and the basal ganglia is the ventromedial prefrontal cortex (e.g., Bechara et al., 1999; Sanfey et al., 2003). Thus, this region is believed not to be involved in primary emotional processing, but rather in secondary emotional integration. A recent patient study demonstrated that the amygdala and the ventromedial prefrontal/orbitofrontal cortex are differentially involved in decisions that present some degree of uncertainty (Weller et al., 2007). While patients with amygdala lesions showed deficits only in gain related decisions, patients with lesions to the ventromedial prefrontal cortex showed deficits in both gain-related and loss-related decisions. The authors concluded that decisions that are associated with losses are more difficult to disrupt by brain lesions compared with decisions that are associated with gains because losses are more redundantly processed, i.e., they are processed not only in the amygdala but also in the insula (see also Weller et al., 2009). There are also circumstances under which patients with lesions of the ventromedial prefrontal/orbitofrontal cortex or the insular cortex have outperformed healthy participants, namely those situations in which taking risks was associated with a better final outcome (Shiv et al., 2005a,b). Healthy participants tended to overestimate the probability of a loss and were loss averse, whereas the patient groups took more risks. Recent neuroimaging studies have pinpointed further neural correlates of decisions that present some degree of uncertainty or involve a conflict between a first automatic response and deliberate thinking. de Martino et al. (2006) investigated brain activation in a financial decision-making task. In this paradigm, intuitive frame-congruent decisions or deliberate frame-incongruent decisions can be made. Frame-congruent decisions are those that are biased by the instruction whereas frame-incongruent decisions are not biased. Results revealed that frame-congruent choices were associated with increased amygdala activation, whereas frame-incongruent choices were associated with significant activation of the anterior cingulate cortex. Activation of the orbitofrontal cortex and the ventromedial prefrontal cortex were negatively related to susceptibility to the framing effect. A study on intertemporal choice demonstrated that parts of the limbic system that are associated with the midbrain dopamine system were activated when the immediate reward was chosen. Conversely, fronto-temporal activity was related to choosing the delayed reward (McClure et al., 2004). Another study (Xue et al., 2010) demonstrated that choosing a less certain option (i.e., a gamble) over a certain option was associated with the activation of the insular and dorsal medial prefrontal cortex. In studies that measured the response to unfair offers in social decisions, unfair offers elicited activations in the dorsolateral prefrontal cortex, the anterior cingulate cortex and the insula. The strength of insular activation was related to the rejection of unfair offers (Sanfey et al., 2003). In moral dilemmas, activity has been observed in the right dorsolateral prefrontal cortex and the bilateral inferior parietal lobe, the medial prefrontal cortex, the posterior cingulate/precuneus, regions of the superior temporal sulcus/inferior, the parietal lobe, the amygdala, and the anterior cingulate cortex (Greene et al., 2001, 2004). Whether areas that are associated with cognitive or emotional processes are activated depends on the emotionality of the dilemma and the strength of the conflict included. Compared with healthy participants, patients with lesions or dysfunctions of the ventromedial prefrontal/orbitofrontal cortex respond more quickly to highly emotional moral dilemmas (Ciaramelli et al., 2007; Koenigs et al., 2007; Mendez et al., 2005). While healthy participants likely experience a conflict between automated emotional vs. calculative cognitive responses, this response conflict appears to be blunted in this group of patients. Thus, empirical evidence suggests that brain regions that are thought to underlie the intuitive system and the deliberate system are both involved in decisions that present some degree of uncertainty or that offer a conflict between the first automatic response and a deliberate adjustment from this response.

Decisions that are made under conditions of high uncertainty should particularly rely on the brain regions that are involved in feedback processing and reward and punishment sensitivity. A region that is crucial for reward processing is the striatum (Delgado, 2007). Both the dorsal and ventral striatum show increased activation when primary rewards such as food or drinks are delivered. Secondary rewards such as money most likely elicit activation when participants experience action-outcome contingencies. While both ventral and dorsal striatum show different activation patterns in response to reward versus punishment, the dorsal striatum differentiates between different magnitudes of reward and punishment. Patients with Parkinson's disease who possess low levels of dopamine in the striatum are slower in learning associative paradigms (Myers et al., 2003); they also show deficits in feedback learning (Shohamy et al., 2004) and they have difficulties in balancing reward and punishment in decisions under high uncertainty (Kobayakawa et al., 2010). Note, however, that there are also conflicting results and that treatment with dopaminergic medication should be taken into account when investigating decision making in Parkinson's disease. Patients with lesions or dysfunctions of the amygdala or the ventromedial prefrontal/orbitofrontal cortex often show impaired decision-making abilities for decisions under high uncertainty (e.g., Bechara et al., 1999; Brand et al., 2007). The patients prefer the options that are disadvantageous in the long run, and their preference is often accompanied by reduced electrodermal reactions. These patients are described as 'myopic' about future consequences and impaired in generating the appropriate somatic markers that are thought to guide decisions in an advantageous direction (e.g., Bechara et al., 2003; Brand et al., 2007; Goudriaan et al., 2006). However, as mentioned previously in this section, patients can outperform healthy participants in situations in which loss aversion is associated with disadvantageous outcomes (Shiv et al., 2005a). Furthermore, an asymmetric relationship between decision-making abilities and working memory was found in patients with lesions of the dorsolateral prefrontal cortex or the ventromedial prefrontal cortex (Bechara et al., 1998; Manes et al., 2002). While patients may have impaired decision making even with normal working memory, working-memory problems were associated with impaired decision making. Conversely, there are studies that indicate that amnestic patients who possess hippocampus damage may perform normally in feedback-based decision-making tasks (e.g., Turnbull and Evans, 2006), indicating that intact episodic memory is not a precondition for feedback learning. Imaging studies have demonstrated that decisions made under uncertain conditions elicit brain activity in the ventromedial prefrontal/orbitofrontal cortex (Bolla et al., 2003, 2004, 2005; Hsu et al., 2005; Thiel et al., 2003), the anterior cingulate cortex and the dorsolateral prefrontal cortex (Adinoff et al., 2003).

In summary, a complex neural network is involved in decision making. Each region serves a more or less specific function as indicated by the studies on decision making and the studies that examined the underlying functions more directly. Thus, although it is assumed that each region serves a specific function, the regions listed and the functions they serve are highly interconnected.

3.3. Theoretical and methodological approaches to stress

Stress research began in the 1930s with Hans Selye, who defined stress as unspecific bodily reaction to stressors, such as heat or cold (Selye, 1956). The existence of psychological stressors was introduced by Mason (1968). In the following decades, research has focused on cognitive factors, such as appraisals (Lazarus, 1999). Despite the heterogeneous models of the stress genesis, there is a broad consensus that stress elicits psychological, physiological and behavioral reactions and that there is a large interindividual difference in stress reactions (Kudielka et al., 2009). Recent reviews and meta-analyses postulate that stress occurs whenever a demand exceeds the regulatory capacity of an organism, particularly in situations that are unpredictable and uncontrollable (Dickerson and Kemeny, 2004; Koolhaas et al., 2011).

Laboratory stressors are used to simulate the natural stressors that reliably elicit stress reactions. An exception to this method is the direct application of stress hormones that directly induce a physical stress reaction, such as adrenaline or cortisol. Most laboratory stressors contain either a physical challenge (e.g., heat, cold, pain, exercise, inhalation of CO_2), a cognitive demand (e.g., mental arithmetic, vigilance-reaction time tasks, analytical tasks), and/or a social-evaluative threat (e.g., anticipation of or actual performance of a public speech, verbal interaction and direct or virtual observation of an individual while he/she is doing something). In the current review, stressors are used to investigate the effects of stress on a decision-making task. Therefore, it is important to note that stressors differ in their timing relative to the other task. Most stress protocols are assessed prior to the task of interest and are timed to ensure maximal stress reaction during the task, particularly a high cortisol response during task performance (see Section 3.4). A common procedure for physical challenge is the Cold Pressor Test (CPT; Hines and Brown, 1932), in which one hand must be immersed in ice water for 3 min (or even longer durations). This test is usually performed approximately 15 min before the onset of the decision-making task (e.g., Lighthall et al., 2009). A recent modification of the CPT is the Socially Evaluated Cold Pressor Test (Schwabe et al., 2008), in which researchers pretend to analyze facial expression during the CPT by placing a camera in front of the participants' face. This modified version of the CPT elicits stronger endocrine stress reactions compared with the original version of the CPT. A common stress induction task that combines a social-evaluative threat and a cognitive demand is the Trier Social Stress Test (TSST; Kirschbaum et al., 1993). This procedure lasts approximately 15 min and begins prior to decision making (e.g., Starcke et al., 2011). The participants must deliver a public speech (a mock job interview) in front of a committee that behaves in a very cold and reserved manner. Afterwards, the participants must perform an arithmetic task as quickly and accurately as possible. The entire performance is videotaped. A placebo version (Het et al., 2009) and a group version of this task (von Dawans et al., 2011) were recently established. The announcement that a public speech must be delivered, without a subsequent speech performance, is also a common method for inducing stress (Preston et al., 2007; Starcke et al., 2008). The announcement is made prior to the task of interest and the participants anticipate the speech during task performance. Another method for inducing stress that occurs during task performance is the announcement of a physical threat, such as an electric shock that will be administered in response to a mistake (Keinan, 1987). Thus, methods for inducing stress in the laboratory are manifold.

To investigate the effects of stress on decision-making performance it is essential to ensure that stress induction was successful. Behavioral stress reactions, such as fidgeting, are accessible to observation, but the observation of such reactions is not common in stress research. Instead, such reactions are predominantly assessed using questionnaires that also include psychological stress reactions, such as feelings of tension or pressure. Examples of the questionnaires that assess behavioral and subjective reactions are the state part of the State Trait Anxiety Inventory (Spielberger et al., 1977), which measures acute anxiety reactions, or the Positive and Negative Affect Schedule (Watson et al., 1988), which measures current affect. The stress levels that occur over a specific time period, for example, can be assessed using the Daily Hassles Scale (Kanner et al., 1981), which measures daily hassles, the Life Experiences Questionnaire (Norbeck, 1984), which measures positive and negative critical life events, the Perceived Stress Scale (Cohen et al., 1983), which measures the extent to which participants perceive their lives as unpredictable, uncontrollable and overloaded, or the Impact of Event Scale (Horowitz et al., 1979), which measures the reactions that follow a specific traumatic event. There are various other questionnaires that are suitable for assessing acute and chronic stress levels.

