INFLUENCE OF EMOTION ON COGNITIVE CONTROL FROM ADOLESCENCE TO ADULTHOOD

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Adolescence is a period of development with high incidence of affective disorders representing poor cognitive control over affect, but little is known about how adolescent emotional systems compare to those of adults and how emotion influences still-maturing cognitive control systems. The ability to inhibit a response, which is crucial for cognitive control of behavior, continues to improve through adolescence. Though the core cognitive processes for inhibitory control are available in adolescence, the ability to utilize them in a reliable manner continues to mature, making adolescents susceptible to making errors. This study aimed to explore the vulnerabilities of the adolescent inhibitory control system to emotion by manipulating autonomic arousal. Adolescents (age 15-16) and adults (age 24-29) performed an oculomotor inhibitory control task as they heard sequences of temporally unpredictable tones (increased arousal condition) and temporally predictable tones (lower arousal, control condition) while autonomic arousal was assessed via pupillometry. Results indicated that adolescents have higher levels of arousal compared to adults, but less awareness of their arousal levels. Secondly, adolescents' inhibitory control was comparable to adults' even under arousal conditions but they showed greater effects of arousal reflected in optimal performance with higher levels of arousal. Thirdly, in adolescents but not adults, individuals who scored higher on measures of

dysregulation showed greater sensitivity of inhibitory control to arousal. Together, these results indicate that emotional and inhibitory control processes are more susceptible to external stressors in adolescence than in adulthood. This may underlie known limitations during this period in higher level regulation of behavior, particularly in the face of stressors.

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PREFACE

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1.0 INTRODUCTION

Adolescence is a unique period in development when an individual's behavior can appear adult-like, but there is still evidence for immaturities in higher level control that is distinct from adulthood (Spear, 2007). This period is roughly defined as the time between the onset of sexual maturation and the attainment of adult status in society, which usually spans the teenage years (approximately ages 12 to 17) and includes the duration of puberty (Dahl & Hariri, 2005). It is the developmental period when psychopathologies including schizophrenia, mood disorders, and anxiety disorders typically emerge (APA, 2000) and risk of their onset is at its peak (Castle, Wessely, Der, & Murray, 1991). During this time there are significant brain maturational processes (Giedd et al., 1999; Gogtay et al., 2004; Sowell, Thompson, Holmes, Jernigan, & Toga, 1999; Sowell et al., 2004) (Huttenlocher, 1990) (Yakovlev & Lecours, 1967) that likely underlie enhancements in brain functional connectivity (Stevens, Kiehl, Pearlson, & Calhoun, 2007) and the efficiency of processing within neural circuitries (Klingberg, Vaidya, Gabrieli, Moseley, & Hedehus, 1999). These processes facilitate complex neuronal processing that support controlled behavior in adulthood (Luna, Velanova, & Geier, 2008), but adolescent immaturities in brain processing undermine the ability to demonstrate adult-like control over behavior during this period of development.

Understanding the development of the relationship between *emotional* and *cognitive* changes can inform us regarding the vulnerability for psychopathology during adolescence

(Nelson, Leibenluft, McClure, & Pine, 2005). In the mood and anxiety disorders that emerge during this period, there is evidence for heightened emotional reactivity and impairments in higher-level cognitive functioning, particularly in emotional contexts (Ettinger et al., 2004; Everling & Fischer, 1998; Hutton & Ettinger, 2006; Jazbec, McClure, Hardin, Pine, & Ernst, 2005; Ladouceur et al., 2006; Petersen et al., 1993; Rich et al., 2005). An understanding of emotion-cognition interactions may also contribute to an understanding of enhanced sensation-seeking behaviors among healthy adolescents (Dahl, 2004; Spear, 2000; Steinberg, 2008), particularly since adolescents demonstrate that they adequately comprehend the potential consequences of their actions when completing risk assessment questionnaires (Reyna & Farley, 2006). However, little is known about emotional reactivity and how its effects on emerging cognitive control systems during healthy adolescence.

This study sought to gain insight into the differences in the effects of emotion on cognitive control between adolescents and adults. We used an approach of focusing on basic, core components of these larger constructs, choosing to study the effects of autonomic arousal on inhibitory control. In choosing more "basic" levels to conceptualize emotion and cognitive control, we sought to explore fundamental processes that can later be more fully understood using methods with greater ecological validity. Towards this end, we utilized paradigms with well-delineated neural mechanisms that can enhance our understanding of the association between brain maturation and behavioral findings. Due to continuing developmental changes in emotion recognition abilities (Herba & Phillips, 2004; Scherf, Behrmann, Humphreys, & Luna, 2007; Thomas, De Bellis, Graham, & LaBar, 2007), paradigms were selected for minimal developmental confounds and sensitivity to developmental change.

