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Acute psychosocial stress effects on memory performance: relevance of age and sex

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Abstract

In recent decades, there has been a growing interest in investigating the effects of chronic and acute stress on cognitive processes, especially memory performance. However, research focusing on acute stress effects has reported contradictory findings, probably due to the many factors that can moderate this relationship. In addition to factors related to the individual, such as sex and age, other factors, such as the type of memory assessed, can play a critical role in the direction of these effects. This review summarizes the main findings of our research group and others about the effects of acute psychosocial stress on memory performance in young and older people of both sexes, taking into account the type and phase of memory assessed. In our opinion, an approach that addresses individual factors and other factors related to the type of stressor and temporal relationship between exposure to the stressor and performance will contribute to better understanding the mechanisms underlying the complex relationship between acute stress and memory. Finally, some new directions for future studies on this research topic are suggested.

Keywords

Psychosocial Stress; Memory; Cortisol; Aging; Sex;

Contents

1. Introduction

In recent decades, there has been a growing interest in investigating the effects of stress on cognitive processes, especially memory performance. We are constantly exposed to different sources of stress, and memory is an essential cognitive process in the individual's functionality and independence. Understanding the effects of stress on memory is an important goal for the scientific community, due to its importance for society as a whole. Here, we review the main results found about psychosocial stress effects on memory performance, in order to shed light on the existing knowledge about the mechanisms underlying the stress-memory link.

There is a high degree of overlap between the neurobiological systems that regulate the stress response and the memory function. Stress provokes a fast activation of the sympathetic nervous system (SNS) and, shortly after, the hypothalamus-pituitary-adrenal axis (HPA-axis), resulting in a large secretion of catecholamines and cortisol (i.e. the main glucocorticoid in humans), respectively. These stress hormones exert their action on memory in different ways. On the one hand, the catecholamines (especially adrenaline), which cannot cross the blood-brain barrier, activate the β-adrenergic receptors on vagal afferents projecting to the nucleus of the solitary tract in the brainstem and directly induce the release of noradrenaline in the basolateral amygdala or indirectly via the locus coeruleus. Then, noradrenaline is bonded to β- and α_{1}- adrenergic receptors activating adenosine 3',5'-cyclic monophosphate (cAMP) and protein kinase formation (McGaugh and Roozendaal, 2002), thus affecting other brain areas such as the hippocampus and prefrontal cortex (Schwabe, Joëls, Roozendaal, Wolf, & Oitzl, 2012). On the other hand, cortisol crosses the blood-brain barrier and binds to glucocorticoid receptors (i.e. mineralocorticoid and glucocorticoid receptors) located in the hippocampus, prefrontal cortex, and amygdala. Cortisol both potentiates the noradrenaline release in the basolateral amygdala and increases the response of this area (McGaugh and Roozendaal, 2002). Clearly, the hippocampus, prefrontal cortex, and amygdala are related to the stress response, and studies have shown that changes in cortisol due to stress modify the activity of these structures (Roozendaal, 2002; Roozendaal, McEwen & Chattarji, 2009). According to the model proposed by Herman and colleagues, during acute stress, a salience network is active, whereas the executive control network is actively suppressed. However, in the recovery phase, this activation pattern changes (Herman, Henckens, Joëls & Fernández, 2014). Thus, based on this model, it seems that cortisol increases the amygdala's activity and, in turn, reduces the activity in the prefrontal cortex, whereas cortisol's effect on hippocampus activity is not clear (Herman et al., 2014). In addition to their involvement in the stress response, the hippocampus, prefrontal cortex, and amygdala are also key structures in several cognitive functions (e.g., executive function, attention), and especially memory (Lupien & Lepage, 2001; Lupien, Maheu, Tu, Fiocco & Schramek, 2007; Roozendaal et al., 2009). Stress-related changes in these brain areas result in changes in memory performance.

In recent decades, several theoretical models have been proposed to explain the effects of acute stress on memory (for a review see: Shields, Sazma, McCullough & Yonelinas, 2017). In this regard, the model proposed by Schwabe and colleagues (2012) is, in our opinion, a comprehensive model that could explain this relationship. As an integration of the initial models proposed by Roozendaal and colleagues (see Roozendaal, Barsegyan & Lee, 2008; Roozendaal et al., 2009; Roozendaal, Okuda, De Quervain & McGaugh, 2006) and Joëls and colleagues (Joëls, Pu, Wiegert, Oitzl & Krugers, 2006), the authors state that the stress response shifts the organism into two modes depending on the time course of the stress hormones. First, when the levels of cathecolamines and glucocorticoids are high, the "memory formation mode" takes place. This mode facilitates the encoding and retention (or consolidation) of important information during the stressful situation, but it is expected to impair the encoding and retention of non-relevant information that is not related to the stressor. In this mode, rapid cathecolamine and non-genomic glucocorticoid actions are involved, interacting in the basolateral amygdala. Later, when the levels of cathecolamines are low, but the levels of glucocorticoids are still high, the "memory storage mode" occurs. During this mode, retention memory is facilitated to the detriment of encoding and retrieval processes. This effect would be driven by genomic glucocorticoids actions. Importantly, this model predicts that emotional material would be more affected by stress than neutral material. Overall, this model assumes that the stress hormone levels and the memory phase are crucial factors in understanding the discrepancies in stress effects on memory.

However, many other factors related to the stressor, the memory function assessed, and the individual can also affect the relationship between stress and memory. First, it is important to note that several stress tasks have been proposed to investigate the effects of acute stress on memory function. However, depending on the nature of the stressor, the stress response elicited is different. Thus, it is well known that physical and cognitive stressors (e.g., the Cold Pressor Test, cognitive challenge) provoke a robust SNS response, whereas psychosocial stressors trigger the activation of both the SNS and HPA-axis (Allen, Kennedy, Cryan, Dinan & Clarke, 2014). The Trier Social Stress Test (TSST; Kirschbaum, Pirke & Hellhammer, 1993), considered the gold standard for investigating the response to acute stress in humans, has been widely used because it is able to induce a consistent stress response at different levels (i.e. endocrine, cardiovascular, immune, and subjective) (Kudielka, Hellhammer & Kirschbaum, 2007). Other paradigms, such as the Socially Evaluated Cold Pressor Test (SECPT; Schwabe, Haddad & Schachinger, 2008), a combination of ice water and social evaluation, has also been used, due to its social-evaluative character, which is known to boost cortisol responses (Dickerson & Kemeny, 2004). Based on the idea that both SNS (especially noradrenaline) and cortisol responses are needed to observe the stress effects described by Schwabe et al (2012), in the present review, we focus on studies that use acute psychosocial stressors (e.g., TSST, SECPT, etc.).