3.4. Neurobiological correlates of stress reactions

The most prominent method for the measurement of stress reactions is the assessment of physiological and endocrine reactions.

Stress triggers two systems in the brain and body: the fast-reacting neural path, also referred to as the sympathetic adrenomedullary system (SAM-system) (Cannon, 1914) and the slower hypothalamus pituitary adrenal axis (HPA-axis) (Selye, 1956). The neural stress reactions occur immediately after stress exposure. They originate in the hypothalamus, which stimulates sympathetic nuclei in the medulla, triggering the release of the catecholamines adrenaline and noradrenaline from the adrenal medulla. This release leads to various reactions within the sympathetic nervous system, such as increases in heart rate, pulse, blood pressure, and electrodermal activity. These reactions occur immediately after stress onset and return to baseline approximately 10 min after cessation of the stressor (e.g., Het et al., 2009; Kirschbaum et al., 1993). Adrenaline also leads to an increased release of glucose. Therefore, reactions of the SAM-system allow a fast adaptation to the stressful situation and allow a 'fight-or-flight' response (Cannon, 1914). Catecholamines can in turn affect the brain via the sensory vagus transmitting information to adrenergic neurons in the nucleus tractus solitary projecting to the locus coeruleus which is the main source of noradrenaline inputs to the basolateral amygdala. Further projections reach to the thalamus, hypothalamus, hippocampus, and prefrontal cortex (review in Chrousos and Gold, 1992; De Kloet et al., 2005; Joels and Baram, 2009; Roozendaal et al., 2009). Catecholamines can be directly measured in the blood. Recently, saliva measures have become popular to analyze the enzyme alpha-amylase as a marker of adrenergic and noradrenergic activity (Nater and Rohleder, 2009; Rohleder and Nater, 2009).

Reactions of the HPA-axis lead to a secretion of corticotropin-releasing hormone from the peri–paraventricular nucleus of the hypothalamus and adrenocorticotropic hormone from the anterior pituitary, stimulating the release of glucocorticoids from the adrenal cortex (Sapolsky et al., 2000). The primary glucocorticoid in humans is cortisol, which mobilizes energy resources by elevating blood glucose levels. The peak cortisol response is approximately 21–40 min after the onset of a stressor (Dickerson and Kemeny, 2004). Therefore, many studies on stress and subsequent performance include the time period approximately 21–40 min after stress onset (see Section 3.3). If the cortisol peaks were high, then cortisol elevation persists up to 60 min after stressor termination; otherwise cortisol levels return to prestressor levels within 41–60 min after cessation of the stressor. Cortisol can be measured in the blood, urine and saliva (Kirschbaum and Hellhammer, 1994). Within the central nervous system, the HPA-axis is regulated via excitatory and inhibitory loops of limbic and prefrontal structures that are involved in emotion and stress processing, such as the amygdala, hippocampus and prefrontal cortex (De Kloet et al., 2005; Herman et al., 2005). These regions have receptors to which glucocorticoids can bind. Glucocorticoids bind to two receptor subtypes: mineralocorticoid-receptors (type I) and glucocorticoid-receptors (type II). Type I receptors have a higher affinity and are exclusively present in the limbic system while type II receptors have a lower affinity and are also present in the prefrontal cortex. During circadian low levels and under rest conditions, most of the type I receptors are occupied and the type II receptors are not occupied, whereas during circadian high levels or under stress conditions, the type I receptors are saturated and 67–74% of the type II receptors are also occupied (reviews in Lupien et al., 2007; McEwen and Sapolsky, 1995). Recent research has also suggested that the SAM-system and the HPA-axis act in concert (Joels and Baram, 2009). For example, glucocorticoids facilitate the effects of noradrenergic stimulation in the basolateral amygdala (Roozendaal et al., 2009). Thus, while the fast-reacting SAM-system and the slower reacting HPA-axis have different neuro-endocrine correlates, there are also intersections between the two systems.

Recent neuroimaging studies have shown that current stress leads to metabolic changes in different brain regions, particularly in those regions that possess receptors for stress hormones (Dedovic et al., 2009a; Pruessner et al., 2010). Studies that used fMRI or PET have indicated that the acute exposure to stress leads to metabolic reactions in the prefrontal, limbic, basal ganglia and other regions. Although results were not always consistent, a decrease in activity was observed in the orbitofrontal cortex, the hippocampus and the hypothalamus (Pruessner et al., 2008), while an increase in activity was observed in the dorsolateral prefrontal cortex, the anterior cingulate cortex, the basal ganglia and the ventral striatum (Pruessner et al., 2004). Mixed results (either a decrease in or an increase in activity) were found for the amygdala, the thalamus and the insular cortex (Dedovic et al., 2009b; Pruessner et al., 2008; Tillfors et al., 2002; Wang et al., 2005). These mixed results may be explained by individual differences in stress responses (Kudielka et al., 2009). Therefore, the interaction between hormonal stress reactions and neural reactions should also be taken into consideration. Pruessner et al.'s (2008) is one example of these differences between responders and nonresponders to experimentally induced stress. The authors divided their participants into cortisol responders and nonresponders after their responses to stress were evaluated and demonstrated that the responders showed a deactivation of specific parts of the limbic system, including the hypothalamus, hippocampus, amygdala, and medio-orbitofrontal cortex. In contrast, the cortisol nonresponders did not show this deactivation pattern. The authors concluded that the limbic system has a high basal activity that can serve as an alarm system. Once an alarm has been given after exposure to a stressor, the activity is curtailed. The question of why some participants respond to a challenge with a cortisol response while others do not has been addressed by recent research (Kudielka et al., 2009). There are many factors that could influence HPA-axis reactivity, such as gender, age, oral contraceptive use, chronic alcohol or nicotine consumption. These factors should be controlled for in stress research. However, many other factors may also impact this reactivity, such as genetic factors, early life stress and personality. Early life stress (e.g., Luecken and Appelhans, 2006) and some personality variables, such as low self-esteem and low locus of control (Pruessner et al., 2005) are thought to increase the reactivity of the HPA-axis. Additionally, a habituation effect occurs in most participants after repeated exposure to the same stressor (e.g., Schommer et al., 2003), and therefore prior experience with the respective challenge may be a confounding factor. One may assume that individual factors determine the threshold for hormonal responses to stress exposure.

In conclusion, the brain regions that possess receptors for stress hormones show metabolic changes during acute stress exposure. Furthermore, the hormonal stress response interacts with neural responses.

3.5. Integration and hypothesis

The former sections were intended to summarize the research that indicates that the brain regions that are associated with decision making are sensitive to stress-induced changes (see Fig. 1). Therefore, it seems reasonable to assume that stress affects decision making. Various types of decisions should be affected by increased activation of the ventral striatum, which leads to an increased sensitivity to reward; decisions that are made under risky conditions should be affected by stress effects on the dorsolateral prefrontal cortex that alter functional strategy use; decisions that present a moderate degree of uncertainty should be affected by stress effects on prefrontal as well as limbic regions, which interferes with the balance between automated emotional responses and deliberate calculative responses; decisions that are made under high uncertainty should be especially affected by stress effects on the

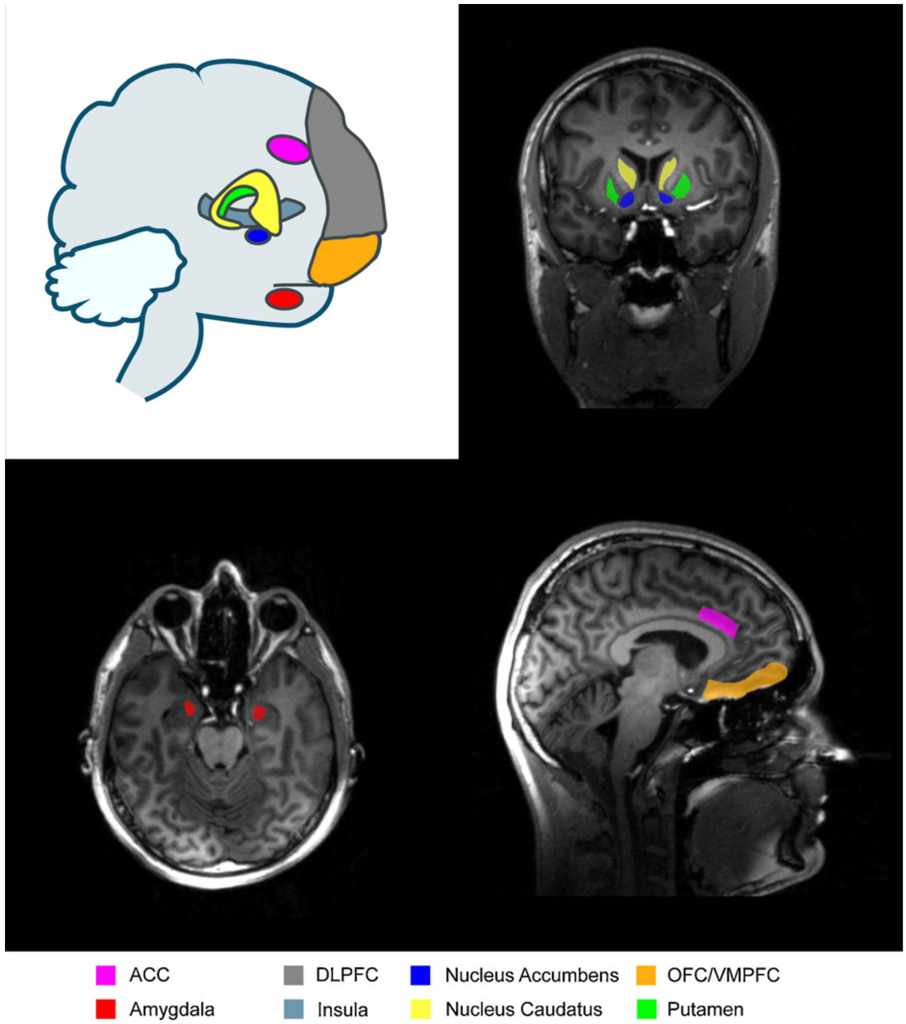

Fig. 1. Key brain regions for intact decision making that are potentially sensitive to stress-induced changes. ACC = anterior cingulate cortex; DLPFC = dorsolateral prefrontal cortex; OFC = orbitofrontal cortex; VMPFC = ventromedial prefrontal cortex.

limbic system and the orbitofrontal cortex, which alter feedback-processing abilities. It should be emphasized that whether stress leads to more advantageous decisions or more disadvantageous ones probably depends on the situation. For example, increased risk seeking under stress due to decreased punishment sensitivity is expected to be disadvantageous in some circumstances but not in others.