1.1 EMOTION

Emotions are defined as temporary psychological and physiological phenomena that represent adaptation to changing environmental demands (Levenson, 2003). Crucial to this definition is the recognition that emotions are states that are contextually-determined, temporary, and internally experienced. Thus, they are a mechanism by which environmental factors drive people's responses and influence behavior. Emotions, however, are a broad and complicated construct with multiple levels of experience ranging from physiological states to appraisal processes which vary to the degree that they are modulated by conscious thought processes (Ochsner & Gross, 2005). To begin our exploration of emotion in adolescence, we chose to focus on the least complex level of emotion: autonomic arousal. This is the physiological state that is usually elicited by a stimulus and is under control of the sympathetic and parasympathetic branches of the autonomic nervous system. Autonomic arousal is a basic component of emotion that may shed light on how emotional processes may differ in adolescence. A focus on autonomic arousal (which will henceforth also be referred to as "emotional arousal" or "arousal") is advantageous because it represents a core component of emotion that is mediated by the limbic system and which organizes disparate biological systems to produce an optimal bodily state for effective responding to a given situation (Lang, 1995; Levenson, 2003). In this study, we were particularly interested in an autonomic arousal that was elicited by a stressor because of its relevance for psychopathology. Acute stressors include events or situations that are unpredictable, uncontrollable, and for which there is no outlet for frustration (McEwen, 1998), and additively increase the risk of developing psychopathology (Caspi et al., 2003; Gross & Hen, 2004; Heim, Owens, Plotsky, & Nemeroff, 1997). This study explored developmental differences on arousal levels and reactivity as well their effects on cognition.

Studies of emotion in adolescents have documented that the prevalence of negative affect increases, with reports that one-third to one-half of adolescents report sadness, depressed mood, anxieties, or other negative emotions at a given point in time (Abe & Suzuki, 1986; Compas, Hinden, & Gerhardt, 1995; Holsen, Kraft, & Vittersø, 2000; Larson & Richards, 1994; Petersen et al., 1993; Petersen, Sarigiani, & Kennedy, 1991; Rutter, Graham, Chadwick, & Yule, 1976). From childhood into adolescence, individuals report feeling negative affect more frequently (from 12% to 20% of the time), with concomitant but lesser declines in the frequency of positive affect (Larson, Moneta, Richards, & Wilson, 2002). There is evidence that adolescents experience greater extremes of emotions (Buchanan, Eccles, & Becker, 1992), and that they experience greater emotional lability on a daily basis than adults (Buchanan et al., 1992; Larson et al., 2002), which highlights the emotional volatility of the adolescent years (Arnett, 1999). Given the difficulties in comparing responses to stressors experienced at different points in the lifespan, studies using standardized laboratory stressors provide initial evidence for adolescents' comparative stress reactivity. These studies provide evidence that adolescents have increased hypothalamus-pituitary-adrenal (HPA) axis activity to stressors as compared to children (Gunnar, Wewerka, Frenn, Long, & Griggs, 2009; Stroud et al., 2009), pointing to the role of neurobiological factors in affective differences across the lifespan.

Neuroimaging studies suggest that over-reactivity in limbic regions may be one contributing factor to immaturities in emotional reactivity in adolescence. Adolescents, like adults, demonstrate a reliable amygdala response to negatively valenced facial expressions of emotion (Baird et al., 1999). Several studies have shown that adolescents show greater amygdala response magnitudes to these stimuli in adolescents as compared to adults (Guyer et al., 2008; Hare et al., 2008; Monk, McClure et al., 2003). Studies that do not use facial stimuli,

which are less confounded by developmental differences in emotion recognition (Herba & Phillips, 2004; Thomas et al., 2007), have also shown exaggerated amygdala responses (to omission of a large monetary reward and to aversive air puffs to the larynx)(Ernst et al., 2005; Monk, Grillon et al., 2003).

The amygdala innervates nuclei of the autonomic nervous system (Sah, Faber, Lopez De Armentia, & Power, 2003), which is involved in generating the physiological experience of emotion, and its dysregulation may contribute to heightened emotionality during adolescence. Surprisingly little is known about the development of autonomic reactivity to emotional stimuli in healthy development (Beauchaine, 2001), but emerging data suggests that changes may continue into adolescence. One study using a metric of pupillary reactivity, which reflects a combination of sympathetic and parasympathetic activity, to emotional words and reported continued changes in autonomic reactivity across adolescence (Silk et al., 2009). Studies examining parasympathetic activity alone suggest no differences between adolescents and children (Allen & Matthews, 1997), but studies of sympathetic reactivity to laboratory stressors are inconsistent. A study by Quigley & Stifter (2006) concluded that sympathetic reactivity may be may be adult-like by late childhood, but this study excluded adolescents and only compared children and adults. Studies comparing adolescents to children have alternately reported that adolescents show increased sympathetic reactivity to a stressor (Allen & Matthews, 1997; Stroud et al., 2009) as well as decreased sympathetic reactivity to a stressor (Gunnar et al., 2009). Further clarification of developmental differences in autonomic nervous system reactivity to stressors is needed because immaturities in the autonomic nervous system may be an aspect of emotional processing that may underlie adolescent limitations in emotional processing.

