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Authors

Quas, Jodi A
Castro, Amy
Bryce, Crystal I
et al.

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Stress Physiology and Memory for Emotional Information: Moderation by Individual Differences in Pubertal Hormones

Jodi A. Quas[1], **Amy Castro**[1], **Crystal I. Bryce**[2,3], and **Douglas A. Granger**[1,2,4,5]

[1]Department of Psychology and Social Behavior, University of California, Irvine, CA, USA

[2]Institute for Interdisciplinary Salivary Bioscience Research, University of California, Irvine, CA, USA

[3]Sanford School of Social and Family Dynamics, Arizona State University, Tempe, AZ, USA

[4]School of Nursing, [4]Bloomberg School of Public Health, Johns Hopkins University, Baltimore, MD, USA

[5]School of Medicine, Johns Hopkins University, Baltimore, MD, USA

Abstract

In contrast to a large body of work concerning the effects of physiological stress reactivity on children's socio-emotional functioning, far less attention has been devoted to understanding the effects of such reactivity on cognitive, including mnemonic, functioning. How well children learn and remember information under stress has implications for a range of educational, clinical, and legal outcomes. We evaluated 8–14 year olds' (N = 94, 50 female) memory for negative, neutral, and positive images. Youth had seen the images a week previously as a part of laboratory stress task. At encoding and retrieval, and in between, youth provided saliva samples that were later assayed for cortisol, salivary alpha amylase (sAA), testosterone, and dehydroepiandrosterone (DHEA). Overall, higher cortisol reactivity to the lab task predicted enhanced memory for emotional but not neutral images. However, cortisol further interacted with pubertal hormones (testosterone and DHEA) to predict memory. Among girls with lower pubertal hormone levels, greater cortisol reactivity was associated with enhanced memory for negative information. Among boys with higher pubertal hormone levels, however, cortisol reactivity was associated with enhanced memory for positive information. sAA, was unrelated to memory. Overall, our findings reveal that individual differences in hormone levels associated with pubertal development have implications for our understanding of how stress-responsive biological systems directly and interactively influence cognitive outcomes.

Direct Correspondence to Jodi Quas, Department of Psychology and Social Behavior, 4201 Social and Behavioral Sciences Gateway, University of California, Irvine, CA 92697-7085 (jquas@uci.edu).

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Keywords

hypothalamic pituitary adrenal axis; autonomic nervous system; stress; emotion; memory; pubertal hormones

Over the past two decades, interest in physiological stress reactivity in children has moved beyond simple investigations of bivariate relations between responses in individual systems and socio-emotional and mental health outcomes and toward more complex evaluations of how responses across systems, directly and interactively, shape such outcomes (El-Sheikh, Erath, Buckhalt, Granger, & Mize, 2008; Gordis, Feres, Olezeski, Rabkin, & Trickett, 2010; Gordis, Granger, Susman, & Trickett, 2006; Obradović, Bush, & Boyce, 2011). Results are beginning to shed light on potential patterns of responsivity, particularly in the hypothalamic pituitary adrenal (HPA) axis and autonomic nervous system (ANS), that are both shaped by familial and environmental experiences and shape children's subsequent well being (Afifi et al., 2015; Del Giudice, Benjamin Hinnant, Ellis, & El-Sheikh, 2012). What remains missing from these investigations is complimentary research investigating the associations between cross-system responses and cognitive outcomes. This omission is especially noteworthy given that learning and memory, especially under stress, have implications for children's and adolescents' functioning in a range of educational, clinical, social, and even legal settings.

We sought to begin to fill this knowledge gap by examining the links between children's HPA axis and ANS arousal and memory for emotionally valenced and neutral information. We tested whether these associations vary with age and across pubertal indices. We were particularly interested in the relations between individual differences in hormones associated with pubertal development and children's and adolescents' memory for emotionally laden information. Our interest was spurred by the need to test whether attention to and processing of emotional information are shaped by both stress and development. Before we describe our work, we review literature concerning arousal and memory in adults, the effects of stress on memory in children, and finally how emotional processes and pubertal development may shape memory during the transition to adolescence.

Arousal and Memory in Adults

A large and well-established literature exists concerning how stress and arousal affect memory in adults (see Schwabe, Joëls, Roozendaal, Wolf, & Oitzl, 2011; Wolf, 2009, for reviews). This literature has focused on how biological and neurological stress-related processes influence core components of memory: encoding, consolidation, and retrieval. Studies have relied on rigorous experimental designs that allow for strong causal inferences regarding the precise effects of stress on memory (Buchanan & Lovallo, 2001; Payne et al., 2007; Smeets, Jelicic, & Merckelbach, 2006; Smeets et al., 2009). Methodologically, stress has been manipulated by exposing adults to well-established laboratory-based stress tasks (e.g., surprise speeches, submerging one's arm in ice water) or comparable non-stressful activities, or by administering pharmacological agents that vary levels of physiological arousal (Cahill et al., 1996; Cornelisse, Joëls, & Smeets, 2011; Roozendaal, Hahn, Nathan, Dominique, & McGaugh, 2004; Schwabe et al., 2011). Shortly before or after the stress manipulation, adults complete standardized or widely used memory encoding tasks. The

tasks require adults to remember images, words, or sometimes videos that vary in emotional content. Their memory is later tested via recall or recognition tests, the latter of which often include previously seen ("old") and never-seen ("new") material to examine how stress affects memory accuracy, errors, and response biases (Schwabe, Bohringer, Chatterjee, & Schachinger, 2008; Smeets et al., 2006; Smeets, Otgaar, Candel, & Wolf, 2008).

Results consistently reveal positive effects of stress at encoding on memory. This has been most consistent when stress is measured via physiological responses and when the to-be-remembered information is negative rather than neutral, suggesting that the benefits of stress may be valence-specific (Kensinger & Corkin, 2003; McGaugh, 2013; Wolf, 2009). Of relevance to the present work, the most robust effects have also often emerged when stress has been reflected in *joint* activation of the sympathetic branch of the autonomic nervous system and HPA axis rather than activation of only one system (Buchanan, Tranel, & Adolphs, 2006; Cahill & Alkire, 2003; Payne et al., 2007; Schwabe et al., 2008; Smeets et al., 2009). The significance of joint activation is likely due to these systems' connections to limbic structures, especially the amygdala and hippocampus, that, when stimulated, play an integral part in directing attention toward and increasing consolidation of emotionally laden information.

Effects of Stress on Memory in Children

Developmental research has also focused considerable attention on delineating the effects of stress on children's memory. The methodological approach, though, has often varied from that employed with adults. Specifically, rather than testing children's memory for material learned under stress, studies have typically tested children's memory for the stress-inducing event itself. For example, children have been questioned about their memory for stressful experiences, such as medical procedure, accidents, injuries, or natural disasters (Ackil, Van Abbema, & Bauer, 2003; Goodman, Quas, Batterman-Faunce, Riddlesberger, & Kuhn, 1997; Peterson, 2012). Results provide insight into how well children recall personally significant events. However, variations in individual children's experiences and the complex array of emotions endured during the events preclude clear conclusions about how stress or arousal affects children's basic memory, including whether those effects vary developmentally or across different valences of to-be-remembered information.