Recent research suggests that age is a crucial individual factor. Although a large number of studies have investigated the effects of acute stress on memory in young adults, evidence in older people is surprisingly scarce. Most of the evidence in older people comes from studies focused on the effects of chronic stress on cognitive performance. It has been proposed that chronic stress impairs memory processes that involve hippocampus and prefrontal cortex functioning (i.e., declarative memory formation) and memory processes that require complex and flexible reasoning (Sandi, 2013). By contrast, chronic stress enhances amygdala- and striatum-dependent memory processes, such as implicit memory and well-rehearsed tasks (Sandi, 2013). Furthermore, in addition to these changes in memory performance in non-stressful situations, long-term exposure to stress may also influence the link between acute stress and memory. Based on the "Glucocorticoid Cascade Hypothesis" (Sapolsky, Krey & McEwen, 1986), later known as the "Neurotoxicity Hypothesis" (Gilbertson et al., 2002), memory impairments in older people are due, at least in part, to lifetime cumulative exposure to high levels of glucocorticoids. Moreover, some authors have proposed that exposure to stress forces organisms to actively adjust to both predictable and unpredictable events (McEwen & Wingfield, 2003), producing an ''allostatic load'' or cumulative impairment (''wear and tear'') derived from the frequent or inefficiently managed activation of the mediators of the allostasis (hormones, neurotransmitters, cytokines, etc.) (McEwen, 1998). This cumulative load throughout life could become pathological due to a dysregulation of the mechanisms involved and excessive stress (''allostatic overload'') in some cases. In the long term, changes in the brain provoked by stress may affect how individuals respond to it and the way stress hormones influence memory processes. In fact, studies have proposed that the consequences of excessive exposure to cortisol across the lifespan produces progressive damage to brain structures associated with stress (McEwen & Wingfield, 2003) and a down-regulation of the glucocorticoid receptors in the hippocampus (Sapolsky et al., 1986). Along these lines, several studies have found a reduction in the density and sensitivity of the cortisol receptors with age, especially in some areas of the prefrontal cortex and hippocampus (Bhatnagari et al., 1997; Giordano et al., 2005; Gupta & Morley 2014; Heffelfinger & Newcomer, 2001; Heuser et al., 2000; Mizoguchi et al., 2009; Newcomer, Selke, Kelly, Paras & Craft, 1995; Nichols, Zieba & Bye, 2001; Perlman, Webster, Herman, Kleinman & Weickert, 2007). Together, the changes in the aging brain due to stress might contribute to a decrease in older people's sensitivity to acute increases in cortisol levels (Heffelfinger & Newcomer, 2001; Newcomer et al., 1995). In addition, studies have found a reduced integrity of the locus coeruleus, the brain area with the greatest density of noradrenergic neurons, and a decline in noradrenergic modulation in aged animals (Arnsten & Goldman-Rakic, 1985a; 1985b). This area participates in the connections between key regions involved in memory function, such as the hippocampus, the amygdala, and the prefrontal cortex. Moreover, under stressful situations, the locus coeruleus promotes the activation of the basolateral amygdala, an effect that is needed in order to observe cortisol effects on memory performance. Thus, these age-related changes might contribute to a decrease in older people's sensitivity to acute increases in both cortisol and cathecolamine levels.

In addition to age, another important individual factor to take into account is sex, as well as the sex hormone status, with data showing sex-related differences in the stress response and its effects on memory performance (Shields et al., 2017; Pulopulos, Hidalgo, Puig-Perez & Salvador, 2018). Research has established that men normally have higher cortisol responses to social stress than women in both young and older people (for reviews see: Kudielka, Hellhammer & Wust, 2009; Pulopulos et al., 2018). Moreover, the menstrual cycle phase is also involved in the cortisol response to stress in women (Kirschbaum, Kudielka, Gaab, Schommer & Hellhammer, 1999; Rohleder, Wolf, Piel & Kirschbaum, 2003; Strahler, Mueller, Rosenloecher, Kirschbaum & Rohleder, 2010). Studies investigating the impact of age on the stress response to psychosocial tasks suggest that men, rather than women, would show an increased cortisol response with age (Kudielka, Buske-Kirschbaum, Hellhammer & Kirschbaum, 2004; Strahler et al., 2010). However, although sex, sex hormonal status, and age can modulate the cortisol response to psychosocial stress, this does not seem to be the case for salivary alpha-amylase (i.e. an indirect indicator of SNS activation, Granger, Kivlighan, El-Sheikh, Gordis & Stroud, 2007;

Nater & Rohleder, 2009; Rohleder & Nater, 2009) response (Almela et al., 2011b; Hidalgo, Almela, Villada & Salvador, 2014; Hidalgo et al., 2015). Hence, given that there is sufficient evidence about the importance of these individual factors in moderating the effects of acute stress on memory, this review will be organized around them.

This paper presents an overview of the findings obtained by our research group and others about acute psychosocial stress effects on memory performance in healthy people. Following Schwabe and colleagues (2012), we aim to summarize findings of studies investigating the effects of stress on encoding, retention, and retrieval of declarative memory for neutral and emotional material, and the effects of stress on working memory. We will also describe the effects of stress on non-declarative memory, a type of memory process that has received little attention in human research. Considering previous evidence suggesting age- and sex-related differences in the neuroendocrine mechanisms underlying the stress response and memory processes, in this review we will focus on the role of participants' age and sex as critical factors in understanding inter- individual differences in stress-related effects on memory performance. Finally, we draw some conclusions and raise future research questions.

2. Acute psychosocial stress effects on memory in healthy young men and women

The effects of stress on memory depend on the type of memory (i.e. declarative, working, and non-declarative memory), as well as the memory phase assessed (i.e. encoding, retention, and retrieval). Thus, in the following sections, the main findings related to these factors will be addressed.

2.1. Declarative memory

The relationship between stress and declarative memory, which requires the conscious recollection of previous experience (Milner, Squire & Kandel, 1998), has been more thoroughly investigated in young people. However, it is important to emphasize that, depending on when individuals are stressed, the stress effects observed will be different, given that the stress will impact different memory phases. Thus, to study the *stress effects on encoding*, the stress should be applied prior to or during the encoding phase. To investigate the *stress effects on retention* (or consolidation) of material, the stressor should be applied immediately after the encoding phase. Finally, to study the *stress effects on retrieval*, the stress should be applied prior to or during the retrieval phase. However, stress effects are not always studied in only one memory phase. In other words, sometimes the design used does not make it possible to distinguish what memory phase is affected by the stress. According to Shields et al. (2017), in studies that apply the stressor prior to or during the encoding phase, with a short interval between encoding and retrieval (< 90 min), the stress effects observed can be on encoding, retention, and retrieval. However, in studies that apply the stressor shortly after the encoding phase, with a short interval between encoding and retrieval (<90 min), the stress effects observed can be on retention and retrieval. Therefore, to clarify the psychosocial stress effects on declarative memory performance, the following sections focus on describing the main findings found, considering the different phases (see Table 1 for a complete list of these studies). Finally, the valence (i.e. emotional and neutral) of the material to be remembered seems to be a factor influencing the stress effects on memory performance (Cahill, Gorski & Le, 2003), in addition to the type of memory task (verbal and visual).

2.1.1. Psychosocial stress prior to or during encoding

As mentioned above, in some studies it is impossible to know what memory phase is affected by stress (encoding, retention, or retrieval) because the stressor was applied prior to or during the encoding, and the delay between encoding and information retrieval is short (less than 90 min). Some of the studies employing this design failed to find stress effects (Beato, Cadavid, Pulido & Pinho, 2013; Elzinga, Bakker & Bremner, 2005; Hidalgo et al., 2012; 2014; Hoffman & al'Absi, 2004; but see: Smeets, Jelicic & Merckelbach, 2006b for impairing effects). Other studies, although failing to show stress effects, reported a negative (Kirschbaum, Wolf, May, Wippich & Hellhammer, 1996; Wolf, Schommer, Hellhammer, McEwen & Kirschbaum, 2001) or positive (Nater et al., 2007) correlation between the cortisol response to stress and memory performance.