1.2 COGNITION

Emotional arousal states are of particular importance because of their influence on behavior, particularly that which is voluntary and goal-directed. Cognitive control refers to the ability to exert voluntary control over planned behavior (Fuster, 2002). Understanding the susceptibilities of emotion to cognitive control during adolescence can help clarify the specific vulnerabilities inherent in this period of development. Crucial to cognitive control is inhibitory control, the ability to organize, execute, and regulate goal-directed behavior in the presence of irrelevant external or internal stimuli. Inhibitory control can be used as a model system to study cognitive control more broadly. It is typically assessed using tasks such as the Stroop, go/no-go, stop-signal, and antisaccade tasks that require participants to override a reflexive or prepotent response in favor of a voluntary, goal-related response.

By adolescence, behavioral studies show that inhibitory control can appear similar to that of adults but from adolescence to adulthood the ability to sustain inhibitory control continues to improve significantly (Fischer, Biscaldi, & Gezeck, 1997; Klein, 2001; Klein & Foerster, 2001; Luna, Garver, Urban, Lazar, & Sweeney, 2004; Luna & Sweeney, 2004; Munoz, Broughton, Goldring, & Armstrong, 1998; Romine & Reynolds, 2005). Functional neuroimaging studies show important differences in the brain systems that are recruited to support inhibitory control in adolescence reflecting greater effort (Bunge & Wright, 2007; Luna et al., 2001), limitations in processing inhibitory errors (Velanova, Wheeler, & Luna, 2008), and limitations in maintaining an inhibitory set (Velanova, Wheeler, & Luna, 2009). While adolescents can appear to have adult-level inhibitory control in standard laboratory conditions (Luna et al., 2004), their performance is inferior to that of adults when inside an MRI scanner (Velanova et al., 2008, 2009), a situation which has been shown to elicit some anxiety in this age group (Rosenberg et

al., 1997). In this MRI context, studies have shown that incentive conditions allow adolescents to perform like adults even though their performance during non-rewarded trials is worse than adult performance (Geier, Terwilliger, Teslovich, Velanova, & Luna, 2009). These studies provide evidence that the adolescent cognitive control system is not as reliable as that of the adult system and may be particularly susceptible to error in the presence of increased demands.

Given immaturities in cognitive control in adolescence, inhibitory control systems may be particularly susceptible to error with the additional demands resulting from a state of emotional arousal. At the neural level, there is evidence that emotional stimuli may tax immature and vulnerable inhibitory control systems because they activate subcortical limbic regions including the amygdala that ultimately place demands on cortical association areas involved in cognitive control (Davidson, 2002; Sah et al., 2003). Adolescents may also have an added limitation resulting from the combined immaturities of emotional and cognitive systems, with over-reactive emotional arousal systems taxing newly emergent inhibitory control systems. Understanding the effects of emotion of cognitive control can contribute to our understanding of the vulnerabilities of the dynamic, emerging adolescent neurocognitive systems, and this has implications for understanding why affective disorders tend to emerge at this time. Incorporating the role of emotions can also provide a greater degree of ecological/external validity to the understanding of cognitive control, and clarify how contextual factors may exert an influence on individuals' behavior and decision-making.

1.3 THE PRESENT STUDY

In this study, we explored developmental differences between adolescents and adults in autonomic arousal and its effects on inhibitory control processes. Specifically, we explored developmental differences in: (1) autonomic arousal levels, reactivity, and subjective awareness of arousal, (2) inhibitory control under different arousal states and the relationship between arousal and inhibitory control, and (3) the relationship of behavioral profiles (e.g., impulsivity) to arousal and inhibitory control under arousal. We adopted a neuroscience approach using tasks that isolate basic components of emotion (autonomic arousal) and of cognition (inhibitory control) that can also provide insight into the possible neurobiological basis of developmental change in the effects of emotion on cognitive control.