Some investigations with children have relied on procedures that more closely approximate those used with adults. Stress has been experimentally manipulated and measured via peripheral markers of physiological arousal. Children's memory has been tested for emotional and neutral information learned under stress (Bugental, Blue, Cortez, Fleck, & Rodriguez, 1992; Cordon, Melinder, Goodman, & Edelstein, 2013; Leventon, Stevens, & Bauer, 2014; Potts, Morse, Felleman, & Masters, 1986). Findings, however, are far less consistent than those observed with adults, raising questions about the extent to which mechanisms identified in adults operate similarly across development. For instance, when cortisol levels have been measured before and after children endure medical procedures, no significant associations have been reported between changes in cortisol levels and children's memory (Chen, Zeltzer, Craske, & Katz, 2000; Eisen, Goodman, Qin, Davis, & Crayton, 2007). In contrast, larger autonomic nervous system (ANS) arousal (e.g., increased heart

rate) and HPA axis activation (larger cortisol reactions) to laboratory-based stressors have been linked to better memory, often in conjunction with age (Bugental et al., 1992; Quas, Carrick, Alkon, Goldstein, & Boyce, 2006; Quas & Lench, 2007).

A few studies have relied on stress induction procedures identical to those employed in studies with adults. Specifically, children have completed developmentally appropriate versions of the Trier Social Stress Test (TSST) (Kirschbaum, Pirke, & Hellhammer, 1993), for example, the TSST-Modified (TSST-M) (Yim, Quas, Cahill, & Hayakawa, 2010; Yim, Quas, Rush, Granger, & Skoluda, 2015). The TSST is a widely used 15-minute laboratory protocol that requires individuals give a surprise speech and complete arithmetic in front of neutral observers. Developmental versions make minor adjustments to the content of the speech and arithmetic task so that they are understandable to children (Buske-Kirschbaum et al., 1997; Yim et al., 2010; 2015). Both the TSST and TSST-M reliably increase arousal across multiple physiological systems, in children, adolescents, and adults (Dickerson & Kemeny, 2004; Gunnar, Talge, & Herrera, 2009). A low-stress version of the TSST-M has also been created. Children complete the same speech and arithmetic task as in the standard high stress version, but the social evaluative components are reduced, thereby minimizing levels of arousal (Quas, Rush, Yim, & Nikolayev, 2013; Yim et al., 2015). In memory studies, after taking part in the standard versus low-stress TSST-M, children complete memory tasks. Some tasks assess children's memory for unrelated topics, such as digits, stories, or words, while other tasks test children's memory for what occurred during the TSST-M itself (de Veld, Riksen-Walraven, & de Weerth, 2014; Quas, Yim, Rush, & Sumaroka, 2012; Quesada, Wiemers, Schoofs, & Wolf, 2011).

Few associations have been found between children's physiological arousal during the TSST-M and working memory performance or memory for unrelated, neutral information (e.g., de Veld et al., 2014; Quesada et al., 2011). However, positive associations have been uncovered between arousal and memory for emotional material. For instance, larger changes in children's cortisol levels during the TSST-M predicted better memory for details of the TSST-M (Quas, Yim, Edelstein, Cahill, & Rush, 2011). In one investigation, the strongest associations were uncovered when arousal was reflected in the combined of activation of both the HPA axis and SNS rather than activation of only one system (Quas et al., 2012).

Two additional trends in these studies are worth noting. One is that there may be developmental differences in the effects of stress on memory (Leventon et al., 2014; Quas et al., 2011; Rush et al., 2014). Quas et al. (2013) had 7–8 and 12–14 year olds complete the standard stress-inducing or the low-stress TSST-M. A few weeks later, their memory of the TSST-M was tested. Adolescents in the standard TSST-M condition provided fewer correct answers to recognition questions than adolescents in the low-stress version. However, children's accuracy to these questions did not differ between the two TSST-M conditions. Of interest, adolescents in the standard TSST-M condition did not make more errors than adolescent in the low stress TSST-M condition, but instead answered "I do not know," more often. This may suggest that stress reduced their willingness to answer questions and not their memory per se. As such, perhaps stress leads to different response biases across age, a possibility worth investigating.

A second trend concerns whether the valence of to-be-remembered information further influences the links between stress and memory (Bugental et al., 1992; Potts et al., 1986). Rush, Quas, and Yim (2011) found that arousal during the TSST-M was positively associated with memory for central information about the experience (i.e., event-related details that were emotionally charged or stress-inducing) but unrelated to memory for peripheral details (i.e., details unrelated to the stress-inducing aspects of the TSST-M) (see Christianson, 1992). In another investigation, immediately after completing the standard or low stress TSST-M, children and adolescents learned lists of emotionally valenced and neutral words (Quas et al., 2016). About 45 minutes later, after arousal had largely dissipated, the children's and adolescents' memory for the words was tested via a recognition task that contained the previously presented words and semantically similar but not presented words. Stress induction had a positive effect on memory for negative emotion words, especially in adolescents. Across age, HPA activation during the standard TSST-M predicted better memory for the emotional but not neutral words. Whether memory would have been further affected by joint activation of the HPA axis and SNS, however, is unknown, but important to examine given prior work suggesting that this combination should lead to the strongest effects on memory.

In summary, both stress and the emotional valence of to-be-remembered information likely influence children's and adolescents' memory. Specifically, consistent with evidence emerging from research with adults, greater HPA axis activation, particularly when it co-occurs with SNS activation, should strengthen children's memory for emotional but not neutral information. This possibility has not been adequately tested with well-validated sets of emotional and neutral stimuli. Moreover, some findings suggest that the effects of stress differ between children and adolescents. The developmental mechanisms underlying these potential differences have not been adequately explored. As we turn to next, such mechanisms may include the pubertal transition, which could affect children's stress responses, memory, and the links between them.

Stress, Memory and the Pubertal Transition

Although research has not specifically considered how stress in conjunction with the pubertal transition may influence memory, there are several reasons to suspect such influences exist. Three possible ways are outlined here. These stem from evidence of links between the pubertal transition and children's physiological and behavioral stress reactivity, sensitivity to social evaluation, and attention to emotional contexts and information (e.g., Dahl & Gunnar, 2009; Monk et al., 2003; Spear, 2009; Stroud et al., 2009; Sumter, Bokhorst, Miers, Van Pelt, & Westenberg, 2010).

First, pubertal development may influence memory simply by affecting the magnitude of children's reactions when exposed to stress, which itself affects memory. Specifically some studies have found that physiological stress responses (e.g., activation of the HPA axis) to laboratory-based activities like the TSST increase during the transition to adolescence (Gunnar, Wewerka, Frenn, Long, & Griggs, 2009; Romeo & McEwen, 2006). Insofar as stress response increase during this developmental period, indirect benefits of pubertal development on memory may emerge.

Second, pubertal development may also affect children's memory directly, specifically by influencing their attention to and encoding of emotionally salient information. During the transition to puberty, peers and social relationships become increasingly important (Blakemore, 2008; Forbes & Dahl, 2010; Somerville, 2013; Steinberg & Morris, 2001). This may lead children to focus their attention and hence encode better emotional expressions and emotion communication in interactions with others. For example, adolescents, relative to children and adults, are more sensitive and attentive to others' emotional expressions (McClure, 2000; Monk et al., 2003). Heightened sensitivity to emotions has similarly been uncovered when other developmental markers, such as gonadal (e.g., testosterone) or adrenal (dehydroepiandrosterone or DHEA) hormone levels or self-reported pubertal stage, have been studied (Moore et al., 2012; Pagliaccio et al., 2015; van Honk et al., 1999). Higher levels of testosterone are associated with enhanced attention to threat, especially when engaged in a challenging task (van Honk et al., 1999). Whether direct associations would emerge between pubertal development and memory, particularly for negative emotional information, is not known.