It is important to note that in these studies, the stress effects were investigated with neutral material alone. However, when both neutral and emotional material had to be remembered, different stress effects were found depending on the valence factor. For example, two studies found stress-related negative effects on neutral material, but positive effects on emotional material (Jelicic, Geraerts, Merckelbach & Guerrieri, 2004; Payne et al., 2006). Other studies reported non-effects on emotional material, but negative (Smeets et al., 2006b) and positive (Schwabe, Bohringer, Chatterjee & Schächinger, 2008) stress effects on neutral material. By contrast, Zoladz et al. (2013) found non-effects on neutral material, but impairing stress effects on emotional material. Finally, the stress effects found also depend on the type of memory assessed. As Luethi, Meier and Sandi (2009) reported, the TSST did not affect verbal memory, but it enhanced spatial memory.

Only a few previous studies investigated sex-related differences and considered the menstrual cycle, reporting mixed results. Whereas no differences were found between men and women using oral contraceptives (Schwabe et al., 2008a) or women in the luteal phase of their menstrual cycle (Smeets, Jelicic & Merckelbach, 2006a; Smeets et al., 2006b), a negative correlation was found between cortisol response and memory performance in men, but not in women in the luteal phase (Wolf et al., 2001b). When we studied men, women in the follicular phase, and women using oral contraceptives, no effects of the TSST were found on recall of a neutral word list (Hidalgo et al., 2012). In a later study, we exposed men and women in the follicular phase, women in the luteal phase, and women using oral contraceptives to the TSST or a control task. Results showed that, in the control condition, all the groups of women recalled more words than the men. However, in the stress condition, the men's performance improved, although only to the level of the women (Espin et al., 2013).

Taken together, studies investigating the effects of stress before memory encoding, retention, and retrieval have observed mixed results, possibly related to the idea that stress enhances encoding but impairs memory retrieval. According to Schwabe et al. (2012), because both learning and information retrieval occurred under stressful conditions, the enhancing effects of stress on retention might have been cancelled out by impairing effects on retrieval. However, sex-related differences in this effect have been observed, and more research is needed to understand whether sex, the menstrual cycle phase, and contraceptive use should be considered moderating factors of the effects of stress.

When studying the stress effects only on the encoding phase, it is difficult to draw general conclusions about the direction of these effects, in spite of the large number of existing studies. For example, worsening (Elzinga et al., 2005; Maheu, Collicutt, Kornik, Moszkowski & Lupien, 2005; Quaedflieg, Schwabe, Meyer & Smeets, 2013; Schwabe & Wolf, 2010), enhancing (Hoscheidt, LaBar, Ryan, Jacobs & Nadel, 2014; Smeets, Giesbrecht, Jelicic & Merckelbach, 2007; Wiemers, Sauvage, Schoofs, Hamacher-Dang & Wolf, 2013; Wiemers, Sauvage & Wolf, 2014), or even no effects (Domes, Heinrichs, Rimmele, Reichwald & Hautzinger, 2004; Weymar, Schwabe, Löw & Hamm, 2012; Zoladz et al., 2013) have been found on both long- and short-term memory performance. However, in some cases, the results are complex, and it is necessary to contemplate other moderating factors. Thus, regarding the valence of the material to be remembered, the stressor (i.e. TSST) disrupted memory of neutral material, but it enhanced memory of emotional material (Payne et al., 2006; 2007). By contrast, other stressors (i.e. SECPT) only affected the neutral material, but not the emotional material, enhancing the recall of neutral words (Schwabe et al., 2008a) and the discrimination of neutral pictures (Wirkner, Weymar, Löw & Hamm, 2013). Importantly, Zoladz et al (2011) investigated the impact of the time delay between the stress application and the learning, showing that if stress (i.e. SECPT) was applied immediately before acquisition, enhancing effects on positive word recognition were found. However, if the stressor took place 30 minutes before learning, impairing effects on free recall of negative words appeared (Zoladz et al., 2011). Moreover, as Shields et al. (2017) observed, the enhancing effect of stress on encoding is especially observed for material that is closely related to the stressor.

In addition to the kind of material to be remembered and the time delay between the stress onset and learning, another moderating factor of psychosocial stress effects on acquisition could be the type of memory task. For example, Cornelisse, van Stegeren and Joëls (2011) did not find TSST effects on a free recall task, but the same stressor enhanced recognition of negative pictures. Consistent with the results found by Wolf (2012), the existence or not of immediate recall once the learning has taken place seems to affect the psychosocial stress-related effects on memory acquisition. Therefore, the TSST did not affect memory performance when there was an immediate recall attempt after learning; however, the stressor enhanced memory for negative pictures. Taken together, these results suggest that the immediate recall attempt can interfere with the beneficial effects of pre-acquisition stress on emotional memory (Wolf, 2012).

Finally, despite the large number of studies carried out on declarative memory, it is worth noting that sex, menstrual cycle, and contraceptive use have been understudied. Most of the studies only included only men (Domes et al., 2004; Maheu et al., 2005; Quaedflieg et al., 2013; Weymar et al., 2012; Wolf, 2012), only women (Elzinga et al., 2005), or mixed-sex samples (Hoscheid et al., 2014; Wirkner et al., 2013; Zoladz et al., 2011). When men and women were compared without controlling the menstrual phase or contraceptive intake, the majority of the studies reported no sex-related differences (Payne et al., 2007; Schwabe & Wolf, 2010; Wiemers et al., 2013; 2014). Only two studies clearly investigated the role of the menstrual phase (Smeets et al., 2007) or the intake of contraceptives (Schwabe et al., 2008a), compared to men, although no differences were found. However, sex differences have also been found, with the stress effects being more pronounced in men. For example, Payne et al. (2006) reported a negative correlation between cortisol levels and memory performance in men, but not in women. Accordingly, Zoladz et al. (2013) found that only male cortisol responders recalled fewer words, although the TSST also led young men to improve their recognition of negative pictures (Cornelisse et al., 2011). Hence, there is a need for more research that addresses all of these factors related to the effects of psychosocial stress on declarative memory acquisition.

In conclusion, the results reported by the studies mentioned above suggest that if stress only affects encoding, it enhances memory performance when encoding occurs immediately after the stress task and when the information to be remembered is connected to the stressful event. Moreover, the effect seems to be stronger for emotional material and in men. However, mixed results have also been reported, and more research is clearly needed. For instance, the effects of the menstrual cycle phase and the use of contraceptives have hardly been investigated, and their influence on the link between stress and memory encoding is not well understood.

2.1.2. Psychosocial stress during retention

When the stressor is applied shortly after the encoding phase and the delay between encoding and retrieval is less than 90 min, stress can affect both the retention and retrieval phases, and so the stress effects cannot be distinguished. To our knowledge, only four studies have investigated the psychosocial stress effects on declarative memory performance in young people using this design, and the results are far from conclusive. Thus, while the TSST impaired both immediate and delayed recall of neutral words (Stawski, Sliwinski & Smyth, 2009) and biographical notes (i.e. social memory) (Merz, Wolf & Hennig, 2010), at the same time, it also improved internal source monitoring performance (Smeets et al., 2006c). Moreover, when the stressor used was the Fear-Factor Stress Test (FFST; a combination of TSST and CPT), visuospatial memory performance was also enhanced (Human et al., 2013). Studies that found enhanced effects of stress on memory performance only included men (Smeets et al., 2006c; Human et al., 2013), whereas when both sexes were taken into consideration, no sex differences were found (Stawski et al., 2009; Merz et al., 2010).