4. Intersections of stress and decision-making behavior

In the following sections, the laboratory studies that used acute stress induction and that fulfilled the inclusion criteria described in Section 2 are summarized. Thereafter, some laboratory studies that measured the relationship between naturally occurring stress levels and decision-making performance in healthy participants are described. In both of these sections, the studies are sorted by the type of underlying decision-making processes into 'dysfunctional strategy use,' 'insufficient adjustment from automatic response,' 'altered feedback processing' and 'altered reward and punishment sensitivity.' Note that, under most circumstances, more than one of these mechanisms is involved in a decision. The studies were nevertheless only listed once and were sorted according to their main focus. Finally, some laboratory studies that investigated patients who suffer from stress-related disorders are described.

4.1. *Effects of acutely induced laboratory stress on decision making*

The studies described in this section are summarized in Table 1.

4.1.1. *Dysfunctional strategy use*

As mentioned in Section 3.1, decisions that are made under risky conditions can generally be solved strategically, which means that each alternative can be evaluated concerning its outcome (Brand et al., 2006). According to Janis and Mann (1977), high stress levels can result in premature closure, which means that a decision is made before all of the alternatives are scanned and evaluated concerning their potential outcome. This was observed in real-life situations of acute danger (e.g., Quarantelly, 1954) as well as in laboratory studies in which the participants were told that they would receive an electric shock if they made the wrong decision (e.g., Kelley et al., 1965). A more recent study investigated the effect of announced electric shocks on the performance of an analogies task (Keinan, 1987). The multiple-choice analogy task consisted of questions. For each question, the participants were required to choose the correct answer from six alternatives. The participants were permitted to choose which alternative was displayed on the monitor. Thus, in addition to the quality of performance, dysfunctional decision-making strategies, such as premature closure, non-systematic scanning, and temporal narrowing, could also be

Table 1
Studies examining the effect of acutely induced laboratory stress on decision-making between 1985 and October 2011.

Category	Study	Participants	Decision-making task	Stressor	Stress measurement	Main results
Dysfunctional strategy use	Keinan (1987)	Students 42 m/59 f	Analogies task	Threat of electric shock	STAI	Stress led to a decreased performance, premature closure and non-systematic scanning of alternatives
	Starcke et al. (2008)	Students 18 m/22 f	GDT	Anticipated speech	Cortisol, alpha-amylase, STAI	Stress led to more disadvantageous choices. Cortisol reactions and risky decisions were correlated
Insufficient adjustment from automatic response	Kassam et al. (2009)	32 m/71 f	Anchoring and adjustment	Modified TSST	Heart rate, blood pressure	Stress led to a decrease in adjustment and stress responses predicted decreased adjustment
	Porcelli and Delgado (2009)	Students 14 m/13 f	Modified CGT	CPT	SCL	On gain domain trials, stress led to more conservative choices, on loss domain trials, stress led to more risky choices
	Putman et al. (2010)	Students 29 m	Modified CGT	Application of cortisol	Cortisol, STAI	Stress led to more risky decisions whenever the potential reward was high
	Starcke et al. (2011)	Students 22 m/18 f	Everyday moral dilemmas	TSST	Cortisol, alpha-amylase, STAI	Stress did not lead to more egoistic decisions, but cortisol reactions and egoistic decisions were correlated
	Youssef et al. (in press)	Students 30 m/35 f	Moral dilemmas	TSST	Cortisol	Stress led to fewer utilitarian judgments in personal dilemmas. Stress responses and nonutilitarian judgments were correlated
Altered feedback processing	Driskell and Salas (1991)	Students 78 m	Team decision making in an ambiguous checkerboard task	Announced tear gas drill	Questionnaire	Stressed participants more strongly relied on the judgments of other persons
	Lighthall et al. (2009)	22 m/23 f	BART	CPT	Cortisol	Stress increased risk taking in men, but decreased risk taking in women
	Lighthall et al. (in press)	24 m/23 f	BART	CPT	Cortisol	Stress led to greater reward collection and faster decision speed in men, accompanied by activation of the dorsal striatum and anterior insula, but less reward collection and slower decision speed in women accompanied by decreased activation in the brain regions mentioned
	Mather et al. (2009)	Younger and older adults 43 m/42 f	Driving task	CPT	Cortisol	Stress led to risk aversion associated with dysfunctional decisions, but only in older adults
	Preston et al. (2007)	Students and university staff 20 m/20 f	IGT	Anticipated Speech	Heart rate	Stress led to slower learning of contingencies. In men stress led to more disadvantageous decisions, in women stress led to more advantageous decisions
	van den Bos et al. (2009)	Students and university staff 30 m/34 f	IGT	TSST	Cortisol	Cortisol reactions and disadvantageous decisions were correlated in male participants. In females an inverted U-shaped relation emerged
Altered reward and punishment sensitivity	Oliver et al. (2000)	Students and university staff 27 m/41 f	Food selection	Anticipated speech	Heart rate, blood pressure, PANAS	Stressed emotional eaters ate more sweet, high-fat foods than nonemotional eaters and unstressed participants
	Takahashi et al. (2007)	Students 31 m	Dictator Game	Social evaluation	Alpha-amylase	Stress led to more generous decisions in participants with stress reactions
	Zellner et al. (2006)	Students 34 f	Food selection	Unsolvable anagrams	Questionnaire	Stress led to a preference for unhealthy food
	Zellner et al. (2007)	Students 36 m	Food selection	Unsolvable anagrams	Questionnaire	Stress led to a preference for healthy food

f = female/m = male; BART = Balloon Analogue Risk Task; CGT = Cambridge Gambling Task; CPT = Cold Pressor Test; GDT = Game of Dice Task; IGT = Iowa Gambling Task; PANAS = Positive and Negative Affect Schedule; SCL = skin conductance level; STAI = State Trait Anxiety Inventory; TSST = Trier Social Stress Test.

investigated. Participants were exposed to the announcement of a controllable, performance-based electric shock, an uncontrollable electric shock or no electric shock. Both groups to whom shocks were announced performed worse than the control group and displayed premature closure and non-systematic scanning more frequently than the control group.

A recently developed gambling task, the Game of Dice Task (GDT; Brand et al., 2005a), simulates decisions that offer explicit rules for gains and losses that are stable over time. In this task, participants can chose among different combinations of dice that are explicitly associated with possible gains and losses. The options that are associated with potentially high gains are disadvantageous options because they are also associated with potentially high losses and have very low winning probabilities (less than 34%). Feedback is also provided, thus strategy application and feedback processing are the most influential factors in ensuring optimal task performance (see Brand et al., 2006, 2008). The participants who were stressed due to anticipating a speech performance made more risky and therefore disadvantageous decisions than participants in a control condition, i.e., the stressed participants chose the options that potentially lead to a high reward but more frequently lead to a high punishment more often (Starcke et al., 2008). In this study, cortisol responses and risky decisions were correlated, which suggests that cortisol responses indeed results in risky decision making. Recent studies with the GDT revealed that the dorsolateral prefrontal cortex, the parietal cortex and the amygdala are involved in successful task performance (Brand et al., 2007; Labudda et al., 2008). These results indicate that stress-induced changes may be responsible for both altered executive functioning and altered emotional feedback processing. These stress-induced changes most likely affect the generation and usage of sufficient decision-making strategies.

4.1.2. Insufficient adjustment from automatic response

Decisions that offer a moderate degree of uncertainty have been studied extensively in the research on bounded rationality (Englich et al., 2006; Tversky and Kahneman, 1974). A recent study investigated the influence of social evaluative threat compared to a positive challenge on anchoring and adjustment (Kassam et al., 2009). Anchoring and adjustment is a prominent model for dual-process reasoning because inferences generated through automatic processes are fine-tuned by controlled processes. The anchoring-and-adjustment questions (Epley and Gilovic, 2002) are questions to which participants likely do not know the answer but can make a guess about from facts (anchors) that they do know. The more the participants adjust, the better they perform. Stress was created using modifications of the TSST, either as a threat that included negative feedback or a challenge that included positive feedback, such as nodding, smiling and so on. Participants who were exposed to the challenge adjusted better than the participants under threat. The control participants received no manipulation, and their adjustments were in-between the two experimental groups. Performance was mediated by cardiovascular reactions in response to the manipulation. Challenge was predominantly accompanied by cardiovascular reactions that provided stronger mental and physical resources than threat, i.e., increased cardiac output and decreased vascular reactivity. This study indicates that stress can have positive effects on decision making as well, but only if the stress is not perceived as a threat but as a challenge.