A third and more complicated possibility is that pubertal development moderates the effects of arousal on memory, most noteworthy for negative emotional information. Specifically, as youth transition to adolescence, not only are peers and social relationships becoming increasingly important, but so is the need for self-regulation of emotional responses in social interactions and in response to stress and challenge (de Veld et al., 2014; Silk, Steinberg, & Morris, 2003; Zeman, Cassano, Perry-Parrish, & Stegall, 2006). This may place increasing demands on the youth to attend to emotional information, especially in highly arousing situations, to determine how best to respond and self-regulate. Such enhanced attention, when aroused, should improve memory. Indeed, as mentioned, testosterone levels are more related to enhanced attention to threat, especially when individuals are completing a challenge. Also, adrenal hormone levels (e.g., DHEA) have been shown to interact with salivary cortisol levels to predict increases in general negative affect specifically during the transition to adolescence (e.g., Goodyer, Tamplin, Herbert, & Altham, 2000; Susman, Dorn, & Chrousos, 1991). Finally, as mentioned, Quas et al. (2013) found that, among 8–10 year-olds, greater cortisol reactivity during the TSST-M (regardless of whether it was the standard or low stress version) was associated with increases in how much they recalled about the laboratory task. However, cortisol was unrelated to adolescents' recall. Insofar as the children could be considered in the early phases of puberty, perhaps those who were highly aroused were especially attentive to the unfolding TSST-M, leading to these children's better memory, at least relative to those who were less aroused. By including measures of pubertal development, such a possibility could be tested directly.

Of course, with any consideration of pubertal development, it is imperative to consider the children's sex and how puberty is measured. First, although cognitive sex differences (e.g., in memory performance, including memory for emotional information) have rarely been uncovered, sex differences are robust with respect to both the nature and timing of puberty (e.g., girls begin, on average, one year earlier than do boys), level of hormonal changes that occur across the transition period, and appearance of secondary sex characteristics (Dorn, Dahl, Woodward, & Biro, 2006; Granger, Shirtcliff, Booth, Kivlighan, & Schwartz, 2004; Nelson, 2015). Second, there are robust individual differences in the onset and trajectory of

puberty (Herting et al., 2014; Marceau, Ram, Houts, Grimm, & Susman, 2011), even among same-age children.

Moreover, although different markers of pubertal development are correlated, and all are related to age, the measures are not identical (Dorn et al., 2006), with the associations among them often being moderate in size: Shirtcliff, Dahl, and Pollak (2009), for instance, reported small to moderate β coefficients (e.g., .25–.42) between pubic hair or breast development (in girls) and levels of testosterone; and Angold, Costello, Erkanli, and Worthman (1999) reported a .44 correlation between Tanner stages and morning testosterone levels. We have already mentioned reasons to suspect that puberty-relevant hormones, like DHEA and testosterone, may alter stress reactivity, attention, or memory. Given that the different indices of puberty may be providing somewhat unique information regarding development, it is important to examine hormonal indicators and self-reported puberty separately. For instance, children's sensitivity to secondary physical changes associated with puberty may affect their self-perceptions, desires, or motivation (e.g., to perform well) in ways that affect their memory performance. By including multiple indicators of pubertal development, it would be possible to separate the influence of each on memory for emotional and neutral information and determine whether these influences further vary as a function of stress levels.

Present Study

We examined how well children and adolescents remembered positive, negative, and neutral images. The participants had encoded the images a week earlier immediately after completing a laboratory stress task, the TSST-M. At encoding and retrieval, we collected repeated saliva samples that were assayed for salivary cortisol and alpha amylase (sAA), biological markers indicative of HPA axis and SNS activation, respectively. Samples at retrieval were also assayed for DHEA and testosterone. Finally, between sessions, we collected morning saliva samples that were similarly assayed for sAA, DHEA, cortisol and testosterone. This design allowed us to first examine whether physiological stress was differentially associated with memory accuracy (i.e., hits) and errors (i.e., false alarms) for negative, neutral, and positive images; and second, whether variations in salivary pubertal hormones moderated the associations between stress responses to the TSST-M and memory.

We expected greater physiological arousal at encoding, as reflected by higher HPA axis activation, possibly in conjunction with concurrent sympathetic activation, to be positively related to memory. We anticipated, as well, that the strongest links would emerge between arousal and memory for the negative information, consistent with the large body of work in adults on arousal and memory. We also expected a main effect of valence, with accuracy being highest, across age, for negative images. Beyond these effects, though, were developmental hypotheses. Accuracy was expected to improve, in general, with development, as reflected in pubertal hormones and age. We also predicted that individual differences in pubertal development may moderate the associations between physiological arousal and memory, particularly when puberty-related hormones were considered as an index of development, given that these markers have specifically been linked to variations in attention toward emotional information. Specifically, we thought that the strongest

associations between physiological arousal and memory for negative images would emerge among youth with low levels of pubertal hormones, suggestive of being earlier in this transition. During this period, attention to emotions may be most salient, especially when aroused, driving encoding and hence memory.

Method

Participants

Ninety four children and adolescents ("youth"), ages 8 to 14 years (M = 11.0, 50 females) comprised the final sample. Most were Caucasian non-Hispanic (80%), followed by Asian (13%), and then multi-ethnic (7%). Most parents had graduated college, and annual household incomes ranged from 30k to over 200k (85% of the families reported incomes over 90,000 per year). In combination, these suggested our sample was highly educated and affluent. Ten additional youth began the study but were not included in the final sample because they failed to complete the TSST-M, their memory data were accidentally not recorded, or they failed to show within the required delay for the second session due to scheduling conflicts. No differences emerged between these 10 youth and the larger sample on basic demographic characteristics or baseline arousal in Session 1.

Materials and Procedure

All study procedures were approved by our Institutional Review Board. Families were recruited via local parenting list-serves and word of mouth. Youth individually completed 2 sessions, separated by 1 week (range = 5–17 days, M = 8.17 days). Both sessions started between 13–18 hours (1–5 pm) to control for diurnal cycles of circulating cortisol (Kudielka, Schommer, Hellhammer, & Kirschbaum, 2004).

Session 1—Session 1 began with parent consent and youth assent. The youth and a female research assistant (RA) then built rapport for several minutes. The RA then reviewed instructions for subsequent activities. The youth completed demographic, daily activities, and general health questions. Included in the health questions was the Pubertal Development Scale (PDS; Petersen, Crockett, Richards, & Boxer, 1988) a well-validated self-report measure of pubertal status that asks youth about physical markers of puberty and secondary sex characteristics (e.g., body hair, deepening voice for boys; body hair, menstruation for girls). Youth respond via 4 point scales, ranging from "have not started" to "seems complete" (menstrual cycle beginning was coded as 1 = no or 4 = yes). Next, the RA showed the youth how to provide saliva samples using absorbent swabs, and an initial sample was collected. This was considered the youth's baseline measurement (mean delay between the family's arrival in the parking lot and the first sample was 35 minutes).

The RA then brought youth to a separate room to complete the TSST-M (Yim et al., 2010, 2015). First, youth were given instructions for two minutes and then three minutes to prepare. Next, youth gave a speech and completed arithmetic for five minutes each in front of two neutral observers. At the end, a novel component was added. An unfamiliar adult (male 77% of the time) interrupted and explained that he forgot his notebook. He and the youth looked for it. After 45 seconds, he stated that maybe he left it in his office. He thanked

the youth and left. This component provided youth with an additional experience in the TSST-M that was personally meaningful and required active involvement but was non-evaluative. It was introduced at the end so that it would not disrupt normative responses to the TSST-M.