Only two studies have investigated the psychosocial stress-related effects on retention performance in young men and women (without controlling the menstrual cycle or the intake of contraceptives) (Beckner, Tucker, Delville & Mohr, 2006; Larra et al., 2014). These studies found that anticipation and preparation of a public speech (Beckner et al., 2006) and exposure to the SECPT (Larra et al., 2014) enhanced memory performance. This positive stress effect on memory retention was found on visual, but not verbal, neutral material related to the cortisol response (Beckner et al., 2006), whereas a positive effect was also associated with emotional faces related to SNS activation (Larra et al., 2014). No sex differences were found. Thus, as Shields et al. (2017) suggested, the valence of the material to be remembered may not be a moderator of psychosocial stress effects on memory retention, but it could be related to different components of the stress system (i.e. HPA or SNS).

2.1.3. Psychosocial stress effects prior to or during retrieval

In contrast to stress effects on retention, when stress takes place before retrieval, it usually impairs memory retrieval (Buchanan & Tranel, 2008; Boehringer, Schwabe & Schachinger, 2010; Domes et al., 2004; Espin, Marquina, Hidalgo, Salvador & Gómez-Amor, 2016; Hidalgo et al., 2015; Kuhlmann, Piel & Wolf, 2005; Li, Weerda, Guenzel, Wolf & Thiel, 2013; Schwabe & Wolf, 2014; Smeets, 2011, but see: Beckner et al., 2006; Li, Weerda, Milde, Wolf & Thiel, 2014; Schoofs & Wolf, 2009; Tollenar, Elzinga, Spinhoven & Everaerd, 2009; Wolf, Schommer, Hellhammer, Reischies & Kirschbaum, 2002, for non-effects). According to Roozendaal (2002) and Schwabe et al (2012), these different effects (i.e. enhancement of retention and impairment of retrieval) occur because cortisol has a blocking effect on retrieval processes in favor of retention processes, facilitating the consolidation of new important information that can be necessary in future situations (for a detailed review see: Gagnon & Wagner, 2016). Moreover, psychosocial stress-related retrieval impairments (Domes et al., 2004; Espin et al., 2016; Hidalgo et al., 2015; Kuhlmann et al., 2005; Smeets, 2011; Tollenar, Elzinga, Spinhoven & Everaerd, 2008) or enhancements (Oei, Everaerd, Elzinga, Van Wll & Bermond, 2006; Schwabe et al., 2009) are more robust for emotional material than for neutral material. The cortisol response seems to be especially involved in these impairing effects of stress because a negative correlation between memory retrieval and the cortisol response to stress has consistently been reported (Domes et al., 2004; Hidalgo et al., 2015; Oei et al., 2006; Smeets, 2011). In contrast to the idea that high levels of both stress-induced SNS activation and cortisol levels impair memory retrieval (Schwabe et al., 2012), Schönfeld, Ackermann and Schwabe (2014), although failing to find stress effects on memory retrieval, found that retrieval performance tested under stress was positively related to SNS activation, but not to HPA-axis activation. By contrast, retrieval performance 25 minutes after the stressor was negatively related to the cortisol response. Although these results suggest that each stress system plays a different role (HPA-axis activation would be involved in the negative effects of stress on retrieval, and the SNS would be involved in the positive effects), the question of whether the interaction between SNS activity and cortisol levels would impair memory retrieval was not investigated. Thus, based on Schwabe et al. (2012), one could expect that individuals who show both high SNS activity and high cortisol levels would show worse memory performance.

Regarding the role of sex, most of the aforementioned studies only included men (Boehringer et al., 2010; Domes et al., 2004; Kuhlmann et al., 2005; Li et al., 2013; 2014; Oei et al., 2006; Schwabe et al., 2009; Tollenar et al., 2008; 2009), women (Schoofs & Wolf, 2009), or mixed-sex samples (Wolf et al., 2002). Studies on the role of sex have generally found no sex-related differences (Beckner et al., 2006; Buchanan & Tranel, 2008; Espín et al., 2016; Schönfeld et al., 2014; Schwabe & Wolf, 2009; Schwabe & Wolf, 2014). To the best of our knowledge, only one study reported impairing effects of the TSST on free recall of emotional and neutral pictures in men, but not in women, although no sex-related differences were found in the negative effects on the recognition of positive pictures (Hidalgo et al., 2015). Moreover, only one study considered the effect of the women's menstrual cycle, finding no differences (Smeets, 2011).

In general, studies on the effects of acute stress on memory retrieval support the idea that stress-induced cortisol increases and SNS activation impair memory recall.

2.2. Working memory

To examine the effects of cortisol on working memory (WM), most studies have been performed in young people, and they have shown that stress-induced cortisol increases impair WM (Bogdanov & Schwabe, 2016; Elzinga & Roelofs, 2005; Luethi et al., 2009; Oei et al., 2006; Schoofs, Preuß & Wolf, 2008; Schoofs, Pabst, Brand & Wolf, 2013). This evidence supports the idea proposed by Roozendaal and colleagues that stress impairs WM and memory retrieval, due to the activation of membrane-bound glucocorticoid receptors and non-genomic glucocorticoid actions in the prefrontal cortex (Roozendaal et al., 2010; 2008). However, evidence of enhancing effects (Cornelisse et al., 2011; Schoofs et al., 2013; Stauble, Thompson & Morgan, 2013; Weerda, Muehlhan, Wolf & Thiel, 2010), or no effect (Hoffmann & al'Absi, 2004; Kuhlmann et al., 2005; Smeets et al., 2006b) has also been found. The WM is a PFC-dependent ability that includes both (i) the active maintenance of a limited amount of information (memory span component) and (ii) the executive function of manipulating and/or processing this information (executive component) (D'Esposito, 2007). Studies in young people have shown that WM tasks requiring executive functions (e.g. Digit Span Backward, n-back, O-Span, Letter-Number

Sequencing, and Sternberg paradigm) are more prone to being affected by cortisol than WM tasks that assess only the memory span component (e.g. Digit Span Forward) (Hoffman & al'Absi, 2004; Kuhlmann et al., 2005; Oei et al., 2006; Schoof et al., 2008; Smeets et al., 2006b). These results might be explained by the fact that WM tasks requiring executive functions are more complex, and so less interference in prefrontal cortex functioning is needed to observe behavioral effects.

Only a few studies have investigated the role of sex in the effect of stress on WM, although evidence indicates that sex differences may be a critical moderating factor. Thus, a recent meta-analysis showed that the impairing effect of psychosocial stress on WM is stronger in men than in women (Shields, Sazma & Yonelinas, 2016). We investigated this issue in a recent study (Zandara et al., 2016). We observed that, although both men and women showed a moderate cortisol response, performance on the memory span component of WM (measured with the Digit Span Forward test) was better after the TSST only in women who showed a cortisol decrease after the stress task. This result suggests that when subjects experience moderate stress, small cortisol changes would improve memory span, but only in women. As Shields et al. (2016) acknowledge, most studies have included only males or mixed samples, and further studies are clearly needed to draw solid conclusions about the role of sex in the effects of stress on WM, probably taking into account the severity of the acute stressor and the intensity of the stress response.