A prominent effect that was noted in the research on bounded rationality is the framing effect, the contention that information is processed according to the context of presentation (Kahneman, 2003; Kahneman and Frederick, 2007). The Cambridge Gambling Task (CGT; Rogers et al., 1999) is a frequently used gambling task that simulates the decisions that are made under explicit but unstable conditions and offers different frames. In this task, participants are permitted to choose either a control gamble with a fixed expected value or experimental gambles that vary in their associated potential losses and gains and in their probability of winning and losing. Porcelli and Delgado (2009) investigated the effect of CPT stress in a modified CGT task. The authors used a within subjects design in which participants have undergone the control condition first and the stress condition after that. They found that stress augments the reflection effect (Kahneman and Tversky, 1979), also referred to as preference shift effect (Levin et al., 2002). The participants who were under stress made more conservative decisions in the gain-domain trials compared with participants in the no stress condition, but more risky decisions in the loss-domain trials. This difference was interpreted in light of dual-process approaches as an exaggerated reliance on lower level systems (Masicampo and Baumeister, 2008). Putman et al. (2010) used a similar task and investigated male participants using a within-subjects design. The participants were evaluated either after the application of cortisol or after the application of a placebo. This is the only study found in the database search that applied cortisol directly (40 mg hydrocortisone) and investigated subsequent decision making. The authors also found that, compared with participants who were administered a placebo, participants who were administered cortisol made more high-risk gambles with both a potential high reward and a potential high loss. This study emphasized the causal role that cortisol plays in altering stress-induced decision making. In particular, cortisol leads to a decrease in punishment-sensitive behavior and an increase in reward-sensitive behavior in situations that contain high potential rewards. On a neural level, the CGT elicits activations of different prefrontal regions (Rogers et al., 1999), and patients who possess lesions or dysfunctions in these regions show a decrease in performance (Manes et al., 2002). Stress is thought to alter the functional activity of these regions and lead to a decrease in controlled cognitive processes, such as the application of strategies to overcome automatic choices.

A recent study (Youssef et al., in press) assessed the influence of stress on moral decisions using moral dilemmas that were developed by Greene et al. (2004). Each dilemma offered a utilitarian and a nonutilitarian alternative. A utilitarian decision is defined as an option in which one person is sacrificed to save the lives of a group of people and to maximize the overall benefit amongst all the individuals involved. Additionally, the dilemmas were framed as either personal or impersonal. In personal dilemmas, the decision maker is required to take direct action to sacrifice a person, while in impersonal dilemmas, an existing threat is deflected by the decision maker. Personal dilemmas are thought to elicit stronger aversive emotions than impersonal dilemmas. The stressed participants made fewer utilitarian judgments compared with the unstressed participants in personal dilemmas, but not in impersonal ones. Furthermore, stress reactions were negatively related to utilitarian judgments. The authors concluded that stress diminished the ability to overcome a first automated response. Another study investigated the effects of stress on moral dilemmas that could occur in everyday life (Starcke et al., 2011). Each dilemma offered an egoistic and an altruistic alternative. Again, the dilemmas were framed differently, as either high-emotional or low-emotional. While no group differences were observed between stressed and unstressed participants, cortisol responses in the stress group were correlated with egoistic decisions in high-emotional dilemmas. It could be concluded that both the features of the decision situation and individual stress responses influence the moral decisions.

4.1.3. Altered feedback processing

Gambling tasks have frequently been used to investigate decisions that are made under uncertain conditions that can be solved via the processing of feedback of previous decisions. A prominent task that simulates such decisions is the Iowa Gambling Task (IGT; Bechara et al., 1994, 2000b). In this card game, participants are required to select cards from four card decks, all of which differ in their overall gains and losses. Participants must learn which decks are advantageous via the feedback provided to them. The decks that are associated with initially high gains are also associated with high losses and are therefore disadvantageous in the long run. The IGT has been developed to assess decision-making competencies in patients who suffer from damage to the prefrontal cortex regions or the amygdala. Studies of these patients reveal that they prefer the decks with potentially high gains that are disadvantageous in the long run (Bechara et al., 1999, 2000a, 2003). In recent years, the IGT has also been used to investigate the potential cognitive and emotive correlates of decision making in healthy individuals. In this line of research, the effects of stress on IGT performance have also been studied. Preston et al. (2007) induced stress with the anticipation of a public speech that would be evaluated and videotaped. Participants who were exposed to this stressor did not select more disadvantageous decks in total compared with control participants, but the typical learning curve in the task was slower for the stressed participants than for the control participants. Thus, the typical increase in performance after a number of trials was delayed. Additionally, a gender effect was observed. While stressed men decided more disadvantageously compared with unstressed men, stressed women decided less disadvantageously than unstressed women. The results of a decreased learning curve have been interpreted in the light of the somatic marker hypothesis. While emotions that are relevant to the task, such as experiencing and anticipating a reward or punishment, are supposed to guide the decision in an advantageous direction via somatic markers, emotions that are irrelevant to the task, such as stress-related emotions, should interfere with these somatic markers. Similar results were found in a recent study that used the TSST as a stressor and cortisol responses as a stress indicator (van den Bos et al., 2009). Cortisol reactions and disadvantageous decisions were linearly related in male participants, while an inverted U-shaped relationship was observed in female participants. The more cortisol was secreted, the better the performance was. However, at very high levels of cortisol, performance decreased. Taken together, studies of stress-related changes in IGT performance emphasize that stress, especially hormonal stress responses, affects performance, but it affects men and women differently. These results can be integrated with the studies that have examined the neural correlates of IGT performance and stress response. The secretion of cortisol in particular is thought to disturb the functional integrity of the ventromedial prefrontal/orbitofrontal cortex and the amygdala (Pruessner et al., 2010), both of which have been illustrated by patient studies and neuroimaging techniques as important regions for making advantageous decisions in the IGT (see Section 3.2).

Another prominent task that requires feedback processing and risk taking is the Balloon Analogue Risk Task (BART; Lejuez et al., 2002). In this task, participants must pump up a balloon. The more they pump it up, the more points they win, but if the balloon explodes, then they lose all of the points from the current trial. The point at which the balloon explodes is randomly determined, but participants can estimate the likelihood through trial and error. Thus, early BART trials involve a greater degree of uncertainty while later trials may be more likely to reflect risk tolerance, as probabilities become approximately known. In the BART, risk seeking to a certain extent is related to a better outcome while in the IGT conservative behavior leads to better outcome. In a recent study of the effects of stress on the BART, stress induced with the CPT led to higher risk avoidance (fewer pumps per trial) in women and higher risk seeking (more pumps per trial) in men (Lighthall et al., 2009). In women, the cortisol responses were related to conservative behavior. A study that investigated neural activation during the BART (Rao et al., 2008) revealed activations in the anterior insula, the striatum, the dorsolateral prefrontal cortex, the medial frontal cortex, and the anterior cingulate gyrus during risk taking. These regions are thought to underlie processes of emotional learning, error processing, reward anticipation, executive functioning and working memory. A recent study combined stress induction and neuroimaging during the BART (Lighthall et al., in press). Again, stress pronounced gender differences, i.e., stress led to greater reward collection and faster decision speed in males but less reward collection and slower decision speed in females. The observed behavioral differences between men and women who experienced stress were accompanied by different neural activation. In men, activation of the dorsal striatum and the insula increased under stress, while activation of these regions decreased in stressed women. In men, the cortisol stress response was associated with activation of the dorsal striatum. The same researchers who investigated stress effects on the BART conducted another study that investigated the effect of stress on a simulated driving game in young and older adults (Mather et al., 2009). The task shares some similarities with the BART. Participants must decide whether to brake or to accelerate when traffic lights turn yellow. The duration of the yellow light is random. Crossing the yellow light leads to gains whereas crossing the red light leads to losses of points. Stress, induced with the CPT, did not affect young participants' performance but led to more risk avoidance in older participants. This risk avoidance was associated with fewer points. Contrary to the previous study, no gender effects were found. Thus, despite a shared underlying conceptualization of the decision situation, the different tasks indicated gender effects in the two studies that used the BART, and age effects in the driving game.

One study investigated the effect of another person's disagreement on whether stress alters decisions made in an uncertain task (Driskell and Salas, 1991). Thus, feedback was not conceptualized as the objective outcome but as another persons' opinion. The authors tested whether the participants became more receptive to information from others while under stress. The task consisted of decisions regarding which of two checkerboards contained a greater amount of white area. Participants were required to make an initial choice. Then, they observed their partners' choice and made their final choice. Stress was induced via the announcement of tear gas being introduced in the room and by telling the participants that the group performance would rely only on their final decisions. The results revealed an effect of stress in that the stressed participants became more deferential. The authors concluded that participants who are under stress become more receptive to information from others.

4.1.4. *Altered reward and punishment sensitivity*

As mentioned in Section 3.1, reward and punishment sensitivity should play a central role in decision making independent of the amount of uncertainty associated with the decision. One study (Takahashi et al., 2007) investigated whether stress affects decision making in the Dictator Game (Forsythe et al., 1994). In this game, the participant can divide a sum of money between himself/herself and another participant. The other participant (the responder) cannot accept or reject an offer, which ensures that the decision is not associated with any uncertainty. Furthermore, the game is only played once, which eliminates the role of reciprocity. The player can choose whether to allocate himself/herself a large amount of money. On the one hand, keeping the money for oneself can be rewarding (high gain), on the other hand, egoistic behavior can be punishing (bad conscience). Participants who were exposed to a social evaluation condition subsequently gave more money to a second fictitious participant than participants from a control group did. This effect was only observed in the participants who showed a stress response, i.e., an alpha-amylase response.

The results were interpreted in light of evolutionary theories that postulated that social evaluation triggers reputation formation tendencies. However, alpha-amylase responses and money given were uncorrelated. This lack of effect was also considered an indicator of individual differences in altruistic behavior.