As the adult left, the RA returned and collected a second saliva sample from the youth, one minute after the TSST-M ended (+1). She brought the youth to a separate room where they completed questionnaires about how they felt during the TSST-M. At +5 minutes post-TSST-M, a third saliva sample was collected, and the image encoding phase began. Youth sat at a computer screen and were presented with 36 images. The images were selected from the Developmental Affective Photo System (DAPS), a data base of emotionally valenced and neutral images for use with children (Cordon et al., 2013). A majority of the DAPS images came from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2008), a much larger database containing images that have normed valence ratings available. Those appropriate for children were screened, and valence and arousal ratings were obtained to ensure children's and adults' perceptions of the images were comparable.

A total of 108 images were included in the present study. These contained an equal number of positive, negative, and neutral images depicting an approximately equal number of social (e.g., a couple smiling) and non-social (an animal, a forest fire) scenes. From these, three different sets of 36 images were created, with 12 images per emotion in each set. Youth were shown one of the three sets. Each set began and ended with a positive image, but the remaining images were presented in random order. Across the sets, images within each valence were comparable in arousal.

Images were individually presented on a 21″ computer screen for two seconds. Images disappeared and a fixation screen with three ratings (unpleasant, neutral, or pleasant) appeared. Youth selected which term matched the image they saw. Once they made their selection, the next image was shown. The encoding phase took 5 minutes to complete.

Immediately after the encoding phase, youth completed tasks unrelated to the current study (e.g., questions about their temperament, a working memory activity). Additional saliva samples were collected at +10, +20, +30, +45, and +60 min post-TSST-M. At the end, parents and youth were given instructions regarding how and when to collect saliva samples at home and were provided with kits to do so. Parents were asked not to discuss the session with the youth until after Session 2.

Between sessions, a majority of participants (n= 73) provided saliva samples 30 minutes after waking but before eating anything. This occurred on two consecutive mornings. Parents were given a sheet to record the time when each sample was collected. This procedure was implemented after data collection had begun, and the first 21 youth did not provide morning samples. All samples were collected using absorbent swabs. They were frozen immediately after collection and remained frozen until the day of assay (e.g., Granger et al., 2007; Whetzel & Klein, 2010).

Session 2—Following a one-week delay, the youth returned for a surprise memory test. The session was conducted in a new building by an unfamiliar female assistant who was blind to the study hypotheses and was not present during session 1. The session began with a 20-minute rapport building activity. A saliva sample was then collected to serve as baseline for Session 2.

Next, youth were informed of our interest in how well they remembered the last visit. A two-part memory interview was administered. The first part was an episodic memory task during which youth were asked about what happened during the TSST-M itself. A second saliva sample was collected afterward, and the second part of the memory task, the image recognition portion, was administered. Youth were shown 72 images via computer, half of which were new (equal numbers of positive, negative, and neutral stimuli) and half of which were old, that is, they had been presented in Session 1. The new images were comprised of one of the two sets of images that had not been shown previously. Order of image presentation for the old and new sets was randomized as was valence (the first and last, though, were positive). After each image was presented, youth indicated whether the image was new or old, and the next image was shown.

Following the recognition task, youth and parents completed additional questionnaires. At the end, both were thanked. Youth were debriefed. This included explaining why the TSST-M observers were serious. Youth reported positive feelings about the study and were pleased with their involvement. Saliva samples from Session 2 and those collected at home were stored in a −80 °C freezer.

Coding

Salivary analytes—Saliva samples were shipped on dry ice to the University of Dresden and assayed for cortisol, sAA, testosterone, and DHEA. Assays were performed with commercial chemiluminescence immunoassay kits without modification following the Manufacturers' recommended protocol (IBL International, Hamburg, Germany). The lower limits of sensitivity were 0.44 nmol/l, 1.8 pg/ml, and 3.0 pg/ml for cortisol, Testosterone, and DHEA respectively. On average, intra-assay and interassay precision was less than 11% for all assays.

Physiological arousal—Arousal was indexed via changes in salivary cortisol levels and sAA levels, reflecting activation of the HPA axis and sympathetic nervous system, respectively. Cortisol and sAA reactivity scores were calculated, separately for the first and second session, as follows.

For Session 1, each youth's peak cortisol level during the TSST was identified by comparing their scores across the +1, +5, +10, +20, +30, and +45 minutes post TSST-M. Reactivity scores that accounted for time were computed by subtracting the youth's baseline cortisol level from their peak level and dividing this difference by the time elapsed between the two samples. The same process was utilized to compute sAA reactivity. In Session 2, only two saliva were collected. The first, baseline level, was subtracted from the second, and the difference was again divided by the time elapsed between samples. Separate scores in Session 2 were computed for cortisol and sAA.

Pubertal hormones—Hormone data included testosterone, a gonadal hormone, and DHEA, an adrenal hormone, obtained from the Session 2 samples, and for most participants, from the two morning home samples. Although these two hormones do not originate in the same biological system, they are nonetheless both involved in the transition to puberty and vary considerably across youth during this period of development. In addition, peripheral metabolism of DHEA is a major source of testosterone in pre-pubertal youth and females (e.g., Granger, Schwartz, Booth, Curran, & Zakaria, 1999). By measuring both, a range of differences in hormonal levels could be examined.

DHEA and testosterone levels across all measurement times were significantly correlated. Among girls *r*s ranged from .37 – .43, *p*s ≤ .01, and among boys *r*s ranged from .32–.36, *p*s ≤.02. The only exception was that the correlation between morning 1 testosterone and morning 2 DHEA was slightly lower, $r = .24$, $p = .09$. Principal components analyses (PCA) were thus conducted using the regression method in SPSS to combine the four samples (two DHEA and two testosterone samples) into a single factor for model parsimony and to retain statistical power. This was done separately for girls and boys. The single factor PCA solution converged, resulting in high factor loadings in the model for girls (.68 – .70) and for boys (.54 – .72). The factors accounted for approximately 67% and 63% of the variance in the analytes for girls and boys, respectively. A composite score was extracted using the regression method for each participant and utilized in the analyses. The regression method accounts for correlations between the observed items loadings and the observed items, resulting in an estimated component score for every participant ($M = 0$, $SD = 1$).

Self-reported pubertal status—The PDS was scored per the measure's instructions (Carskadon & Acebo, 1993). Youth's ratings of reproductive changes and secondary sex characteristics (e.g., growth in height/skin changes for boys and girls, emergence of facial hair in boys, start of menstruation in girls) were averaged. Higher scores indicate more advanced self-reported pubertal development.

Recognition memory accuracy—Three sets of memory scores were computed, separately for the positive, neutral, and negative images. Hits were calculated as the number of old images (i.e., presented at encoding and retrieval) correctly reported as old. False alarms were calculated as the number of new images (i.e., only presented at retrieval) incorrectly reported as old. Because hits and false alarms consider memory accuracy and errors independently, they were combined to create d prime (d′) scores, which were used in the main study analyses. D′ refers to youth's standardized hits minus false alarms [Z(hits)-Z(false alarms)]. D′ scores give indices of youth's ability to discriminate between new and old images, separately for positive, neutral, and negatively valenced images. For youth who had either a 1.0 or 0.0, on hits or false alarms, scores were adjusted following standard practice (Macmillan & Kaplan, 1985): Values of 0 were corrected using the formula $\frac{1}{2N}$, where N is number of lures presented, resulting in a corrected value of .0139. Values of 1 were corrected using the formula $1 - \frac{1}{2N}$ where N is the number of targets, resulting in a corrected value of .9861 (Wixted & Lee, n.d.).