2.3. Non-declarative memory

In contrast to declarative memory, psychosocial stress effects on non-declarative memory performance have been studied very little. This type of memory, also known as implicit memory, given that it does not require the awareness of previous experience (Graf, Squire & Mandler, 1984), comprises priming effects, classical conditioning, and non-associative learning, as well as motor, perceptual, and cognitive skill acquisition (Daum & Ackerman, 1997). Only a few studies have investigated the impact of psychosocial stress on non-declarative memory in young people. Thus, the exposure to the TSST prior to encoding seems to affect young people differently depending on the implicit memory task assessed. Whereas it has no effects on perceptual and contextual priming, stress facilitates classical conditioning for negative (but not for positive) stimuli in young men (Luethi et al., 2009), and fear conditioning in men, but not in women (Jackson, Payne, Nadel & Jacobs, 2006). Therefore, a cognitive challenge on a word-stem completion task (i.e. priming) revealed no effects in women (Elzinga, Bakker & Bremner, 2005).

Only Jackson et al. (2006) found that this enhancing effect was related to HPA-axis activation, but there is a lack of studies about whether these effects are only related to HPA-axis activation or also to SNS activation. Therefore, we investigated whether HPA-axis and SNS reactivity (measured by cortisol and sAA responses, respectively) to psychosocial stress affects implicit memory (assessed by a priming effect task) in young men and women. We observed that acute stress applied shortly before the memory task enhanced the priming effect, and this improvement was positively related to the stress-induced sAA increase, regardless of the sex of the participants (Hidalgo et al., 2012). This finding supports the idea that stress favors learning strategies that require less conscious processing (Schwabe et al., 2007), and more specifically, that the crucial stress system to obtain this enhancement would be the SNS.

Notably, studies that included women in their samples, but did not control the menstrual cycle or use of contraceptives, failed to find stress effects on non-declarative memory performance in women (Jackson et al., 2006; Elzinga et al., 2005). However, when these variables were considered, an enhancement effect was found on priming in both women and men (Hidalgo et al., 2012).

3. Acute psychosocial stress effects on memory in healthy older people

Although a large number of studies have investigated the effects of acute stress on memory in young adults, evidence in older people is surprisingly scarce. Important changes in SNS (I.e. reduction in the locus coeruleus integrity and a decline in noradrenergic modulation) and HPA-axis activity (i.e decrease in the number and sensitivity of cortisol receptors) can be observed during the aging process, suggesting that older people might be less sensitive to the acute effects of stress on memory performance than young adults. However, only a few studies have been conducted, and much more research is needed, particularly using a psychosocial stress.

A few studies have been carried out on the effects of psychosocial stress on declarative memory in older people. In the case of the effect of stress applied prior to encoding, earlier studies did not observe any effects (Bohnen, Houx, Nicolson & Jolles, 1990; Domes, Heinrich, Reichwald & Hautzinger, 2002), whereas others observed changes in the encoding of neutral material after acute stress (Almela et al., 2011a; Hidalgo et al., 2014). However, these studies could not distinguish between the stress effects on encoding, retention, and retrieval. In addition, initial studies were carried out only in women from 41 to 69 years of age (Bohnen et al., 1990) and from 32 to 68 years of age (Domes et al., 2002); therefore, it was impossible to investigate the effect of sex. To address this issue, we performed a study with healthy older men and women (from 54 to 72 years old), and we observed that acute stress prior to encoding enhanced word span, but it also impaired immediate recall after interference in older women (Almela et al. 2011a). In addition, the cortisol response to stress was related to retroactive interference, but not to changes in memory span, suggesting that only the effect on retroactive interference was due to the stress-induced cortisol response. When this effect was explored by comparing young and older people, stress impaired immediate recall interference in older people, but not in young people (Hidalgo et al., 2014). In a recent study with older men and women, Smith, Dijkstra, Gordon, Romero and Thomas (*in press*) investigated the effect of acute psychosocial stress on encoding, but not on memory retention and retrieval. These authors failed to find stress effects on free recall of images or on the cued recall test for a video. However, they only found a minimal stress effect on errors of commission on the cued recall test for a video. Thus, participants in the stress condition left more items blank on neutral trials than participants in the control condition. Therefore, the current evidence indicates that, compared to healthy adults, the effect of stress prior to encoding in older people would be specific to memory span and retroactive interference, and no other memory process would be affected. In fact, only the effects on retroactive interference would be due to stress-induced changes in cortisol levels.

Regarding the effect of stress on memory retention, Lupien et al. (1997) observed that acute stress impaired declarative memory performance in older people. In this study, the participants were asked to recall the information shortly after (15-20 minutes) the stress induction, and so the stressor affected both the retention and retrieval phases (Shields et al., 2017). However, memory performance was measured shortly after another similar memory task was performed, and so, as observed in Almela et al. (2011a), the effect may not have been specific to memory retention, but it may have affected retroactive interference. Although both men and women were included, sex differences were not studied.

The current evidence suggests that acute stress does not affect long-term memory retrieval in older people. In a recent study, a sample of older people were asked to learn words, stories, and emotional (positive and negative) and neutral pictures. The next day, they were asked to recall this information after they had performed a stress or a control task. In contrast to what has been consistently found in young adults, we observed that acute stress did not affect long-term memory retrieval in older people (Pulopulos et al., 2013). Moreover, when we directly compared two age groups (18-35 years vs. 54-78 years) of men and women, we confirmed that stress impaired the free recall of pictures only in young men, but not in older men. Additionally, recognition performance was affected in both age groups, but this effect was not related to cortisol levels (Hidalgo et al., 2015).

When studying the effects of psychosocial stress on WM, we found that stress-induced cortisol increases did not affect WM in healthy older people (Pulopulos et al., 2015). This result agrees with studies investigating the effect of cortisol administration on WM (Porter, Barnett, Idey, McGuckin & O'Brien, 2002; Wolf et al., 2001a; Yehuda, Harvey, Buchsbaum, Tischler & Schmeidler, 2007). In this study, we performed two experiments to investigate the effects of acute stress on the memory span (i.e., active maintenance of a limited amount of information in the mind) and the executive component (i.e., manipulation of this information) of WM. The results showed that in older women (but not in men), stress enhances only the memory span component of WM. This enhancement was related to acute circulating cortisol levels, but not to the stress-induced cortisol increase, indicating that the changes in cortisol due to stress might not be responsible for the effect observed. In a previous study using a task designed to assess declarative memory, we found that stress improved the memory span in women from 54 to 72 years old (Almela et al., 2011a). As observed in Pulopulos et al. (2015), the change in memory span was not related to the cortisol response to stress. Overall, the current evidence suggests that the stress would not have a strong effect on the memory span or the executive component of WM.

To the best of our knowledge, acute psychosocial stress effects on non-declarative memory in older people have been understudied. Only two studies have been conducted, showing non-effects in older men and women (Lupien et al., 1997) and in women from middle to older ages (Domes et al., 2002).

Overall, the evidence indicates that psychosocial stress does not affect declarative, working, or non-declarative memory. However, no previous studies have investigated the effects of stress on encoding (except Smith et al., *in press*) and declarative memory retention in older people, and not enough studies have examined the role of sex and age in other types of memory (working and non-declarative memory). Thus, more research is clearly needed to understand the role of age in the relationship between stress and memory performance.

4. Concluding remarks

In this review, we have presented results and findings from studies that have investigated the effects of acute psychosocial stress on different types of memory processes in healthy young and older adults in recent years, taking into account several moderating factors, particularly age and sex (see Table 2 for a summary of the main findings).