One very common decision process that occurs in everyday life is the choice of food. This type of choice is also a topic of interest in health research. Food choice can be assessed very concretely in the laboratory, i.e., participants are allowed to snack on different types of food, for example, healthy or unhealthy snacks. Some studies that investigated the effect of stress on food choice assumed that stress leads to a preference for unhealthy food. This was true for 'emotional eaters,' who generally increased eating under emotional challenge (Oliver et al., 2000), and for women (Zellner et al., 2006). The authors concluded that such food items can relieve stress through the release of endogenous opioids (Mercer and Holder, 1997). The opioid release can be considered a high immediate reward, while long-term negative consequences, such as gain in weight or a decline in health, are neglected. However, the opposite choice pattern emerged in men, such that unstressed men ate more than stressed men (Zellner et al., 2007). Although this contradiction may have been partly due to experimental reasons – stress was induced with unsolvable anagrams, whereas the control group received solvable anagrams that could be finished very quickly, so they had more time to snack – the authors revealed a gender difference in food choice that occurs when people undergo stress. Furthermore, food intake appears to increase under acute stress in overweight participants (Lemmens et al., 2011).

4.1.5. Conclusion: decision making under laboratory stress

The studies that are summarized in this section indicate that stress affects decision making by potentially affecting the underlying mechanisms, such as 'strategy use,' 'adjustment from automated responses,' 'feedback processing' and 'reward and punishment sensitivity.' If these alterations confer an advantage or disadvantage depends on the task and situation. Some studies indicate a decrease in performance under stress conditions (Keinan, 1987; Starcke et al., 2008). Limited attention and reductions in executive functioning due to the stressor were postulated as underlying mechanisms for dysfunctional strategy use. The decrease in adjustment under stress was also explained by limited cognitive resources (Kassam et al., 2009). However, this decrease only occurred when the stress was perceived as a threat while the perception of stress as a challenge led to an increased performance. Participants under threat stress do not overcome their first automatic response and fail to make a controlled rational adjustment. Stress may lead to an exaggerated reliance on lower level automatic response tendencies and to a decrease of controlled cognitive processes (Masicampo and Baumeister, 2008). This reliance on lower level systems should make participants particularly prone to framing effects when stressed. Studies indicate that stress exacerbates a preference for conservative decisions in gain-domain trials, and it exacerbates a preference for risky decisions in loss-domain trials (Porcelli and Delgado, 2009). Note, however, that the reliance on lower level systems under stress is not necessarily detrimental. There are many situations in which automatic processing in decision making may be beneficial. This relates to the hypothesized evolutionary value of 'fight-or-flight' stress responses. Frames that guide behavior in moral decisions are also prone to stress-induced changes (Youssef et al., in press), but whether this confers an advantage or disadvantage is not to determine by definition. The studies that examine decisions in tasks that require feedback learning and involve risk taking indicate that individual stress responses may be related to the decisions. In tasks in which increased risk seeking is disadvantageous for the overall outcome such as the IGT, a high individual stress response appears to be related to disadvantageous decisions (van den Bos et al., 2009), whereas tasks in which risk seeking to a certain extent is advantageous such as the BART, a high individual stress response may be related to advantageous decisions (e.g., Lighthall et al., 2009). However, these results do not apply to all participants; these studies have indicated gender differences (Lighthall et al., 2009, in press; van den Bos et al., 2009) and age differences in performance (Mather et al., 2009). In those participants, stress has a detrimental effect, stress-related emotions unrelated to the task are supposed to interfere with learning. Furthermore, stress may increase reward sensitivity, which might be advantageous in some tasks but disadvantageous in others. In those scenarios in which increased reward sensitivity leads to disadvantageous outcomes, the participants may neglect negative long-term consequences such as punishment. This increase in reward sensitivity could lead to a preference for options that potentially offer both high rewards and high punishments (Starcke et al., 2008). Animal studies (Shaham et al., 2000) and human studies (Buchmann et al., 2010; Lemmens et al., 2011; Thomas et al., 2011) also indicate that stress increases appetitive behaviors such as drug or food intake. However, this effect has not been found in all participants, as it presents differentially in men and women (Zellner et al., 2006, 2007). In most of the studies cited above, the effects of stress on decision making are most likely based upon a combination of dysfunctional strategy use, decreased adjustment from automatic response, reduced learning from feedback and higher reward sensitivity. The relative impact of these effects, however, is considered dependent upon the specific decision situation.

The secretion of the stress hormone cortisol is discussed as a major mediator between stress and decisions. Relationships have been found between cortisol response after stress induction and decision making (van den Bos et al., 2009; Starcke et al., 2008, 2011). The application of cortisol also affects decision making (Putman et al., 2010) in a similar manner to the application of a cortisol-increasing beta-adrenergic antagonists (Rogers et al., 2004a). Cortisol secretion is thought to disturb the functional integrity of those brain regions that contain receptors for cortisol (see Section 3.4). These brain regions are essential for decision making (see Section 3.2). Cortisol secretion has also been found to affect working memory functioning (Schoofs et al., 2008), executive functioning (McCormick et al., 2007) and feedback learning (Petzold et al., 2010). Animal studies have revealed that glucocorticoids activate dopaminergic neurons and lead to an increased release of dopamine in the nucleus accumbens (George and Koob, 2010; Shaham et al., 2000), which is thought to amplify reward salience. Increased reward salience under stress has also been suggested for humans, particularly in the addiction literature (Buchmann et al., 2010; Lemmens et al., 2011; Thomas et al., 2011), but recently reward circuits under stress have also been investigated in healthy participants using neuroimaging techniques. Scott et al. (2006) found increased dopamine release in the striatum during pain stress and Ossenwaarde et al. (2011) suggest a shift from prefrontal to striatal processing under emotional stress. Until now, only one study that fulfilled the inclusion criteria for this review addressed the neural correlates of decision making that occurs under stress (Lighthall et al., in press). This study suggested that the behavioral indices of decision making that occur under stress co-vary with specific neural activation. In this specific task, activation in the dorsal striatum and the insula was partly related to stress reactions and decision-making performance. More research is needed to address the neural correlates of the various decision-making parameters that can occur under stress.

It becomes clear that stress has a different effect on decisions than time pressure or information overload. Numerous researchers who investigated heuristic vs. analytical judgments do not consider limited cognitive resources to be impedimental to decision making

(Gigerenzer and Brighton, 2009; Gigerenzer and Todd, 1999). Rapid pre-conscious heuristic processes are thought to direct attention toward the relevant aspects of a problem, whereas subsequent analytical processes do not necessarily lead to improved performance. These diverging conclusions indicate that stress triggers different mechanisms than other factors, e.g., time pressure. Stress probably triggers hormonal and neural reactions that may affect decision making which is a disadvantage in certain situations.

4.2. Relationship between current stress levels and decision making

4.2.1. Dysfunctional strategy use

According to Baradell and Klein (1993), naturally occurring stressors are more severe than laboratory induced stress. They investigated the relationship between current life stress, measured by the Daily Hassles Scale, the Life Experience Questionnaire and the State Trait Anxiety Inventory (see description of the questionnaires in Section 3.3), and decision making, measured with the analogies task developed by Keinan (1987). As mentioned in Section 4.1.1, the analogies task measures the ability to select the correct answer out of six alternatives. In addition to errors, dysfunctional strategies can also be assessed using this task. The study's results revealed that state anxiety was related to the number of errors in the analogies task whereas critical life events and daily hassles were not. A moderated regression analysis revealed that critical life events were related to the number of errors as well as dysfunctional decision strategies only in participants who are sensitive to inner sensations such as stress reactions. Daily hassles were also related to the number of perseverations in this subgroup of participants. Thus, while acute anxiety was directly related to poor performance, chronic stress was only related to poor performance in individuals who are sensitive to experience stress reactions.

4.2.2. Altered feedback processing/altered reward and punishment sensitivity

One study (Gray, 1999) examined the relationship between stress in students and performance in a monetary decision-making task that occurred uncertain conditions. In this task, larger long-term vs. smaller short-term rewards are compete with each other, and the contingencies of each choice are implicit. Thus, decisions must be made based on feedback from previous decisions. Students who reported high stress due to impending exams were compared with students who did not report high stress due to impending exams and students without impending exams. The low-stress and the non-exam group earned more money than the stress group. Furthermore, the stress group was faster in making decisions than the other groups. Results indicate that a high current stress level is detrimental for making advantageous decisions in the task used.

Few studies have investigated decision making and current stress levels using questionnaire assessments, and only one recent study has investigated the relationship between basal cortisol levels and performance in the IGT (van Honk et al., 2003). The results indicated that low basal cortisol levels were related to disadvantageous decisions and the loss of money. The authors concluded that low basal cortisol levels caused high reward dependency and low punishment sensitivity through attenuated corticotropin-releasing hormone gene expression in the amygdala, which led to weakened fear. This finding contradicts previous results that indicated a relationship between acute cortisol response and disadvantageous decisions in the IGT (van den Bos et al., 2009).

4.2.3. Conclusion: decision making under natural stress levels

The results from studies that have investigated the relationship between natural stress levels and decision making are generally consistent with studies that have investigated acutely induced laboratory stress and decision-making performance, i.e., current stress is thought to relate to dysfunctional strategy use (Baradell and Klein, 1993), altered feedback processing, heightened reward sensitivity and lowered punishment sensitivity (Gray, 1999). Additionally, critical life events and daily hassles also mediate decision making, but only in those participants who are sensitive to inner sensations, such as stress reactions, that follow critical life events or daily hassles (Baradell and Klein, 1993). One study produced contradictory results compared with studies that investigated decisions that were made under acute laboratory stress (van Honk et al., 2003). The authors found that low basal cortisol levels are related to dysfunctional decisions in the IGT. They considered this situation parallel to the situation of participants with primary psychopathy, who also have low cortisol levels, and who possess high reward dependency and low punishment sensitivity. However, this contradictory finding is consistent with the assumption that chronic stress can also be related to a blunted morning cortisol reaction (Pruessner et al., 1999) or to reduced cortisol reactions that occur under challenge (Rydmark et al., 2006). Thus, low basal cortisol levels may reflect chronic stress that is related to decision-making impairments. This finding would also support the results of the studies that investigated the effects of acute stress on decision-making performance.