Autonomic arousal was elicited by presenting unpredictable (UP) and predictable (P) sequences of tones that have previously been shown to engage the amygdala and elicit emotion in humans and rats (Herry et al., 2007). The basolateral nuclei of the amygdala, an area responsive to stress hormones and emotionally arousing experiences (Pare, 2003; Vyas, Pillai, & Chattarji, 2004) has been shown to fire after the onset of both tone sequences. Habituation occurs in response to the P but not the UP sequences, meaning that there is sustained amygdala activity only in the UP condition. At the behavioral level, the UP sequences elicit anxiety-related biases towards threat in humans and greater anxiety-related behavior (less exploration) in mice (Herry et al., 2007). The speed of the tone presentation is very fast in both conditions (every 200 ms on average), so the tones minimally interrupt a participant's attention during a cognitive task. More importantly, the manipulation of the tone presentation is subtle and not readily detectable, so the two conditions tend to be equally distracting.

We characterized inhibitory control by using the antisaccade task (AS) (Hallett, 1978), an oculomotor inhibitory control task that has been extensively delineated in single-cell monkey studies (Everling, Dorris, Klein, & Munoz, 1999; Funahashi, Chafee, & Goldman-Rakic, 1993; Schlag-Rey, Amador, Sanchez, & Schlag, 1997), human lesion studies (Pierrot-Deseilligny, 1994), and human neuroimaging studies (Chikazoe, Konishi, Asari, Jimura, & Miyashita, 2007; Connolly, Goodale, Menon, & Munoz, 2002; Curtis & D'Esposito, 2003; Ford, Goltz, Brown, & Everling, 2005; Luna et al., 2001; Velanova et al., 2008). The AS task requires subjects to suppress the reflexive tendency to generate a saccade towards a stimulus that appears in the periphery and instead make a voluntary eye movement to its mirror location. The AS task has been found to be particularly sensitive to developmental changes in adolescence (Fischer et al., 1997; Fukushima, Hatta, & Fukushima, 2000; Klein, 2001; Klein & Foerster, 2001; Luna et al., 2004; Munoz et al., 1998; Nieuwenhuis, Ridderinkhof, van der Molen, & Kok, 1999; Romine & Reynolds, 2005). Oculomotor tasks are particularly well-suited for developmental studies because they have minimal verbal processing demands and are not easily amenable to strategy use. This approach allowed us to control for possible developmental differences in information processing of complex stimuli that may be evident in traditional emotion eliciting stimuli.

This experimental study utilizes a within-subject manipulation of emotional arousal states in a sample of healthy adolescents and adults. Three experimental conditions were elicited by the tone paradigm established by Herry et al. (2007): an autonomic arousal condition by playing a sequence of unpredictably patterned tones, an unaroused control condition by playing a sequence of predictably patterned tones that controls for hearing tones, and an unaroused control condition by silence. Participants completed the AS task to assess inhibitory control abilities during each of

these conditions, and their autonomic arousal was monitored throughout via assessments of pupil dilation. Subjective ratings of arousal were obtained in each condition.

We hypothesized that both adolescents and adults would show greater autonomic arousal in the UP condition as compared to the P condition based on the aforementioned results of the previous study (Herry et al., 2007). In light of an emerging literature indicating greater affect sensitivity in adolescence (Spear, 2009), we hypothesized that adolescents would show higher levels of autonomic arousal in both conditions, greater autonomic reactivity to the UP tones as compared to the P tones, and will report higher levels of emotional arousal in both conditions. A number of studies of adults have shown decrements in inhibitory control during emotional conditions (Blair et al., 2007; Hare, Tottenham, Davidson, Glover, & Casey, 2005; Most, Chun, Widders, & Zald, 2005; Wang, LaBar, & McCarthy, 2006), so we predicted that AS error rates and response latencies would be greater in the UP condition for both groups. Given the evidence for immature cognitive control systems in adolescence, we predicted an age group by condition interaction, with adolescents showing greater decrements in performance in the UP condition. Finally, we explored how individual differences in dysregulated behavior would be associated with autonomic arousal as well as inhibitory control under differential arousal conditions at different points in development.

2.0 METHODS

2.1 PARTICIPANTS

A total of 24 adolescents (50% male) ages 15 -16 and 24 adults (50% male) ages 24 - 29 participated in this study. A narrow adolescent age range was selected to minimize variability among adolescents; the choice of 15 to 16 year olds was supported by evidence that this age group performs equivalently to adults on behavioral measures of the AS task (Luna et al., 2004) but shows different patterns of brain activation (Luna et al., 2001; Velanova et al., 2008, 2009). Participants were recruited from the community through mailings and flyers posted throughout the Pittsburgh area that targeted healthy individuals and an ongoing longitudinal study of healthy individuals at the Laboratory of Neurocognitive Development at the University of Pittsburgh.