Most of the research on the effects of stress on memory performance has been carried out in young people, and especially in young men. Overall, these studies confirm that stress enhances retention, but it impairs long-term memory retrieval and the executive component of WM (Gagnon & Wagner, 2016). By contrast, no solid conclusions can be drawn about the effects of stress on memory encoding, the memory span component of WM, or non-declarative memory. Regarding memory encoding, although the current evidence may support the idea that stress enhances encoding when they occur close together in time, this effect seems to be observed more in men. Moreover, when examining the stress effects on encoding, retention, and retrieval, mixed results have been observed. Our findings point to the role of sex, the menstrual cycle, and oral contraceptive use to explain the contradictory results for the effects of stress on memory encoding, the memory span component of WM, and non-declarative memory (Espin et al., 2013; Hidalgo et al., 2012; Zandara et al., 2016). Further studies may benefit from paying special attention to these factors. Taken together, although some of these results provide support for the model proposed by Schwabe et al. (2012), most of the studies just investigate the role of cortisol, and very few investigate the role of the cathecolamines.

Moreover, the results are not easily explained by only one model, given the complexity of the processing of psychosocial situations. Therefore, more research is still needed to better understand the effect of sex and the effect of stress on non-declarative memory.

Regarding the role of age in the effect of stress on memory performance, some data support the idea that memory performance in older people might be less sensitive to the acute effects of psychosocial stress-induced cortisol increases (Gupta & Morley 2014; Heffelfinger & Newcomer, 2001; Newcomer et al., 1995). Consistent with this idea, in older people we failed to find stress effects on WM and long-term memory retrieval, although stress only increased retroactive interference, especially in older women. Evidence from research with animals and humans also supports reduced stress and cortisol effects on memory performance in aging (Buechel et al., 2014; Porter et al., 2002; Wolf et al., 2001a; Yehuda et al., 2007). Apart from age-related changes in cortisol receptors, it is also possible that memory performance in older people is less sensitive to SNS activation in response to acute stress, given that a reduced integrity of the locus coeruleus and a decline in noradrenergic modulation have been reported in aged animals (Arnsten & Goldman-Rakic, 1985a; 1985b). Thus, we can speculate that these age-related changes could also contribute to the lack of stress effects on memory in older people.

According to Roozendaal (2002), the effect of stress-induced cortisol increases on memory performance is an adaptive mechanism that facilitates individuals' adaptation to the environment. Cortisol blocks memory retrieval processes in favor of consolidation processes, reducing the retroactive interference of previously learned information and facilitating the consolidation of new important information related to the stressor. Thus, the information related to the stressor may be recalled in future stressful situations. The current evidence implies that older people might not benefit from learning important information in stressful situations because stress does not impair long-term memory, but it increases retroactive interference. However, it is worth noting that, compared to studies performed in young adults, only a few studies have been conducted in older people. Therefore, more research is clearly needed in this field because these age-related differences might have important implications for stress-related health problems.

Although here we focus on the role of the peripheral SNS and HPA-axis activation in the impact of stress on memory performance, it is important to note that other central factors, such as serotonin and dopamine, can affect this relationship. In fact, after stress, an increase in these monoamines is found in the hippocampus, the amygdala, the prefrontal cortex, and the nucleus accumbens (Joëls & Baram, 2009). In addition, animal studies have found GC receptors in the brain areas involved in dopaminergic and serotoninergic neurotransmission, such as the ventral tegmental area and substantia nigra, and the dorsal raphe nucleus, respectively (Czyrak & Chocyk, 2001; Laaris, Haj-dahmane, Hamon & Lanfumey, 1995). It is widely accepted that dopamine and serotonin affect memory performance (Riedel & Blockland, 2015; Schmitt, Wingen, Ramaekers, Evers & Riedel, 2006). Moreover, cortisol may exaggerate dopamine actions in the prefrontal cortex (Arnsten, 2009). Age-related reductions in both dopamine (for a meta-analysis about this topic see: Karrer, Josef, Mata, Morris & Samanez-Larkin, 2017) and serotonin (Wong & Gjedde, 2009) receptors in healthy aging adults, as well as a higher number of dopamine receptors in the PFC in women (Shansky & Lipps, 2013), have been reported. Thus, in addition to the effects of sex and age on SNS activity and cortisol, differences related to dopamine and serotonin may also explain some of the discrepancies between young and older men and women.

Some other questions and issues remain unanswered. For instance, it is unknown whether memory retention is enhanced by acute stress in older people, as observed in young adults. Additionally, other types of memories also need to be investigated in older people, such as real-life memory tasks (Vogel & Schwabe, 2016), proactive memory (Glienke & Piefke, 2016), or false memory (Pardilla-Delgado, Alger, Cunningham, Kinealy & Payne, 2016). Along these lines, one type of memory that warrants exploration is prospective memory because and its ecological validity and this type of memory can allow us to discover the individual's degree of independence. In addition, studies have shown that noradrenergic activation of the amygdala is necessary in order to observe cortisol effects on memory performance (de Quervain, Aerni & Roozendaal, 2007; Roozendaal et al., 2009; 2002). However, few studies have addressed the role of SNS activation on memory performance, in contrast to what has occurred with the HPA-axis, and even fewer studies have addressed the interaction between the two stress systems. Therefore, there is clearly a need to study the interaction between the HPA-axis and the SNS on memory performance. Furthermore, in order to better understand the mechanisms underlying the impact of stress, further studies using a neuroimaging approach could examine the reduced functional amygdala activity in memory processes associated with healthy aging, suggested by some fMRI studies (Nashiro, Michiko & Mather, 2011). Finally, in the present review, only studies that used a psychosocial stressor were included, so that a comparison of different kinds of stressors would increase the knowledge about acute stress on memory performance.

Although this review provides findings from human studies, it is important to note the contribution of animal studies to knowledge about the stress effects on memory. In general, these studies reported that stress or glucocorticoid administration facilitates retention memory (Roozendaal & McGaugh, 1996; Roozendaal, Okuda, Van der Zee & McGaugh, 2006) and impairs retrieval (de Quervain, Roozendaal, & McGaugh, 1998; Diamond, Park, Heman & Rose, 1999; Roozendaal, 2004; Roozendaal, Griffith, Buranday, De Quervain & McGaugh, 2003). Moreover, in rodents, a memory retention facilitation and a retrieval and working memory impairment produced by the glucocorticoid-noradrenaline interaction have been shown (Roozendaal et al., 2008). However, although animal results support some of these findings from human studies, it is very difficult to compare the results observed with the two models, given the important differences between them, such as the different tasks usually used to assess memory performance or the sex-related differences in the corticosterone response to stress (for a review see: Goel, Workman, Lee, Innala & Viau, 2014).

In conclusion, this review demonstrates the relevance of taking age and sex into account when trying to understand the stress response and its effects on memory performance, and it shows that stress might have important and different influences on memory performance across the lifespan.