Results

Analytic Plan

Preliminary and descriptive statistics were conducted with SPSS 24.0. These included an evaluation of data for skewness and kurtosis, testing for potential confounds (e.g., time of day, day delay), and correlating all study variables. Next, four mixed model analyses of variance (ANOVAs) were conducted as stress induction manipulation checks. Two tested whether youth exhibited physiological stress responses in Session 1 to the TSST-M, as would be expected. Cortisol and sAA levels at the eight time points in Session 1 (pre-TSST-M, and +1, +5, +10, +20, +30, +45, and +60 post TSST-M) were entered as a within-subject measure and sex was entered as a between-subject factor. Two similar ANOVAs with youth Session 2 pre- and post-interview cortisol and sAA levels were conducted. The latter were designed to confirm that youth were not aroused during the memory interview.

Preliminary analyses were also conducted with the memory variables. Three 3 (image valence) x 2 (sex) ANOVAs evaluated whether memory performance (hits, false alarms, d′ scores) varied across the negative, positive, and neutral images. Correlations then tested whether arousal at retrieval, which has been found to inhibit memory (Kuhlmann, Piel, & Wolf, 2005; Nathanson & Saywitz, 2003; Quesada et al., 2011), was related to the youth's memory. Specifically, Session 2 cortisol and sAA reactivity scores were correlated with memory variables, separately for boys and girls.

Our main hypotheses were examined via Mplus 7.11 (Muthén & Muthén, 1998–2014) using a robust full information maximum likelihood estimator with robust standard errors to accommodate missing data. The models were conducted by regressing the memory d′ stores on the three development parameters (age, self-reported pubertal status, and hormone PCA), cortisol reactivity, and the hormone PCA by cortisol reactivity interaction. The interaction tested the hypothesized moderating role of pubertal development on memory for negative images. In addition, both the hormone PCA and the PDS self-report scores were regressed on age (see Figure 1 for conceptual model of the analyses). The models were run separately for boys and girls, given they often follow different timelines for progressing through puberty and likely have different levels of hormones during and after puberty. Model fit was evaluated using four global fit indices, criteria listed in parentheses indicate acceptable fit: χ^2 (p-value ≥ .05); Comparative Fit Index (CFI ≥.95); Standardized Root Mean Square Residual (SRMR ≤ .08); and Root Mean Square Error of Approximation (RMSEA ≤ .06) (Hu & Bentler, 1998). After evaluation of the final models, significant interactions were examined.

Additional models were conducted to clarify the findings and further test our hypotheses. First, because of the significant correlations among the developmental parameters, which were included together in the main models, we re-ran the models with each developmental parameter included separately. This allowed us to test how each indicator, irrespective of its overlap with the others, related to memory. Findings are reported. Second, given prior work suggesting that sympathetic arousal, when paired with HPA axis activation may lead to the strongest positive effects on memory (e.g., Quas et al., 2012; Smeets et al., 2009), we conducted analyses with the sAA reactivity and sAA x cortisol reactivity interaction

included. No effects involving sAA were significant. As such, these models are not described further. We return to the issue of cross-system stress responses and memory in the Discussion.

Preliminary Analyses

Study variables were screened based on the recommended ranges of skewness and kurtosis for normality (i.e., skewness < 2 and kurtosis < 7; Tabachnick & Fidell, 2012). One boy was excluded because his Session 2 sAA reactivity score was five standard deviations above the mean. Cortisol variables were not normally distributed and were thus subjected to a natural log transformation. Following this, cortisol data were normally distributed. The transformed variables were used in the main analyses.

Descriptive statistics and Pearson product moment correlations for all study variables and possible covariates, including session start time, day delay between sessions, and baseline cortisol levels of the day of the recall task are presented in Table 1. Session start time and delay between sessions were not significantly related to the cortisol reactivity scores. Nor was delay related to memory. Sufficient variability was evident in self-reported pubertal level, as indicated by the mean and SD on the PDS, suggesting that we were not studying youth within only a narrow range of pubertal development.

When youth's physiological stress responses to the TSST-M were examined via the Session 1 saliva sample time X sex ANOVAs, robust significant main effects of time emerged for both cortisol, $F(7, 560) = 13.231$, $p < .001$, partial $\eta^2 = .142$, and sAA, $F(7, 525) = 10.611$, $p < .001$, partial $\eta^2 = .124$. No sex differences were evident. Follow-up analyses of the time effects revealed patterns quite consistent with prior research (Gunnar, Talge, et al., 2009; Kirschbaum et al., 1993; Yim et al., 2010). For cortisol, post-hoc tests revealed that youth's baseline and +1 minute post TSST-M levels (*Ms* = 7.99 and 8.78, respectively) were significantly lower than their cortisol levels at +5, +10, and +20 post TSST-M (*Ms* = 9.97, 11.23, and 10.78, respectively). At 30 minutes, youth's cortisol levels decreased significantly (*M* = 9.23). Significant decreases in cortisol continued at the +45 and +60 minute post TSST-M cortisol levels (*Ms* = 7.83 and 6.99, respectively), *p*s < .05, those the latter two did not differ from each other. For sAA, mean comparisons revealed a significant increase in sAA levels one minute after the TSST-M relative to baseline (Baseline *M* = 66.73, +1 minute *M* = 92.63, $p < .01$). The remaining eight sAA samples were all significantly lower than the +1 minute sample, $p < .01$, but none differed from one another or from the pre-TSST-M baseline levels (*Ms* ranged from 56.00 to 66.94).

ANOVAs with the Session 2 pre- and post-interview cortisol and sAA levels entered, along with gender, revealed no significant effects. Thus, youth were not particularly aroused according to HPA axis or ANS responses to the memory interview, and reactivity at Session 2 is not considered further.

Three 3 (valence) x 2 (sex) ANOVAs were conducted, separately for hits, false alarms, and d′ scores. No significant effects emerged for hits (*M*s =.81, .81, and .78, for positive, negative, and neutral images, respectively) or d′ scores (Table 1). For false alarms, the main effect of valence was significant $F(184) = 9.373$, $p < .001$, partial $\eta^2 = .092$. Mean false

alarms for negative images (M = .13) were significantly higher than the means for positive (M = .10) and neutral (M = .08) images, ps < .001 (positive and neutral did not differ from each other). Together, these analyses hinted at valence differences in memory, in that youth were more likely to err and say new images were old for the negative than positive or neutral images. However, valence did not independently influence discriminability.

Finally, no significant correlations emerged between stress at retrieval, according to Session 2 cortisol or sAA reactivity scores (post minus pre-interview scores), and memory. Thus, retrieval arousal, which again was quite low for most youth, did not appear to be affecting memory performance.

Arousal, Puberty, and Memory Performance

The primary goal of the study was to examine how indices of pubertal development in conjunction with physiological arousal related to memory. Our panel models (Figure 1), conducted separately for both and girls, revealed, as expected, that memory for emotional information was indeed shaped by both physiological stress responses and measures of pubertal development. In particular, the final models revealed strong fits across all indicators of interest for girls [χ^2 (4) = 1.05, p = .91; RMSEA <.01 (.00, .10); CFI = 1.0; SRMR = .03) and for boys [χ^2 (4) = 2.22, p = .70; RMSEA <.01 (.00, .20); CFI = 1.0; SRMR = .05]. Table 2 presents unstandardized parameter estimates followed by standardized parameter estimates, separately by gender.

With regard to girls, after controlling for age, hormone PCA, arousal, and the hormone PCA by arousal interaction, relatively strong positive associations emerged between self-reported pubertal development and d′ scores for images across the three valences. This trend is consistent with our hypothesis that memory would improve with age. Here, though, self-reported pubertal status was a better predictor of memory accuracy than chronological age. Also, although somewhat unexpected, a relatively small negative association between girls' chronological age and d′ scores for positive images was evident. Thus, when other indicators related to puberty (self-reported pubertal level and hormone PCA) and arousal were taken into account, chronological age was no longer a robust predictor of enhanced memory. Instead, age was associated with a slight reduction in discriminability for positive images.