2.1.1 Screening Criteria

Participants were screened via phone interview for the presence of current or past diagnosis of Axis I psychiatric disorders, neurological disorders, epilepsy, head trauma resulting in loss of consciousness for an extended period, current or past use of psychiatric medications, family history of Axis I disorders, and eye movement disorders including strabismus and nystagmus. Individuals who were born prematurely (less than 30 weeks gestation) or were Very Low Birth Weight (1500g) were excluded due to known effects on brain development and cognitive

performance (Peterson et al., 2000). Participants that passed the initial screen completed an age-appropriate self-report version of the Child Behavior Checklist (CBCL), a reliable and valid questionnaire that is used to screen for clinically significant DSM-IV-based symptoms (Achenbach, 1991; Achenbach & Rescorla, 2001). Individuals who demonstrated symptoms above a clinical threshold (T=70) for two or more DSM-IV based symptom scales and two or more Internalizing/Externalizing syndrome scales were excluded from the study. Two participants were excluded on the basis of these criteria.

2.2 MATERIALS

Participants completed nine blocks of three cognitive tasks done under three conditions (UP, P, S) in a randomized order. The cognitive tasks consisted of two oculomotor and one button press tasks; only the AS task will be discussed for the purposes of this study. Each of the nine task-condition blocks was a fixed length of time lasting between two and three minutes, and AS blocks were 128 seconds. A set of 24 randomized task orders was generated, each for use with one adolescent and one adult participant of the same sex.

2.2.1 Tone Sequences

Within each task-condition block, the same tone (i.e., the same sound frequency) was played for the full length of the task. To avoid habituation to the tones resulting from repeated presentation of the same tone frequency in all nine blocks, a different tone frequency was played for each of the different task-condition blocks. For the AS task this was 1949 Hz for the UP tones and 1611 Hz

for the P tones. Frequencies were selected to be within the range of peak human sensitivity (1000 – 2000 Hz) and were chosen in logarithmic intervals consistent with the logarithmic scale of human auditory perception.

Tone sequences were modeled after those described by Herry et al. (2007) (see Figure 1). P sequences consisted of 40 ms tones played in 200 ms intervals. The UP sequences were constructed by jittering the presentation of 40 ms tones within a 110 ms window such that the length of the tone interval ranged from 90 ms to 330 ms, with a mean of 200 ms. Tones and tone sequences were generated using programs written in MATLAB (MathWorks, Inc., Natick, MA) using a sampling rate of 22.050 KHz, and they were played in EPrime v. 2.0 (Pittsburgh Software Tools, Pittsburgh, PA). Individual tones during the P condition were sine waves. Tones in the UP condition were saw tooth waves as determined by pilot testing to more optimally to elicit emotional arousal. For all tone variants, each tone was switched on and off smoothly using cosine-shaped increasing and decreasing ramps with duration of 5 ms.

2.2.2 Measure of Autonomic Arousal

Autonomic arousal was assessed via levels of pupil dilation, a valid measure of both sympathetic and parasympathetic nervous system activity (Granholm & Steinhauer, 2004; Siegle, Steinhauer, & Thase, 2004; Steinhauer, Siegle, Condray, & Pless, 2004) across the length of each of the trials. Pupil dilation was recorded in a darkened room using an Applied Science Laboratories (ASL, Bedford, MA) model 504 table-mounted near-infrared eye tracker with a sampling rate of 60 Hz (every 16 ms). Participants were positioned 56 cm from a 15” computer screen in a table-mounted chinrest to minimize head motion and position the eyes at a fixed and constant distance from the screen. Recording began after the right eye was calibrated to an eye tracker. Pupil data was

processed using scripts written in PERL and MATLAB. Blinks were identified as large changes in pupil dilation resulting in a loss of signal. Five samples occurring prior to and after each blink were removed prior to calculating mean pupil diameter in a trial in order to remove artificially low data points reflecting signal loss associated with blink onset and offset. For the purposes of analyzing pupillary time courses, linear interpolations were used to replace blinks throughout the data set (Siegle et al., 2004).

2.2.3 Self-Reported Arousal

The subjective experience/awareness of state arousal was assessed with the Self-Assessment Manikin (SAM), a pictorial likert scale (Bradley & Lang, 1994). Participants were introduced to the nine-point SAM arousal scale (see Figure 2) and the meaning of the images depicted on the scale during a practice session. At the end of each task-condition, the SAM arousal scale appeared on the computer screen. Subjects were instructed to "indicate how you feel right now" by pressing a number key. This measure is validated for adolescents (McCormick, Leen-Feldner, & Zvolensky, 2003) and adults (Bradley & Lang, 1994). Adult SAM arousal ratings correlate with other valid, verbal self-report measures of internal feeling states (Bradley & Lang, 1994).