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Table 1. Psychosocial stress effects on declarative memory performance

Authors	Participants	Type of Stressor	Memory Task	Memory phase studied	Main Results
Almela et al. (2011a)	16 ♂ + 16 ♀ (PM) (54-72 years)	TSST	Neutral words	E/RT/R	Only in ♀: enhanced attention (trial 1) and impaired working memory (trial 6)
Beato et al. (2013)	Ex.1: 44 (♀: 71%) (*M*= 20.21 years) Ex.2: 54 (♀: 80%) (*M*= 19.8 years)	TSST	Neutral words	E/RT/R	Stress had no effect on true and false recognition in the two experiments Sex differences were not studied
Beckner et al. (2006)	157 (♀: 64%) (*M*= 18.77 years)	Anticipation and preparation of a public speech	Film recognition and paragraphs	RT R	Stress facilitated retention Stress did not affect memory retrieval No sex differences
Boehringer et al. (2010)	51 ♂ (*M*= 24.57 years)	TSST	Neutral and emotional words	R	Stress reduced retrieval performance In SG: participants with high changes in energetic and tense arousal showed best memory retrieval
Bohnen et al. (1990)	12 ♀ (41-49 years) 12 ♀ (61-69 years)	4-hour mental task	Neutral words	E/RT/R	No stress effects on memory performance No age differences
Buchanan & Tranel (2008)	20 ♂+ 20 ♀ (*M*= 20 years)	TSST modified	Neutral and negative pictures	R	Cortisol responders showed reduced memory retrieval Men and women in SC with no cortisol response: increased retrieval for negative pictures versus CC
Cornelisse et al. (2011)	23 ♂ + 54♀ (39 OC, 6F, 7L) (*M*= 20.44 years)	TSST	Neutral and emotional pictures	E	Stress did not affect free recall (long-term) Stress enhanced negative recognition, only in men
Domes et al. (2002)	32 ♀ (4 RC, 5 IR, 23 PM) (32-68 years)	TSST	Neutral words	E	No stress effects on memory performance regardless of experimental condition, high responders showed increased memory performance
Domes et al. (2004)	60 ♂ (*M*= 25.3 years)	TSST	Neutral and emotional words	E R	E: Stress did not affect long-term memory (1 week) R: Stress before retrieval impaired the recognition of

					positive words Positive correlation between cortisol response and errors of commission
Elzinga et al. (2005)	16 ♀ (*M*= 21.4 years)	Cognitive challenge	Paragraphs	E E/RT/R	E: Stress impaired memory performance E/RT/R: No stress effects on memory performance
Espín et al. (2013)	32 ♂ + 87 ♀ (30 F, 34 L, 23 OC) (18-25 years)	TSST	Neutral words	E/RT/R	In CC, all groups of women recalled more words than men, but these differences disappeared in the group exposed to the TSST, given that men's performance improved to the level of women's.
Espín et al. (2016)	47 ♂ + 48 ♀ SG (*M*= 19.4 years)	TSST	Neutral and emotional pictures	R	Stress did not affect free recall but impaired the recognition of positive pictures No sex differences
Hidalgo et al. (2012)	18 ♂ + 34 ♀ (17 F, 17 OC) (*M*= 21.56 years)	TSST	Neutral words	E/RT/R	Stress did not affect memory performance No sex/group differences
Hidalgo et al. (2014)	16 ♂ + 16 ♀ (PM) (*M*= 62.1 years) 18 ♂ + 17 ♀ (F) (*M*= 21.1 years)	TSST	Neutral words	E/RT/R	Stress impaired recall after interference only in the older group This effect was negatively correlated with the sAA/C ratio No sex differences
Hidalgo et al. (2015)	27 ♂ + 25 ♀ (PM) (56-76 years) 26 ♂ + 24 ♀ (18-27 years)	TSST	Neutral and emotional pictures	R	Stress impaired free recall only in young men, but only free recall of negative pictures was negatively related to cortisol response Stress impaired recognition of positive pictures in all participants
Hoffman & al'Absi (2004)	10 ♂ + 15 ♀ (*M*= 24.8 years)	Public-speaking exercise	Neutral words Paragraphs Complex Figure	E/RT/R	No stress effects on memory performance No sex differences
Hoscheidt et al. (2014)	38 ♂ + 30♀ (*M*= 19 years)	TSST	Neutral and negative pictures	E	Stress enhanced short-term (48 hours) memory Sex differences were not studied

Human et al. (2013)	38 ♂ (18-23 years)	FFST (TSST + CPT)	Complex Figure	RT/R	Stress enhanced visuospatial memory performance
Jelicic et al. (2004)	9 ♂ + 31 ♀ (*M*= 20.1 years)	TSST	Neutral and emotional words	E/RT/R	Stress impaired recall of neutral words, whereas it enhanced recall of emotional words Sex differences were not studied
Kirschbaum et al. (1996)	8 ♂ + 5 ♀ (Students, age not specified)	TSST	Neutral words	E/RT/R	Negative correlation between stress-induced cortisol levels and memory performance No sex differences
Kuhlmann et al. (2005)	19 ♂ (*M*= 24.58 years)	TSST	Neutral and emotional words	R	Stress impaired free recall of memory retrieval Emotional words were affected, but not neutral words
Larra et al. (2014)	100 ♂ + 106 ♀ L SG (*M*= 23 years)	SECPT	Emotion-expressing face portraits	RT RT/R	RT: High HR responders showed enhanced recognition memory RT/R: Stress did not affect memory performance No sex differences
Li et al. (2013)	45 ♂ (*M*= 23.63 years)	TSST	Neutral and emotional faces	R	Stress impaired recognition memory for faces
Li et al. (2014)	35 ♂ (18-31 years)	TSST	Neutral and fearful faces	R	Stress did not affect recognition memory for faces
Luethi et al. (2009)	35 ♂ (*M*= 24.8 years)	TSST	Neutral words Route on a map	E/RT/R	No stress effects on verbal explicit memory, but spatial episodic memory was enhanced
Lupien et al. (1997)	7 ♂ (*M*= 73.3 years) 7 ♀ (*M*= 73.1 years)	Public speaking task	Neutral word pairs	RT/R	Stress impaired declarative memory Sex differences were not studied
Maheu et al. (2005)	40 ♂ (*M*= 22.5 years)	TSST	Neutral and emotional narrated slides	E	Stress impaired long-term memory (1 week) for emotionally arousing material, but not for neutral material This result was found only in the group assessed in the morning, but not in the afternoon group
Merz et al. (2010)	14 ♂ (*M*= 22.7 years) 15 ♀ (OC users) (*M*= 23.6 years)	TSST	Biographical notes	RT/R	Stress reduced social memory retrieval This negative effect is linked to the stress-induced cortisol increase No sex differences

Nater et al. (2007)	20 ♂ (*M*= 23.75 years)	TSST	Neutral words	E/RT/R	No general stress effect on memory performance High responders: better immediate free recall after stress
Oei et al. (2006)	20 ♂ (*M*= 21.86 years)	TSST	Neutral and emotional paragraphs	R	Stress disrupted long-term memory of neutral material, but facilitated long-term memory of emotional material
Payne et al. (2006)	53 ♂ + 64 ♀ (Psychology students, years not specified)	TSST	Neutral and emotional narrated slides	E E/RT/R	In both: Stress disrupted memory of non-emotional material, whereas it preserved or even enhanced memory of emotional material Higher cortisol levels were associated with poorer memory performance in men, but not in women
Payne et al. (2007)	32 ♂ + 44 ♀ (Undergraduate students, age not specified)	TSST	Neutral and emotional narrated slides	E	Stress disrupted long-term memory (1 week) of neutral material, but facilitated long-term memory of emotional material No sex differences
Pulopulos et al. (2013)	38 ♂ + 38♀ (PM) (56-76 years)	TSST	Neutral and emotional pictures Neutral words Paragraphs	R	Stress did not affect memory retrieval on any memory task
Quaedflieg et al. (2013)	64 ♂ (*M*= 21.25 years)	MAST	Neutral and negative pictures	E	Stress impaired long-term (24 h) free recall and recognition Stress increased the number of false alarms
Schönfeld et al. (2014)	36 ♂ + 36 ♀ (*M*= 23.2 years)	Oral examination	Neutral and emotional words and pictures	R	Stress did not affect memory retrieval Retrieval performance under stress was positively correlated with the SNS response Retrieval performance 25 min post stress was negatively correlated with HPA-axis response No sex differences
Schoofs & Wolf (2009)	36 ♀ (L) (*M*= 24.47 years)	TSST	Neutral and emotional words	R	Stress did not affect memory retrieval No differences between cortisol responders and non-responders No correlation between stress-induced cortisol increase and memory