Consistent with our expectation that arousal would be positively related to memory, cortisol reactivity was positively associated with d′ for the negative images but was unrelated to d′ for the neutral or positive images. However, this effect was subsumed by a significant arousal and hormone interaction. To evaluate the interaction, we plotted d′ scores for negative images based on predicted low v. high levels of cortisol and low v. high hormone PCA scores using the parameter estimates from the models (Table 2) at one standard deviation below and above the means.

Results, presented in Figure 2, revealed that, among girls who exhibited strong cortisol reactions to the TSST-M, those with lower hormone PCA scores evidenced better discriminability of negative images relative to those with higher hormone PCA scores. Among girls who responded less vigorously according to their HPA axis activation, however,

hormone levels were unrelated to their negative image discriminability. The simple slopes for the low cortisol reactivity (−1 SD) was .06, t (36) = .06, p = .95, and high cortisol reactivity (+1 SD) was −.26, t (36) = −.26, p = .80 (the non-significant simple slopes indicate that slopes were not significantly different from zero at the chosen levels of the moderator).

When boys' memory was examined, some patterns were similar to those in girls, for instance, greater cortisol reactivity predicted better discriminability for negative images. Other patterns diverged. Greater cortisol reactivity also predicted better discriminability for the positive images. This latter trend further varied depending on hormonal levels. A plot of the interaction, in Figure 3, showed that, among high cortisol reactive boys, those with higher hormone levels according to their PCA scores evidenced better memory for positive images than those with lower hormone levels. Among boys who were only minimally aroused to the TSST-M as reflected in their HPA axis activation, no differences based on hormone levels emerged in their positive image d′ scores. The simple slopes for the low cortisol reactivity (−1 SD) was −.04, t (34) = −.12, p = .90. The significant simple slope for high cortisol reactivity (+1 SD) 2.44, t (34) = 9.02, p < .01.

In subsequent analyses, models were conducted with the developmental indicators (chronological age, self-reported pubertal level, and PCA hormones) entered separately. For girls, results were similar to those reported above: When chronological age was entered, no significant predictors of memory (positive, negative, or neutral) emerged. When self-reported puberty was entered, PDS scores were positively associated with d′ scores for the positive, b=.33, p = .04, and neutral, b = .48, p = .04 images, consistent with trends evident in the main models. When girls' hormone PCA scores were examined, cortisol reactivity, b = .71, p = .02, and the hormone X cortisol interaction, b = −.53, p = .03, were significant for negative images (the interaction was also significant for positive images, b = .46, p = .02). The pattern of findings for negative images paralleled the interaction pattern in the main models (see Figure 2).

Among boys, analyses including chronological age and self-reported puberty separately revealed positive associations between cortisol reactivity and d′ scores for negative images, bs > 1.02, ps < .03. Self-reported puberty, however, was also negatively associated with d′ scores for negative images, b = −.54, p = .02. Finally, when the PCA hormone scores were considered, higher cortisol reactivity was associated with better memory for the positive images, b = .97, p = .05, and marginally better memory for the negative images, b = .93, p = .06. In addition, lower hormone PCA scores were associated with better memory for the negative images, b = −.30, p = .01. The significant interaction, uncovered in the full model when the overlap among the developmental indicators was considered, however, was non-significant when only hormonal PCA scores were included in the model.

Discussion

The overarching goal of the current investigation was to examine whether the associations between physiological arousal and memory varied across the pubertal transition and varied depending on the valence of the to-be-remembered information. Most central to this goal, our results indeed revealed that not only did physiological arousal matter, but it did so

differentially based on pubertal hormone levels and gender. That is, greater arousal was associated with enhanced memory for negative images in girls with lower levels of hormones linked to pubertal development, but poorer memory among girls with higher hormone levels. In boys, greater arousal was associated with enhanced memory for positive images when they had higher puberty-related hormone levels but poorer memory when they had lower levels. When arousal was low, pubertal hormone levels did not appear to matter for memory--in girls or in boys.

Together, these results suggest that the effects of physiological stress responses, reflected via HPA axis activation, at encoding on memory are likely shaped in important ways by key developmental processes across later childhood and into early adolescence. Hence, existing models of emotion and memory in adults may not be directly applicable to some developmental periods. Findings also inform theorizing about stress-responsive physiological systems and development, showing that these systems' response tendencies, in combination, are important for not only socio-emotional outcomes (Allwood, Handwerger, Kivlighan, Granger, & Stroud, 2011; Gordis et al., 2010; Koss et al., 2014) but cognitive and mnemonic outcomes as well (Keller, El-Sheikh, Granger, & Buckhalt, 2012). That is, the present study highlights that investigations of cross-system physiological response proclivities and functioning must consider developmental processes as another source of influence: The systems and their links to outcomes likely vary across puberty.

Turning to our results specifically, several findings supported our hypotheses, with some noteworthy caveats. For example, HPA axis activation during encoding was positively associated with memory for emotional images. This was evident for negative images in girls, and for both positive and negative images in boys. HPA axis activation was unrelated to memory for neutral images. Similar findings have been reported in adults: HPA axis activation at encoding is associated with better later memory for emotional but not neutral information (Schwabe et al., 2011; Smeets et al., 2009). At the same time, however, memory for the negative images was not uniformly better than for neutral images. In fact, with age, memory for positive images actually decreased somewhat.

On the one hand, our findings diverge from work that has revealed that emotional information (separate from being aroused) is remembered better than neutral information, in adults and in children (Bookbinder & Brainerd, 2016; Cordon et al., 2013; Levine & Edelstein, 2009; Potts et al., 1986). On the other hand, a few studies of children's and adolescents' memory for emotional versus neutral words have similarly reported either no differences or poorer memory for emotional than neutral information, possibly in conjunction with age (Brainerd, Stein, Silveira, Rohenkohl, & Reyna, 2008; Howe, Candel, Otgaar, Malone, & Wimmer, 2010). Studies have also reported an increased tendency to falsely remember negative information more so than neutral information (Otgaar, Candel, & Merckelbach, 2008). Until the present research, however, studies have not considered how indices of pubertal status, separate from age, influence attention, encoding, and retrieval accuracy and errors. Our findings hint that pubertal development may be important to consider in its own right. Further investigations are warrented to pinpoint which mnemonic processes are influenced by valence and pubertal development, and in which directions.

We had expected the positive association between physiological arousal and memory for the negative images to be strongest among youth during the early part of the pubertal transition. This expectation was confirmed in girls, at least insofar as lower pubertal hormone levels are indicative of earlier developmental periods (Shirtcliff, Dahl, & Pollak, 2009). Perhaps, as girls transition into puberty, they become particularly attentive, especially when aroused, to negative information in their immediate environment. Many of the negative images displayed social scenes, such as injuries, accidents, and adults arguing. These themes may be particularly important to girls, leading better encoding and better memory for the images when aroused.

An alternative explanation for our findings focuses not on memory performance of girls early in the pubertal transition, but instead, on performance among girls with higher hormone levels, who are likely more advanced in pubertal development. These girls may be more skilled at emotion regulation, which could include strategies that help them divert attention away from negative information when aroused as a means of self-regulation or that help them not think about the information afterward. Whether such attentional control is beneficial, for instance, because girls are not attending to or ruminating about negative information, or problematic, because it signals a form of disengagement after girls transition to puberty (Silk et al., 2003), is an important question worthy of further study.