4.3. Decision making in stress-related disorders

Stress is discussed as a pathogenetic factor in many psychiatric and psychosomatic disorders, such as depression, general anxiety disorder, borderline personality disorder, post traumatic stress disorder, dissociative disorders, burn out syndrome and fibromyalgia (reviews in Heim et al., 2000; Holsboer, 2001; Wingenfeld et al., 2010). Particularly, a dysregulation of the HPA-axis is thought to play a major role in the genesis of stress-related disorders. Early life stress and traumatic events are considered underlying mechanisms for a dysregulation of the HPA-axis. They are thought to induce a hyper-reactivity of the central corticotropin releasing system (Heim and Nemeroff, 2001) and may change the normal functioning of glucocorticoid receptors (McGowan et al., 2009). Early life stress is also thought to impact the development of the prefrontal cortex, which may lead to both a helpless response to stressors and to executive dysfunctions (review in Loman and Gunnar, 2010). Thus, early life stress is proposed as a risk factor for the development of psychiatric and psychosomatic disorders and neurocognitive deficits, but there is also evidence that patients, who suffer from these disorders also currently experience chronic and extreme stress. Therefore, these patient groups should be taken into consideration when investigating decision making under extreme and chronic stress levels. However, one must keep in mind that stress is considered as one pathogenetic factor among many. Nevertheless, studies of these patient groups may provide insights into the potential relationship between chronic stress and decision making that cannot be obtained using experimental designs in healthy participants. The studies that investigated decision making in patients who suffer from depression and post traumatic stress disorder are described below. Note that this review only describes studies about those disorders that have been directly have examined in conjunction with decision-making behavior.

4.3.1. Depression

Depression is commonly associated with hypercortisolism both in the morning (e.g., Aubry et al., 2010) and under challenge (e.g., Aubry et al., 2007; Kunugi et al., 2004). In atypical depression, no such pattern has been observed, and in some cases, a decreased cortisol secretion was observed (see Gold and Chrousos, 2002). In addition to the altered cortisol secretion that was observed in a substantial number of patients, metabolic abnormalities in cortico-limbic circuits have been observed. Hyperactivity of limbic structures during induction of negative affect has been reported frequently (Fitzgerald et al., 2008; Kessler et al., 2011; Mayberg, 1997; Siegle et al., 2002). Conversely, the activation rate of the dorsolateral prefrontal cortex has been found to decrease (Drevets, 1999; Harvey et al., 2005). These factors have been purported to interact with each other, i.e., that sustained emotional reactivity may result from decreased executive control. Empirical evidence supports this assumption. A decreased relationship between amygdala activity and activity of the dorsolateral prefrontal cortex has been observed (Siegle et al., 2007). In summary, these findings suggest that decision making may be altered in patients who suffer from depression. This alteration may be partly explained by an interaction between the HPA-axis and functional brain changes. Indeed, decision-making deficits are one diagnostic criterion for major depressive disorder (American Psychiatric Association, 1994).

Empirical evidence also suggests that patients who suffer from depression show alterations in neuropsychological decision-making tasks. One case study of a single individual indicated that the patient was severely impaired in the GDT, which mirrored her everyday decision-making difficulties (Brand et al., 2004a). Another recent study examined decisions made by pediatric patients using a modified CGT and also assessed neural responses (Forbes et al., 2006). While the authors found no behavioral differences between patients and control participants, the neural responses differed during anticipation and in the reward phase of the task. More precisely, participants who suffered from depression exhibited less neural response in reward related brain areas. Some recent studies have measured IGT performance in patients who suffer from depression. Cella et al. (2010) found that patients with depression performed worse than control participants in both the standard IGT and a version in which the contingencies of reward and punishment change. The authors concluded that altered sensitivity to reward and punishment and difficulties in re-learning contingencies were responsible for disadvantageous decisions. Must et al. (2006) found similar results using the standard IGT. The authors also used a modified version of the task in which the advantageous decks offered immediate large punishments followed by even larger gains. In this task version, the patients performed as well as control participants, but the authors come to the same conclusions as Cella et al. (2010) concerning reward and punishment sensitivity. Another recent study (Shankman et al., 2007) examined reward sensitivity in depression more directly by recording electroencephalogram waves while the participants played a slot machine game. Patients with early onset depression did not exhibit the expected increase in left frontal activity during reward processing. However, other results conflict with those found above. Smoski et al. (2008) found better IGT performance in depressed patients compared with healthy participants. The authors concluded that patients with depression avoid the potential high rewards in the task the same way they do in everyday life. Patients with partially remitted depression did not differ from healthy control participants in their IGT performance (Westheide et al., 2007), which indicates that performance is state dependent. Taken together, the results from these studies suggest that some patients who currently suffer from depression show altered decision making or altered neural responses while making a decision. However, the moderating or mediating roles of subjectively experienced stress and endocrine levels of stress reactions on decision making in patients with depression must be investigated systematically in future studies.

4.3.2. Posttraumatic stress disorder

Posttraumatic stress disorder is associated with heightened baseline catecholamines (Yehuda et al., 1998) and baseline hypocortisolism (Neylan et al., 2005; Yehuda et al., 2005). However, when exposed to an emotional challenge, patients appear to hypersecrete cortisol (Elzinga et al., 2003; Lieberzon et al., 1999). On a functional level, a number of studies indicate increased metabolism in the amygdala under resting state conditions and under emotional challenge (Bremner et al., 2005; Chung et al., 2006; Rauch et al., 2000; Semple et al., 2000). Conversely, the medial prefrontal cortex shows decreased metabolism under resting conditions and under challenge (Britton et al., 2005; Hou et al., 2007; Semple et al., 2000). Again, it has been proposed that a hyperresponsive amygdala cannot be regulated by a hyporesponsive prefrontal cortex, which may lead to deficits in emotion regulation and to impaired extinction of traumatic events. The results about hippocampal metabolism under resting state conditions and under challenge are currently inconsistent. While some studies found decreased metabolism (Astur et al., 2006; Bremner et al., 1999; Molina et al., 2010), others found an increased metabolism (Geuze et al., 2007, 2008; Semple et al., 2000). One result that has been replicated repeatedly is a volume decline of the hippocampus (reviews in Karl et al., 2006; Smith, 2005); however other results contradict this finding (e.g., Bonne et al., 2001; Carrion et al., 2001; Pederson et al., 2004). Decision-making deficits are not core symptoms of posttraumatic stress disorder, but the patients' endocrine, functional and structural brain changes suggest that decision-making abilities may also be altered.

Empirical evidence concerning decision making in posttraumatic stress disorder is scarce so far. One recent study (Sailer et al., 2008) investigated patients and healthy controls in a decision-making task during which neural responses were measured. The task (adapted from Gehring and Willoughby, 2002) consisted of gains and losses that followed a choice pattern that the participants could learn from feedback. The patients differed from control participants both behaviorally and on the neural level. The patients learned the correct response pattern more slowly than the control participants. Functionally, the patients and the control participants differed in their neural responses to gains but not losses. During the processing of gains in the late phase of learning, patients showed lower activations than the control participants in the nucleus accumbens and the medial prefrontal cortex. These results were interpreted as reduced reward sensitivity. Future studies are needed to systematically examine decision-making performance in patients with PTSD to better understand the potential link between extreme stress and decision making.

4.3.3. Conclusion: decision making in stress-related disorders

Studies of decision making in patients with stress-related disorders offer the option of investigating persons suffering from severe and chronic stress that cannot be induced experimentally. Studies of patients who suffer from depression and posttraumatic stress disorder have been described exemplarily for this line of research. The results from these studies indicate altered decision making in these patient groups, predominantly a decreased performance or a decreased neural response. The results are interpreted as reflecting alterations in strategy use, feedback processing, reward sensitivity and punishment sensitivity. One can speculate that the interaction between HPA-axis dysregulation and metabolic brain changes is one underlying mechanism of decision-making impairments. Interestingly, in the patient groups described, heightened and lowered basal levels of cortisol were observed, both of which have been associated with poor decision making in healthy participants (Putman et al., 2010; van den Bos et al., 2009; van Honk et al., 2003). However, it is not currently possible to determine whether decision-making difficulties are partly attributable to current stress and the dysregulation of the stress system or to overwhelming factors, such as the emotional/cognitive deficits associated with the respective disorder. To fill this gap, future research should address the potential relationships between current stress levels/current hormonal status and decision-making performance in patients who suffer from stress-related disorders. In addition to depression and posttraumatic stress disorder, there are many other disorders that are considered stress-related, such as burn out syndrome or general anxiety disorder. Disorders that are directly related to a dysfunction of the HPA-axis, such Cushing's syndrome, could also provide insights into the relationship between cortisol levels and decision making. So far, no studies investigating decision-making performance in these patient groups have been published internationally. Future research should also determine if there are any differences in decision making in chronic stress populations versus acutely stressed participants or healthy participants with high natural stress levels.