Schwabe et al. (2008a)	48 ♂ + 48 ♀ (OC) (*M*= 23.3 years)	SECPT	Neutral and emotional words	E E/RT/R	E: Stress enhanced the recall of neutral words E/RT/R: Stress enhanced the recall of neutral words; Cortisol responders: better free recall of negative words
Schwabe et al. (2009)	44 ♂ (*M*= 23.7 years)	SECPT	Neutral and emotional words	R	Stress enhanced memory retrieval for emotional but not for neutral words
Schwabe and Wolf (2009)	36 ♂ + 36 ♀ (*M*= 25.1 years)	SECPT	Object location	R	Stress impaired memory retrieval tested in incongruent contexts, but not in congruent contexts No sex differences
Schwabe & Wolf (2010)	16 ♂ + 32 ♀ (20 OC) (*M*= 23.6 years)	SECPT	Neutral and emotional words	E	Stress impaired long-term (24 h) free recall and recognition No sex differences
Schwabe & Wolf (2014)	60 ♂ + 60 ♀ (*M*= 23.61 years)	SECPT	Neutral and emotional words	R	Stress impaired memory retrieval tested 25 min and 90 min after the stressor, but not immediately No sex differences
Smeets (2011)	34 ♂ + 42 ♀ (31 L, 11 F) (*M*= 19.9 years)	SECPT	Neutral and negative words	R	Stress impaired memory retrieval This effect was larger for negative than for neutral words and associated with cortisol response
Smeets et al. (2006a)	Ex.1: 30 ♂ + 30 ♀ (L) (*M*= 19.91 years) Ex.2: 46 ♂ + 46 ♀ (*M*= 19.74 years)	TSST	Neutral words	E/RT/R	Ex.1: No stress effects on false recollections Ex.2: Stress impaired recall, but cortisol responses were not related to false recall or recognition rates
Smeets et al. (2006b)	30 ♂ + 30 ♀ (*M*= 19.65 years)	TSST	Neutral and emotional words	E/RT/R	Stress only impaired recall of neutral words No sex differences
Smeets et al. (2006c)	40 ♂ (*M*= 19.2 years)	modified TSST	Source monitoring	RT/R	Stress improved internal-internal source monitoring performance
Smeets et al. (2007)	13 ♂ + 39 ♀ (19 F, 11M, 4L) (*M*= 23.08 years)	modified TSST	Personality and memory words	E	Stress enhanced recall (24 hours) of context-congruent words, but only for personality words No sex differences
Smith et al. (*in press*)	25 ♂ + 35 ♀ (*M*= 71.90 years)	TSST	Short video and pictures	E	No stress effects, except on errors of commission on the cued recall test for a video Sex differences were not studied

Stawski et al. (2009)	26 ♂ + 74 ♀ (*M*= 18.94 years)	TSST	Neutral words	RT/R	Stress impaired immediate and delayed recall and provoked the commission of intrusions and perseverations No sex differences
Tollenar et al. (2008)	70 ♂ (*M*= 21.34 years)	TSST	Idiosyncratic emotional and neutral word pairs	R	Stress only impaired long-term (5 weeks), but not short-term (1 day), memory retrieval of negative words tested during and after stress Only during the stress task, impaired retrieval was related to enhanced cortisol response
Tollenar et al. (2009)	40 ♂ (*M*= 21.7 years)	TSST	Autobiographical memory	R	Stress did not affect autobiographical memory Negative correlation between cortisol response and specificity of recent, neutral memories in physically aroused SG
Weymar et al (2012)	40 ♂ (*M*= 23.08 years)	SECPT	Neutral and emotional pictures	E	No stress effects on long-term memory (24 hours)
Wiemers et al. (2013)	32 ♂ + 31 ♀ (19-30 years)	modified TSST	Office objects Committee members' faces	E	Stress enhanced recognition of objects and the committee's faces (24 hours) No sex differences
Wiemers et al. (2014)	48 ♂ + 47 ♀ (18-32 years)	modified TSST	Objects	E	Stress enhanced recognition of objects, especially for central visual objects in congruent odor situation No sex differences
Wirkner et al. (2013)	29 ♂ + 23 ♀ (6F, 17L) (*M*= 23 years)	SECPT	Neutral and emotional pictures	E	Stress enhanced the discrimination of neutral pictures Sex differences were not studied
Wolf (2012)	Ex. 1: 24 ♂ (*M*= 24 years) Ex. 2: 32♂ (*M*= 24.84 years)	TSST	Neutral and emotional narrated pictures	E	Ex.1 (with immediate recall): Stress did not affect memory performance (24 hours) Ex. 2 (without immediate recall): Stress enhanced negative pictures Conclusion: The immediate recall attempt can prevent or even reverse the beneficial effects of pre-encoding stress on emotional long-term memory
Wolf et al. (2001b)	33 ♂ + 25 ♀ (L) SG (*M*= 24.9 years)	TSST	Neutral words	E/RT/R	No stress effects on memory performance Negative correlation between stress-induced cortisol levels

	CG (*M*= 23.6 years)				and memory performance This correlation was solely caused by the strong association in men
Wolf et al. (2002)	22 ♂ + 18 ♀ L SG (*M*= 24.2 years) CG (*M*= 24.8 years)	TSST	Neutral words	R E/RT/R	Both: No stress effects on memory performance Sex differences were not studied
Zoladz et al. (2011)	20 ♂ + 52 ♀ (*M*= 19.68. years)	SECPT	Neutral and emotional words	E	Ex.1: Stress (immediately prior to learning) enhanced the recognition of positive words Ex.2: Stress (30 min prior to learning) impaired free recall of negative words Sex differences were not studied
Zoladz et al. (2013)	38 ♂ + 59 ♀ (*M*= 19.18 years)	SECPT	Neutral and emotional words	E E/RT/R	E: Stress did not affect free recall E/RT/R: Stress did not affect free recall, but impaired recognition, particularly positive and non-arousing words; Male cortisol responders recalled fewer words

M: mean

TSST: Trier Social Stress Test. FFST: Fear-Factor Stress Test. CPT: Cold Pressor Test. MAST: Maastricht Acute Stress Test. SECPT: Socially Evaluated Cold Pressor Test

SG: Stress Group. CG: Control Group. CC: Control Condition.

F: Follicular. M: Mid-cycle. L: Luteal. OC: Oral Contraceptive. PM: Postmenopausal. RC: Regular cycle. IC: Irregular cycle

E: encoding. RT: retention. R: retrieval

sAA: salivary alpha-amylase. C: cortisol. HPA-axis: hypothalamic-pituitary-adrenal axis

Table 2. Summary of the main results of the psychosocial stress effects on memory performance

	Young people	Older people[1]
Declarative memory		
Encoding	Not clear	No effects
Retention	Enhancing effects	No studied
Retrieval	Impairing effects	No effects
Working memory		
Span component	Not clear	Enhancing effects[2]
Executive component	Impairing effects	No effects
Non-declarative memory	Not clear	No effects
Sex	Stronger effects on encoding and WM in men No differences in retention, retrieval, or non-declarative memory	Understudied

[1]In declarative memory, psychosocial stress only enhances memory span and impairs retroactive interference on a word-list task
[2]only in women