Boys, in contrast to girls, evidenced no significant interactive links between puberty-related hormones and HPA axis activation predicting memory for the negative images. Instead, there were some hints that boys with higher pubertal hormone levels, and hence who may have been further along in their development, evidenced better memory for positive emotional information when more rather than less aroused. While this trend was not robust, in that it only emerged when hormone levels, age, and self-reported puberty were entered concurrently, it remains of interest for several reasons. One is that the trend was in the opposite to that observed in girls, who evidenced better memory under stress when they had lower levels of pubertal hormones. Numerous studies have revealed differences in how males and females (adolescents and adults) experience and express emotions (e.g., Brody & Hall, 2010; Nolen-Hoeksema & Girgus, 1994). Females tend toward greater expression of negative emotion than boys. In contrast, boys are also socialized to attend more to positive emotions and not to attend to or express as strongly negative emotions, with the exception of anger (Eisenberg, Cumberland, & Spinrad, 1998; Klimes-Dougan et al., 2007). As boys internalize this socialization, which could continually improve with development, their encoding of positive information may increase. Second, our negative images largely concerned sad, frightening, or mildly disgusting topics. Few depicted violence or anger-related themes, as these were screened out to ensure that the images were developmentally appropriate. Had we included anger-related images, emotions more consistent with boys' socialization (Chaplin, Cole, & Zahn-Waxler, 2005), perhaps the more developed boys would also have evidenced enhanced memory for negative images, at least when aroused. Overall though, given that the hormone PCA x cortisol reactivity interaction only emerged when all markers of development were considered concurrently, these interpretations are tentative without additional investigations of stress, puberty, and memory for a host of different types of information, among girls and among boys.

Of note, we collected hormonal measures at a single point in time. Such an approach is consistent with that of numerous other investigations of pubertal development and the links between this development and behavioral and emotional outcomes (e.g., Angold et al., 1999; Goddings, Heyes, Bird, Viner, & Blakemore, 2012; Shiftclilff et al., 2009). However, single time point measurements do not take into account individual differences in hormones that may be independent of pubertal phase and do not provide insight into the speed with which pubertal changes are occurring in individual youth. Longitudinal research in which pubertal measures are collected on multiple occasions over time would help distinguish among pubertal influences, social influences, and variations in absolute hormonal levels on girls' and boys' encoding and retrieval of emotionally laden information during this pivotal developmental window.

An additional point regarding the gender-specific trends concerns their relevance to understanding the emergence of mental health disorders, like depression, that have strong mnemonic components, increase markedly during adolescence, and vary between the sexes (Angold, Costello, & Worthman, 1998; Hollenstein & Lougheed, 2013; Nolen-Hoeksema & Girgus, 1994). Perhaps, during the early hormonal phases of puberty, being particularly attentive to negative information when aroused places girls at risk for greater perseveration on negative information. Such perseveration may act as a catalyst for depressive symptoms, which indeed increase sharply mid-way through puberty in girls (Susman et al., 1991). Alternatively, perhaps our study design simply identified girls who tend towards negative affect generally. When this tendency is combined with high arousal, it may lead to increased encoding of and memory for negative information. Why this occurs primarily in girls with lower levels of puberty-related hormones, though, is not clear. Longitudinal studies of the links between girls' heightened attention to negative information when aroused during the early part of pubertal development and later depressive symptoms would be worthwhile. Results would provide much-needed new knowledge concerning whether memory for negative information in girls is a precursor of risk.

Two broader points are worthwhile to note about the current findings. One concerns the unexpected associations between self-reported pubertal status and memory. Among girls, self-reporting more advanced pubertal development was associated with better overall memory, regardless of the valence of the images. Such a trend is consistent with prior work showing age-related improvements in general mnemonic abilities even between childhood and adolescence. Here, however, it was not chronological age but instead self-reported pubertal level that predicted memory. Given the lag between self-reported puberty, which reflects overt knowledge of secondary sex characteristics, and hormonal indicators of pubertal development, which occur much earlier (Shirtcliff et al., 2009), it is of interest that secondary characteristics, or at least girls' reports of them, were associated with better memory. Though speculative, perhaps with development, girls become more confident in themselves and their abilities. This confidence could influence their performance on a task requiring that they not only identify correctly old images but also reject new images. Compared to girls who reporting being less well-developed, the more developed girls may simply be more willing to distinguish between old and new. Of note, in our sample, most girls were from middle-class families and were of either Caucasian or Asian descent. Very few could be considered early maturers or at least early relative to their peers (Deardorff et

al., 2011; Wierson, Long, & Forehand, 1993). Had a large percent of early maturing girls been included, the positive association between self-reported pubertal status and memory may not have been evident. Future research needs to evaluate whether the trends evident in these youth are generalizable to other populations.

Second, our results inform emerging questions about multi-system approaches to understanding behavioral and developmental outcomes. Based on past work, including some of our own research, we had expected the combination of HPA axis and sympathetic activation to be the best predictor of memory. We found no evidence, however, that sympathetic arousal, reflected in changes in sAA to the TSST-M, directly or interactively, predicted memory. This lack of association emerged for emotional and neutral to-be-remembered information. Perhaps sympathetic arousal is most important in facilitating encoding of information directly related to the cause of the stress, which in this case would be the TSST-M itself (see Quas et al., 2012). When memory is tested for unrelated, albeit emotional, images, activation of the sympathetic system, in conjunction with the HPA axis, may not direct encoding in significant ways toward this information. We should add, however, that the lack of significant associations between sAA (directly or in conjunction with cortisol) and memory does not mean that multi-system investigations are uninformative. Instead, investigations of the combined influence of multiple stress-responsive systems on developmental outcomes are imperative. Findings provide critical insight into the conditions under which the systems are jointly important versus the conditions under which individual system responses take precedence. Knowledge of both is key to advancing the field.

In closing, the present study took a novel approach to studying the associations between stress and memory across development by assessing whether such associations vary depending on pubertal status and hormone levels in both girls and boys. The findings highlight important expansions in scientific research concerning stress-responsive hormonal systems in childhood: to consider in increasingly complex manners how different physiological systems' response tendencies do—and do not—directly predict socio-emotional and cognitive outcomes, and to consider whether and how developmental processes, particularly those associated with the pubertal transition, further shape stress responses' links to those outcomes. Results of this work will continue to advance theoretical understanding of risk and development. Results will also have implications for educational, clinical, and other settings in which children, across development, must function, grow, and interact.

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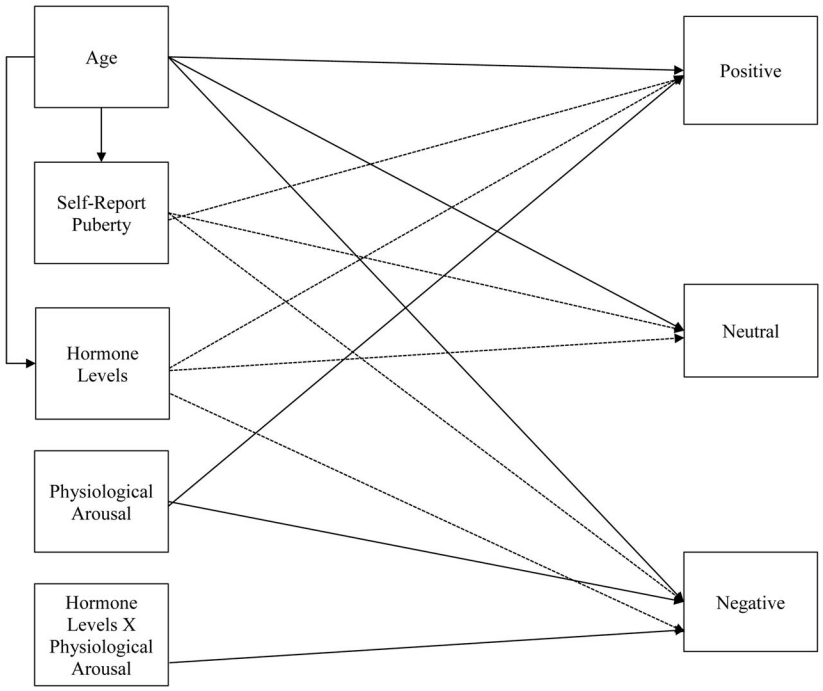

Figure 1.
Conceptual model.