5. General discussion

5.1. Consistent results

Results from the studies that were included in this review support the assumption that stress affects decision making. If stress confers an advantage or disadvantage in terms of outcome depends on the specific task or situation. Studies that investigated decision-making performance under acute laboratory stress in healthy participants indicated that stress may alter the underlying mechanisms of decision making, such as 'strategy use,' 'adjustment from automated response,' 'feedback processing' and 'reward and punishment sensitivity.' It is thought that decision situations that vary in their degree of uncertainty invoke the above-mentioned underlying decision mechanism to different extents. Decision situations that offer explicit rules and low uncertainty chiefly require strategy use; decision situations that present some degree of uncertainty require the decision maker to balance automated and calculative responses; and decisions that are made under high uncertainty particularly require feedback processing. Reward and punishment sensitivity should play a role in all situations that offer reward or punishment (see Section 3.1). However, most of the studies reviewed in this paper are not suited to address which specific decision-making component has been affected by the stressor. One exception to this lack is the study by Keinan (1987), in which attention and decision strategies were monitored and were observed to decrease under stress. Studies from other lines of research support the assumption that stress may interfere with executive functions, such as working memory (e.g., Schoofs et al., 2008, 2009), categorization and set shifting (McCormick et al., 2007). The insufficient balance between automatic response tendencies and controlled rational adjustment under stress is attributed to an exaggerated reliance on lower level automatic response tendencies and to a decrease in controlled cognitive processes. This reliance on lower level systems should make participants particularly prone to framing effects when stressed. The link between stress and exaggerated reliance on lower level systems has not been tested directly, but results are in line with those previously mentioned; i.e., cognitive resources such as executive functions required for making adjustments are supposed to be deteriorated by stress. Altered feedback processing has been proposed to underlie changes in decision making, particularly under conditions of high uncertainty. Recent studies have addressed this mechanism more directly. Stress reduced participants' explicit knowledge of action-outcome contingencies in an instrumental learning task (Schwabe and Wolf, 2009) and reduced punishment learning (Petzold et al., 2010). Working memory is also prone to stress-induced changes that may influence feedback learning. While some authors consider working memory an important mediator for learning under uncertain conditions (Hinson et al., 2002; Jameson et al., 2004), others emphasize that learning through somatic markers may occur with low executive involvement (Turnbull et al., 2005) and without intact episodic memory (Turnbull and Evans, 2006). Reward and punishment sensitivity should play a role in all decisions that offer reward or punishment. Stress-induced changes could moderate many decisions, but the studies reviewed provide mixed results. While some studies indicate that stress led to a focus on potential high short-term rewards and a neglect of potential high long-term punishments (e.g., Putman et al., 2010; Starcke et al., 2008), one study demonstrates the opposite pattern (Takahashi et al., 2007). The results from studies that examined decision making in relation to natural stress levels in healthy participants generally support the results from the studies that used acute stress induction. More precisely, natural stress levels that are assessed by questionnaires are related to dysfunctional strategy use, altered feedback processing and altered reward and punishment sensitivity.

Stress-induced changes are largely attributed to physiological and endocrine stress reactions that affect the brain regions that are associated with intact decision making for the particular situation tested. Regions that are known to underlie decision making, such as prefrontal, limbic and basal ganglial regions, have numerous receptors for stress hormones. These regions also show changed neural activation under conditions of stress, predominantly in those participants who exhibit substantial cortisol responses (see Section 3.4). Therefore, it is not surprising that some studies did not find an overall effect of stress induction on decision making, but did find a relationship between individual hormonal stress response and performance (Starcke et al., 2011; van den Bos et al., 2009). Animal studies reveal that glucocorticoids activate dopaminergic neurons and lead to an increased release of dopamine in the nucleus accumbens (George and Koob, 2010; Shaham et al., 2000), which is thought to amplify reward salience. Increased reward salience under stress has also been postulated for humans, particularly in the addiction literature (Buchmann et al., 2010; Lemmens et al., 2011; Thomas et al., 2011). However, the exact mechanisms between cortisol secretion, increased reward salience and the addictive behavior remain to be elucidated.

In summary, studies indicate that stress can lead to a performance shift in decision making. Stress likely triggers cardiovascular, hormonal and neural reactions that may affect fine-tuned decision making. This appears to be detrimental in situations that require risk avoidance, strategy use or the reliance on higher level systems in general. There are, however, also situations in which increased risk taking, heightened reward sensitivity and automatic processing may be beneficial. This corroborates the proposed evolutionary value of 'fight-or-flight' stress responses. Additionally, if stress is not perceived as a threat but as a challenge, cardiovascular reactions may occur that provide even more cognitive resources and allow more fine-tuned decision making compared to resting conditions (see Kassam et al., 2009). Fig. 2 illustrates the potential effects of stress on decision making. These factors are most likely moderated and mediated by several individual factors, as suggested by the convergent results of the studies reviewed above.

5.2. Implications

If the effects of (high) stress on decision making that were found in the laboratory studies reviewed could be transferred to real-life decision making, the implications would be far-reaching. As mentioned in the introduction, many important real life decisions must be made under stressful circumstances, e.g., in traffic situations, during examinations, financial decisions or in emergency situations. Additionally, recent studies have noted that difficult decisions are also accompanied by stress reactions. In financial traders, who are considered professional decision makers, electrodermal activity and cardiovascular variables were related to the volatility of the market (Lo and Repin, 2002). The traders'

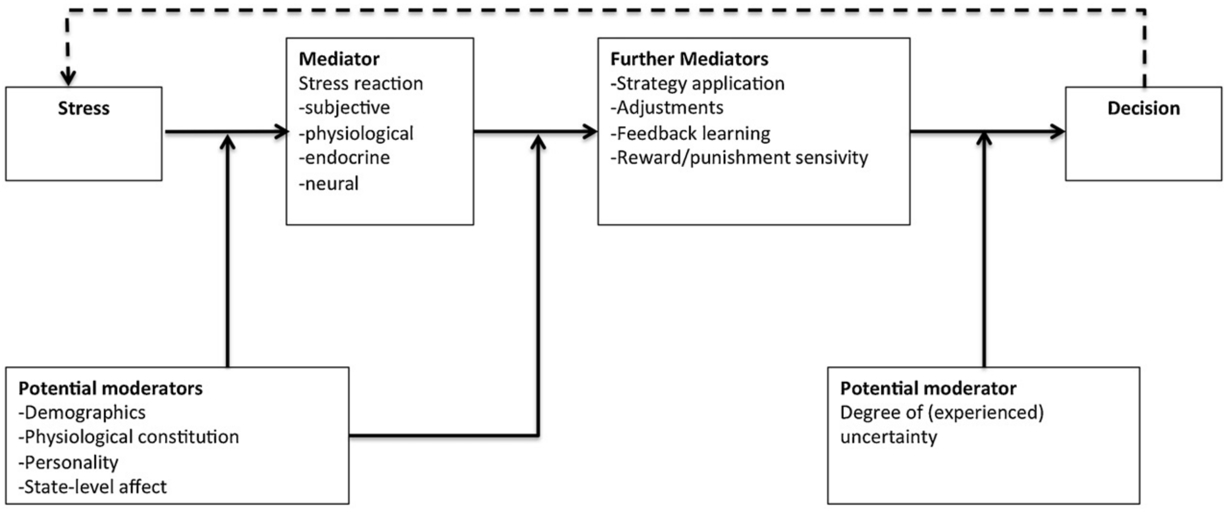

Fig. 2. Proposed mediators and moderators between stress and decision making.

cortisol levels were also related to the variance of the traders' returns and to the volatility of the market, independent of the overall economic return (Coates and Herbert, 2008). Thus, decisions that are made under uncertain conditions appear to be associated with physiological and endocrine stress reactions. These decisions in particular are associated with variation and volatility, which likely reflects uncontrollability and unpredictability. That the relationship between decision situations and stress reactions may be reciprocal enlarges both the scope and the impact of how decisions are affected by stress. Thus, if the decision-making process is affected by not only external stress but also stress related to the decision itself, then many difficult decision situations could result in suboptimal decisions. Some professions are trained to deal with stressful situations (pilots or emergency doctors), but whether this prevents them from making suboptimal decisions under real conditions is questionable. Most people are not specially trained to make optimal decisions in all of the situations that occur under suboptimal circumstances such as stress. This reciprocal relationship between a difficult decision situation, stress reactions and the subsequent effects of stress reactions on the quality of the decision has not been investigated in laboratory experiments to the best of our knowledge.

The review proposed that the effects of stress on decisions are also relevant to public health by increasing the risk for unhealthy decisions, such as smoking, drinking or unhealthy diet (Juster et al., 2010; McEwen, 2008; Schneiderman et al., 2005). Recent reviews imply that the HPA-axis plays a crucial role in developing and maintaining substance abuse. This effect has been documented in both animal studies (Koob, 2008) and human studies (Uhart and Wand, 2009). Experimental studies of humans that induce stress and then measure the subsequent substance (ab)use are rare due to ethical reasons. Nevertheless, some studies investigated the effects of acute laboratory stress on substance consumption and relapse in alcohol- and tobacco-addicted participants and the effects of stress on eating behavior in overweight participants or participants with eating disorders. The results from these studies indicate that acute stress leads to increased alcohol consumption in alcohol-dependent participants (Thomas et al., 2011), increased cigarette craving in smokers (Buchmann et al., 2010) and increased food intake in overweight participants (Lemmens et al., 2011). While chronic alcohol consumption has been associated with high baseline cortisol levels (Gianoulakis et al., 2003) and nicotine consumption acutely stimulates the HPA-axis (Matta et al., 1998), the acute response to a psychosocial stressor appears to be blunted in participants who regularly drink, smoke or have disordered eating behavior (al'Absi et al., 2005; Ginty et al., in press; Higley et al., 2011). This may reflect some processes of habituation on an HPA-axis level, but nevertheless, reduced functioning of prefrontal and limbic regions in the course of the disorder. The impacts of the results reviewed in this article on a better understanding of a broader range of everyday life decisions and the development and maintenance of psychological disorders are still speculative. However, this review may inspire future research to elucidate the still-unknown pattern of potential interactions between stress, the individual factors that mediate stress responses and dysfunctional behavior.

5.3. Limitations: individual factors as potential moderators and mediators

The studies reviewed have some limitations that should be addressed here. First, the concepts of stress and decision making are both quite heterogeneous. The laboratory stressors that were used in the studies differed in their timing (prior to the decision-making task vs. ongoing) and operationalization (physical or socio-evaluative threat) and likely also differed in their intensity (e.g., unsolvable anagrams vs. announced tear gas drill). The decision situations varied in terms of their degree of uncertainty and in terms of other factors, including topic (e.g., moral decisions vs. food choice) or involvement (e.g., earning money in the Dictator Game vs. earning fictitious money in gambling tasks). Thus, more studies are needed to support and generalize from the existing results.