2.2.4 Assessment of Inhibitory Control

The antisaccade (AS) task (Hallett, 1978) is an oculomotor task requiring subjects to suppress the reflexive tendency to generate a saccade towards a visual stimulus that appears in the periphery and to generate a voluntary eye movement to its mirror location. To obtain measurements of antisaccade accuracy and latency, eye tracking data was collected using the

aforementioned ASL eye tracker data collection parameters. Each trial proceeded as follows: 1) a central red fixation cross hair subtending 1.5º degrees visual angle appeared for either 500, 2000, or 4000 ms, providing the instruction that an AS is to be made when the cue appears 2) 200 ms of a black screen (a gap period to release fixation), 3) yellow cue subtending 1.5º visual angle appeared for 1000 ms in an unpredicted location 10º or 20º left or right of the fixation stimulus location, 4) a black screen appeared for 100 ms to serve as an intertrial interval. A total of 36 trials were administered to obtain reliable estimates of performance as determined by previous studies (Luna et al., 2004).

Eye movement responses were scored off-line by trained raters using a combination of ILAB (Gitelman, 2002) and in-house programs written in MATLAB. Saccades were identified using a velocity algorithm employing a 30 deg/sec criterion. Trained raters inspected the graphical and numerical results to identify blink artifacts and to correct occasional failures of the software to identify primary saccades. Two metrics of AS performance were of interest: error rates (1 minus the number of correct trials divided by the number of scorable trials) and latencies to initiate the AS on correct trials. Correct trials were defined as trials where the initial eye movement during the saccade response epoch met the following criteria: a velocity greater than or equal to 30º/s (Gitelman, 2002), the movement was made in the direction toward the mirror location of the peripheral cue, and the eye movement extended beyond a 2.5º visual angle central fixation zone. Express saccades characterized by an initial saccadic latency of less than 100 ms reflecting anticipatory errors were coded as error trials (Fischer & Ramsperger, 1984). Trials where no eye movement was generated (<1%) were considered unscorable. AS errors were almost always followed by a correct response in the mirror location, indicating that subjects

understood the instruction but were unable to suppress a reflexive response. One individual did not correct any of their errors, and this block was excluded from further analyses.

2.2.5 Questionnaires

Participants completed three questionnaires to assess dysregulated behavioral traits at the end of the experiment. Questionnaire items are listed in Tables 2 through 4.

The Abbreviated Dysregulation Inventory (ADI) is a 30-item scale that assesses behavioral, cognitive, and emotional dysregulation. Participants rated items on a 4-point scale (0 = "never true" to 3 = "always true"), with high scores indicating greater dysregulation. Items on the ADI have good internal consistency, evidence for construct validity, and were designed for use with adolescents (Mezzich et al., 1997; Pardini, Lochman, & Frick, 2003).

The Sensation Seeking Scale is a 40-item scale that assesses preferences for achieving excitement. The 10-item Disinhibition/Impulsiveness subscale (SSS-DI) is a measure of sensation seeking behaviors that reflect disinhibition and impulsivity. This subscale was chosen because it represents the domain of sensation seeking that also reflects poor control over behavior, whereas other subscale domains (Experience Seeking, Boredom Susceptibility, Thrill and Adventure Seeking) do not (Dahl & Gunnar, 2009; Steinberg et al., 2008). Participants selected one of two items which best described their likes or the way they feel, and high scores indicate greater disinhibition/impulsivity. The SSS was designed for use with adolescents and adults and is a reliable and valid measure (Zuckerman, 1979).

The Adult Temperament Questionnaire – Effortful Control scale (ATQ-EC) is a 35-item scale that assesses the means by which individuals control their internal emotions and external behaviors, which involves the capacity to focus and shift attention when desired, to suppress

inappropriate approach behavior, and to perform an action when there is a strong tendency to avoid it. Participants rated items on a 7-point scale (1 = "extremely untrue" to 7 = "extremely true"). The ATQ-EC has demonstrated validity and reliability (Derryberry & Rothbart, 1988; Rothbart, Ahadi, & Evans, 2000).

Additional brief questionnaires were administered to assess developmental differences in traits that may modulate reactivity to the stressor: trait anxiety, negative affect related to auditory stimulation, and sensitivity to auditory stimuli from the external environment. The State Trait Anxiety Inventory – Y (Spielberger & Vagg, 1984) is a 20-item scale that assesses trait anxiety. The trait instructions were administered ("indicate how you generally feel"). Participants rated items on a 4-point scale (1 = "Almost Never" to 4 = "Almost Always"). This scale is reliable and valid and has been used with adults and adolescents (Spielberger & Reheiser, 2004). Negative affect related to auditory stimulation was assessed via the auditory discomfort subscale of the Adult Temperament Questionnaire – Negative Affectivity scale (Derryberry & Rothbart, 1988; Rothbart et al., 2000). Sensitivity to auditory stimuli from the external environment was assessed via the auditory subscale of the Adult Temperament Questionnaire – Orienting Sensitivity scale (Derryberry & Rothbart, 1988; Rothbart et al., 2000). Each subscale consisted of 3 items rated on a 7 point scale (1 = "extremely untrue" to 7 = "extremely true").