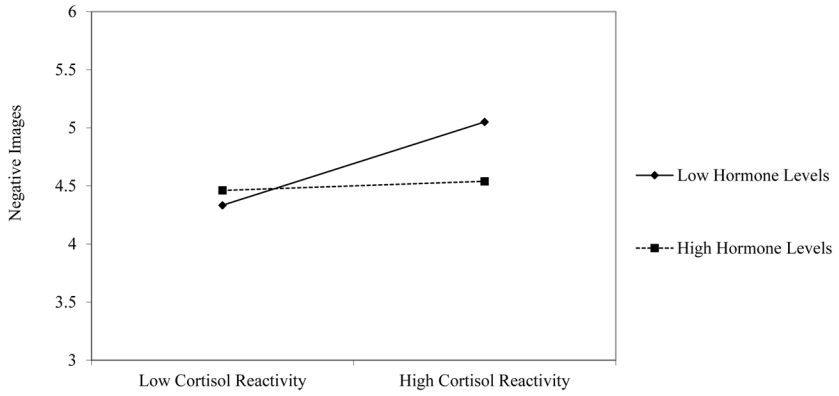

Figure 2.

Girls' d' scores (memory discriminability) for negative images. Plot end points reflect 1 SD below and above the mean for PCA hormone levels and cortisol reactivity.

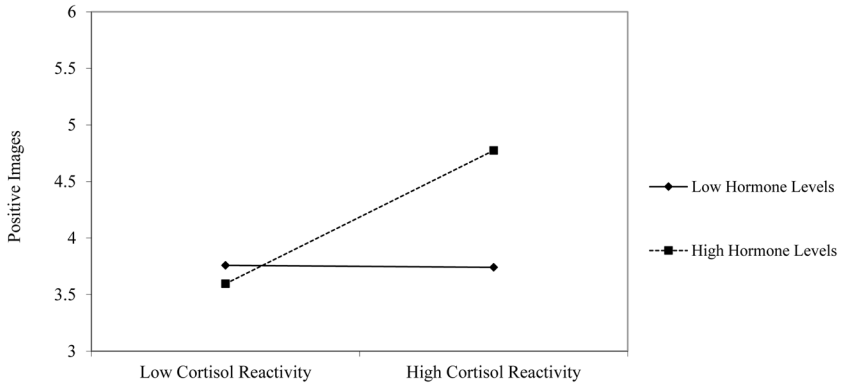

Figure 3.

Boys' d' scores (memory discriminability) for positive images. Plot end points reflect 1 SD below and above the mean for PCA hormone levels and cortisol reactivity.

Table 1

Correlations and descriptive statistics for all study variables and possible covariates, presented separately for girls and boys.

		1	2	3	4	5	6	7	8	9	10
1	Age		**0.49** **	**0.02**	**0.11**	**0.33** *	**−0.05**	**0.03**	**−0.12**	**0.20**	**0.01**
2	Hormone Levels	0.60 **		**−0.07**	**−0.11**	**0.28**	**0.22**	**0.12**	**−0.24**	**0.02**	**−0.01**
3	Cortisol Reactivity	−0.05	−0.10		**0.07**	**−0.08**	**0.21**	**0.10**	**0.27**	**0.06**	**−0.16**
4	sAA Reactivity	0.09	0.05	0.06		**0.27**	**−0.26**	**−0.09**	**0.03**	**0.11**	**0.06**
5	Self-Reported Puberty	0.61 **	0.46 **	0.01	0.04		**−0.23**	**0.01**	**−0.20**	**− 0.03**	**−0.08**
6	*d*′ Positive Images	−0.21	−0.14	0.01	−0.02	0.17		**0.40** **	**0.38** **	**−0.05**	**−0.10**
7	*d*′ Neutral Images	0.02	−0.01	0.20	0.05	0.10	0.42 **		**0.46** **	**−0.01**	**−0.11**
8	*d*′ Negative Images	−0.24	−0.23	0.19	−0.14	−0.06	0.30 *	0.19		**0.16**	**0.07**
9	Start-time	0.09	0.13	−0.20	0.13	0.10	−0.01	−0.05	0.08		**−0.09**
10	Day Delay	0.13	0.05	−0.06	0.17	−0.20	−0.27	−0.26	−0.15	0.33 *	
	M	11.87/**11.53**	−0.05/**0.12**	0.07/**0.10**	4.04/**3.57**	3.52/**2.26**	2.57/**2.62**	2.72/**2.63**	2.34/**2.60**	879.24/**899.90**	8.17/**8.13**
	SD	1.81/**1.60**	1.01/**0.97**	0.23/**0.24**	3.37/**3.08**	0.99/**0.83**	0.70/**0.83**	1.03/**0.90**	0.79/**0.98**	84.73/**111.13**	2.26/**2.25**
	Min.	8.15/**8.37**	−2.59/**−2.85**	−0.91/**−0.63**	−1.14/**0.30**	2.00/**1.00**	1.20/**1.17**	0.91/**0.49**	1.05/**0.44**	720.00/**720.00**	6.00/**5.00**
	Max.	14.95/**14.98**	1.57/**2.47**	0.88/**0.88**	14.54/**17.62**	5.00/**4.00**	4.40/**4.40**	4.40/**4.40**	4.40/**4.40**	1025.00/**1080.00**	15.00/**17.00**

Note.

* p<.05,

** p <.01.

For correlations, boys are in bold on the upper diagonal, girls are on the lower diagonal. For descriptive statistics, boys' values are in bold. Start-time was computed in minutes. Cortisol values are in nmol/L, sAA values are in U/ml.

Table 2

Parameter estimates for hypothesized models

	Boys Outcomes			Girls Outcomes		
	Positive	**Neutral**	**Aversive**	**Positive**	**Neutral**	**Aversive**
Age	−.11 (−.23)	−.04 (−.08)	−.01 (−.03)	−.20* (−.47)	−.08 (−.14)	−.19 (−.39)
Self-Reported Puberty	−.28 (−.18)	−.41 (−.25)	−.42 (−.24)	.62* (.55)	.56* (.36)	.55* (.42)
Hormone Levels	.26* (.31)	.15 (.18)	−.20 (−.22)	−.02 (−.03)	−.02 (−.02)	−.10 (−.11)
Cortisol Reactivity	1.06* (.32)	.38 (.11)	.97* (.27)	−.04 (−.01)	.84 (.20)	.81* (.23)
Interaction Term	1.31* (.28)	.24 (.05)	.04 (.01)	.29 (.11)	.63 (.17)	−.68* (−.22)

Note.

* $p \leq .05$.

Unstandardized estimates are followed by standardized estimates in parentheses. P-values are for the unstandardized parameter estimates. Interaction term= hormone levels X cortisol reactivity.