Second, even the same tools may affect individuals differently because the participants display substantial variance at baseline during decision-making tasks. Additionally, the same stressor may lead to different stress reactions. Individual factors, such as susceptibility to stress, age, gender or personality variables, should moderate the effect of stress on decision making (Kudielka et al., 2009), as suggested in Fig. 2. The differential gender effects of stress on decisions that have been found in some decision scenarios were attributed to the interaction between different behavioral and endocrine stress responses and different behavioral and neural involvement in decision making in men and women. Women in particular showed risk-avoiding responses and men showed risk-seeking stress responses (Taylor et al., 2000). In decisions that were made under uncertainty, the right prefrontal areas were observed to be stronger involved in men than in women (Bolla et al., 2004;

Tranel et al., 2005). Animal (Stalnaker et al., 2009) and human studies (Lueken et al., 2009) have shown right prefrontal areas to be more sensitive to cortisol. Despite these findings, gender effects were not found in all decision scenarios. The interaction between stress and age is attributed to a volume decline in prefrontal brain regions and to decreased dopamine transmission effectiveness at higher ages (Raz, 2000; Volkow et al., 2000) but not much is known about the exact mechanisms of how age, stress and decisions interact. Personality variables are also considered potential moderators of decision-making performance that may affect stress-induced changes in decision-making performance. When automated response tendencies are exacerbated, the response preferences that were prevalent before stress exposure may play a major role. Individual preferences for risk should be considered in this context. Bechara et al. (2000a) found that 20–30% of healthy participants who did not undergo any experimental manipulation showed disadvantageous IGT performance; the authors named these participants 'high-risk takers'. Some studies reported relationships between IGT performance and facets of impulsivity (Billieux et al., 2010; Suhr and Tsanadis, 2007; Zermatten et al., 2005), whereas GDT performance does not appear to be related to measures of impulsivity (e.g., Brand et al., 2005b). Nevertheless, the possibility exists that individual preferences in terms of cognitive styles substantially moderate the effect of stress on decision making (e.g., Brand et al., 2008). There are other personality variables, such as trait anxiety that may be relevant to investigating the effects of stress on decision making (Miu et al., 2008). Participants with high trait anxiety showed dysfunctional decisions in the IGT. While this result is in line with the assumption that stress may impair decision making by eliciting task-irrelevant emotions such as anxiety, this personality variable may also be a confounding factor. Participants who differ in their trait anxiety may react in a specific way when exposed to a stressor and may also differ from each other in their decision-making performance at baseline. Another personality trait that may moderate the relationship between stress and decision making is neuroticism. A recent study found a relationship between neuroticism and poor IGT performance, but only in older adults (Denburg et al., 2009). The authors concluded that neuroticism is associated with a heightened stress response to daily stressors (Bolger and Shilling, 1991) and with elevated levels of cortisol (van Eck et al., 1996). Compared with younger adults, older adults were thought to have had more time to experience the negative effects associated with neuroticism, such as chronic stress. An interacting effect of trait-level punishment sensitivity and state-level affect on feedback processing under stress has been found by Cavanagh et al. (2011). Higher punishment sensitivity predicted better punishment learning and poorer reward learning while the opposite pattern was found in low punishment sensitive participants. Increasing negative affect was related to punishment learning performance in highly punishment sensitive participants, but the inverse relationship was observed in less sensitive participants. In summary, there are many factors that may confound the relationship between stress and decision making, such as personality, demographics, state-level affect or an interaction between the factors. However, many of the current studies that examined the effects of acutely induced stress on decision making only investigated those participants who fulfilled certain inclusion criteria due to ethical reasons. Participants with any acute or chronic diseases, psychiatric diseases, psychological problems, stressful life circumstances or signs of social phobia were excluded in many stress protocols. Thus, although subclinical personality traits cannot all be ruled out, the typical participant population in stress experiments was very homogenous. This homogeneity results in another problem, namely that the results from the reviewed studies cannot be generalized to different kinds of populations. However, the authors suppose that the aforementioned effects of stress on decision making may be even more pronounced in people who also suffer from high trait anxiety or high neuroticism.

5.4. Remaining questions

Some decision-making abilities have not yet been tested under stress, for example, intertemporal choice. A more general point is that only one study investigated the neural correlates of decisions that were made under stress (Lighthall et al., in press). The authors believe that this lack of research is a shortcoming because the results of stress effects on decisions are frequently discussed with respect to underlying neural processes. Thus, conclusions about the neural correlates of decision making under stress and the differential impact that stress has on the various brain regions that are required for different kinds of decisions are usually drawn indirectly via the neural mechanisms that are thought to underly stress and decisions. To investigate the neural correlates of stress effects on decisions more directly, more studies are needed in which acute stress induction is combined with functional imaging during subsequent decisions. One stressor that was designed for functional imaging studies is the Montreal Imaging Stress Task (Dedovic et al., 2005) which could be undertaken in the scanner immediately prior to the decision-making task of interest. The stressor combines mental arithmetic with an adaptive algorithm (inducing failure in approximately half of the trials) and a social comparison and evaluation component. However, combining stress and neuroimaging has some limitations. Neuroimaging may be stressful itself, at least to some individuals (Raz et al., 2005), making the comparison between stressed and unstressed participants more difficult. Thus, neuroimaging studies that aim to address stress and decision making should have an appropriate sample size to have sufficient stress responders in the stress group and stress nonresponders in the control group.

The results from the majority of the studies that investigated current stress levels and decision making support and supplement the results from the studies that used acutely induced stress. There is, however, one study that demonstrated that low basal cortisol levels are related to dysfunctional decisions (van Honk et al., 2003). This result appears to contradict the assumption that high cortisol secretion due to acutely induced stress is related to dysfunctional decisions in the specific task used. However, there are two lines of research that are able to explain this contradiction. First, some studies suggested that chronic stress can lead to a blunted cortisol reaction (Pruessner et al., 1999), i.e., that low basal levels could be indicators of chronic stress. If this were the case, then the assumption that high stress has deteriorating effects on the specific task could be maintained; however, the mediating role of cortisol would have to be reconsidered. Second, the results summarized above suggest that an optimal level of stress may exist for making advantageous decisions, a level that is neither too high nor too low. Such an inverted U-shaped relationship between arousal and performance was proposed long ago by Yerks and Dodson (1908), who investigated habit formation in mice. The Yerks–Dodson law has been applied to numerous fields of human performance. In memory research, an inverted U-shaped relationship between glucocorticoids and performance has been postulated for both declarative memory for neutral and emotional material and for working memory (reviews in Lupien et al., 2007; McEwen and Sapolsky, 1995). The relationship is most pronounced when the glucocorticoids are applied exogenously; for endogenous secretion after a stressor, the results vary more depending on the nature of the task, time of day, testing environment and so on. In general, it is assumed that endogenous glucocorticoid secretion mirrors the effects of applied glucocorticoids but underlies stronger variations. Studies indicate that working memory is more strongly affected by glucocorticoid levels, and some studies indicate that emotional material is more strongly affected than neutral material, but other findings contradict the latter result. The inverted U-shaped relationship is attributed to the ratio of type I to type II glucocorticoid receptors. When most of the type I and only some of the type II receptors are activated (increased type I/type II ratio), performance can be enhanced; when circulating levels of glucocorticoids are decreased or increased (low type I/type II ratio), performance can be impaired. The differential impact on working memory and declarative memory for neutral vs. emotional material is explained by the different distribution of type I and II receptors in the brain. Type I receptors are exclusively present in the limbic system while type II receptors are present in both the limbic system and the prefrontal cortex. One can speculate whether an inverted U-shaped relationship between stress and decision making may also exist. A U-shaped curve would explain why low levels of basal cortisol are suboptimal for decision making. One study (van den Bos et al., 2009) found an inverted U-shaped relationship between the level of cortisol and performance in the IGT in female participants. No studies have yet investigated the relationship between the dose of exogenously manipulated (applied or depleted) glucocorticoids and decision making. Only one study (Putman et al., 2010) compared decision-making performance after cortisol vs. placebo application, but this study did not address the issue of dose–response relationships. Most studies about stress and decision making used laboratory stressors that elicited stress responses, such as endogenous hormone secretion. Thus, currently the mathematical relationship between glucocorticoids and decision-making performance can only be calculated using individual stress responses. Patients with stress-related disorders can be considered one extreme of the inverted U-shaped relationship (intense stress). Their decision-making performance could provide knowledge that is not accessible from examinations of healthy participants. The results from patient studies generally indicate decreased decision-making abilities or decreased neural activation in patients who currently suffer from depression and posttraumatic stress disorder. However, studies that investigated decision making in patients with stress-related disorders are rare so far. Furthermore, as in all patient studies, conclusions concerning the relationship between stress and decision making can only be drawn very indirectly because stress is considered only one pathogenetic factor for each disorder. Other pathogenetic factors must be also considered, as well as confounding factors, such as emotional/cognitive deficits, comorbid disorders, medication, subclinical personality traits and so on. Therefore, patient studies that will evaluate the effects of stress on decision making should assess the patients' present stress level and stress hormones more directly. Additionally, other patient groups should be examined, such as for example patients with Cushing's syndrome who suffer from a dysregulation of the HPA-axis which leads to heightened cortisol levels (WHO, 1994). In summary, most of the studies reviewed indicate that stress responses and decision making are linearly related. However, some few studies raise the possibility that the relationship may be nonlinear and may be best represented by an inverted U.

Thus, there are many points for future research beyond supplementing, supporting and generalizing existing results. Future research should address the interactions between stress (reactions) and decision-making performance on a neural level. Generally, moderating and mediating variables such as personality, current affect and demographic variables and subjective and physiological stress responses should be examined and analyzed systematically, to better understand the paths of the effect of stress on decision making. Additionally, the relationship between current stress levels and decision-making performance should be investigated more intensively in both healthy participants and in patients who suffer from stress-related disorders. A further topic for future research could be the elucidation of the reciprocal relationship between stress and decision making, i.e., investigating how difficult decision situations elicit stress responses and how these stress responses subsequently affect the decision.

Conflict of interest

The authors declare that they have no conflict of interest.

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