Socioeconomic information was obtained about participants' families in light of evidence that socioeconomic status may modulate emotional reactivity (Gallo & Matthews, 2003; Manuck et al., 2005). Parents completed the form for adolescent participants. Analyses used the level of education reached by the highest-achieving parent to reflect the highest socioeconomic resources available to the participants (Phillips et al., 2009).

Participants were asked about their recent sleep because this has been shown to modulate emotional reactivity to stressors (Franzen, Buysse, Dahl, Thompson, & Siegle, 2009) and there may be developmental differences in quantity of sleep (Dahl & Lewin, 2002). Participants were asked to report the amount of sleep they obtained in the previous night, whether this was a sufficient amount of sleep, and whether there were recent changes to their sleep.

At the end of the study visit, participants were interviewed using a standardized questionnaire to understand how they perceived the tone sequences and to determine which features of the tone stimuli manipulations they were consciously able to detect.

2.3 PROCEDURE

Participants who met study criteria were asked to refrain from drinking caffeinated beverages on the day of the assessment. Participants signed consents and assents, if necessary, with parents providing consent for participants under the age of 18, and individuals who wore corrective eyewear removed contacts and wore glasses to improve eye-tracking signals. Participants were told that they would hear some sounds while they completed computer games, and then they were situated into a headrest for the purposes of eye-tracking. The study began with a calibration for eye-tracking (looked at fixation crosses), and then participants completed the nine task-condition blocks in a randomized order. Between each block, participants rested for one minute until the start of the next task. After every set of three tasks, the participants were given five minute break. At the end of testing, a two minute baseline measure of pupillary dilation was acquired as participants looked at fixation crosses (the calibration paradigm). After the oculomotor studies,

participants completed a short interview about their experience, rated tones, and completed behavioral questionnaires.

2.4 STATISTICAL ANALYSES

A repeated measures ANOVA with age group as the between-groups variable (adolescents, adults) and condition as the within-groups variable (UP, P, S, baseline - for arousal measures only) was used to examine the effects of these variables on pupillary dilation, subjective reports of arousal, and AS performance. Regressions were used to examine relationships of inhibitory control on arousal across age groups. Correlations were used to explore the significance and directionality of relationships between pupil dilation, AS performance, and self-reported dysregulated behavior.

3.0 RESULTS

Demographic, personality, and sleep characteristics of the sample are displayed in Table I. The table illustrates that there are no age group differences in gender, race, ethnicity, familial socioeconomic status, sensitivity to auditory stimuli, or trait anxiety. There is a trend for adolescents participants to have slept longer than adults the night prior to the study.

3.1 EMOTIONAL AROUSAL

3.1.1 Refinement of Measures

As expected, analyses of pupillary data indicated that arousal levels were lower at baseline (assessed at end of experiment) as compared to the UP ($F_{(1,32)} = 11.862$, $p = .002$), P ($F_{(1,32)} = 6.984$, $p = .013$), and S ($F_{(1,32)} = 16.221$, $p = .000$) conditions. However, arousal levels in S were equivalent to those in the UP ($F_{(1,44)} = .711$, $p = .404$) and P ($F_{(1,44)} = 1.602$, $p = .212$) conditions. Among adults, arousal levels in the S condition did not differ from arousal in the UP ($F_{(1,21)} = .490$, $p = .491$) and P ($F_{(1,21)} = .381$, $p = .544$) conditions. Among adolescents, arousal levels in the S condition did not differ from those in the UP condition ($F_{(1,23)} = .205$, $p = .655$) and were actually higher than in the P condition ($F_{(1,23)} = 6.173$, $p = .021$). Such results indicate that the S condition was not an independent condition, and it may instead reflect carryover effects from the

other condition or a period when participants were anticipating or reflecting upon the stressful nature of the other conditions. Therefore it was not used further as a comparison condition. All remaining analyses use pupil diameter as a dependent variable, and focus on comparisons between performance in the UP condition and the P condition as the control condition.

3.1.2 Arousal

There was a trend for a main effect of increased pupil dilation in the UP condition ($F_{(1,45)}$ = 2.743, p = .065). This effect was driven by adolescents who showed significantly greater pupil dilation in the UP condition ($F_{(1,23)}$ = 5.503, p = .028) relative to the P condition, whereas adults did not ($F_{(1,21)}$ = .046, p = .833), indicating adolescents show stronger arousal *reactivity* (see Figure 3). Compared to adults, adolescents demonstrated greater arousal in the UP condition ($t_{(45)}$ = 2.974, p = .005) as well as the in the control (P) condition ($t_{(44)}$ = 2.242, p = .030), indicating developmental differences in arousal *levels*. Subjective ratings indicated participants felt more aroused in the UP condition relative to the P condition ($F_{(1,46)}$ = 6.578, p = .014). This effect was driven by adults reporting elevated perception of arousal in the UP vs. P condition ($F_{(1,23)}$ = 10.302, p = .004), while adolescents did not show differences in subjective reports by condition ($F_{(1,23)}$ = .796, p = .381). Teens reported feeling less aroused than adults in the UP condition ($t_{(45)}$ = -2.247, p = .030), though this did not reach significance in the P condition ($t_{(45)}$ = -1.400, p = .168).

3.1.3 Arousal Time Courses

Time courses of pupil dilation were examined to explore temporal dynamics in arousal (see Figure 4). Pupillary data was averaged across 15 second intervals for the purposes of statistical analyses. Comparisons revealed that adolescents' increased pupil dilation relative to adults was sustained across the first seven of the eight 15-second intervals in both the UP (0-15s: $t_{(46)}$ = 3.446, p = .001; 15-30s: $t_{(46)}$ = 3.575, p = .001, 30-45s: $t_{(46)}$ = 3.599, p = .001, 45-60s: $t_{(46)}$ = 3.064, p = .004, 60-75s: $t_{(46)}$ = 2.787, p = .008, 75-90s: $t_{(46)}$ = 2.725, p = .009, 90-105s: $t_{(46)}$ = 2.885, p = .006, 105-130s: $t_{(46)}$ = 1.876, p = .067) and P conditions (0-15s: $t_{(45)}$ = 2.730, p = .009; 15-30s: $t_{(45)}$ = 2.406, p = .020, 30-45s: $t_{(45)}$ = 2.198, p = .033, 45-60s: $t_{(45)}$ = 2.300, p = .026, 60-75s: $t_{(45)}$ = 2.198, p = .033, 75-90s: $t_{(45)}$ = 2.507, p = .016, 90-105s: $t_{(45)}$ = 2.050, p = .046, 105-130s: $t_{(45)}$ = 1.903, p = .063) indicating that teens' elevated arousal relative to adults' was sustained for 105 seconds, the majority of the testing block.

We examined main effects of time to explore whether arousal levels changed over the course of the task. Across age groups, there was no main effect of time in either the UP ($F_{(4.218, 194.011)}$ = 1.769, p = .133) or the P condition ($F_{(3.505, 157.735)}$ = 1.931, p = .117). There was no age by time interaction in the P condition ($F_{(3.505,157.735)}$ = .337, p = .828), which paired with no main effects of time suggest stable levels of arousal in the P condition across both age groups. There was a significant age by time interaction in the UP condition ($F_{(4.218,194,011)}$ = 2.704, p = .029). Adolescents showed a significant effect of time in the UP condition ($F_{(3.740, 86.029)}$ = 2.813, p = .033), with a negative slope indicating higher levels of arousal at the beginning of the trial that subsequently stabilized. Adults did not show differences across the trial in the UP condition ($F_{(3.812, 87.685)}$ = .905, p = .461), indicating stable arousal levels comparable to their pattern of arousal in the P condition.

Contrasts comparing teens' arousal across conditions showed significantly higher levels of arousal in the first 30 seconds of UP condition relative to the P condition, but not thereafter (0-15s: $t_{(23)} = 2.419$, $p = .024$; 15-30s: $t_{(23)} = 2.846$, $p = .009$; 30-45s: $t_{(23)} = 1.701$, $p = .102$; 45-60s: $t_{(23)} = 1.405$, $p = .174$; 60-75s: $t_{(23)} = 2.033$, $p = .054$; 75-90s: $t_{(23)} = 1.324$, $p = .199$; 90-105s: $t_{(23)} = 1.747$, $p = .094$; 105-130s: $t_{(23)} = .564$, $p = .578$). Adults did not show differences in pupil dilation to the UP and P conditions at any time point (0-15s: $t_{(22)} = .409$, $p = .687$; 15-30s: $t_{(22)} = -.509$, $p = .616$; 30-45s: $t_{(22)} = -.699$, $p = .492$; 45-60s: $t_{(22)} = .600$, $p = .555$; 60-75s: $t_{(22)} = .463$, $p = .648$; 75-90s: $t_{(22)} = 1.148$, $p = .263$; 90-105s: $t_{(22)} = .266$, $p = .792$; 105-130s: $t_{(22)} = 1.497$, $p = .149$).

3.2 AROUSAL AND INHIBITORY CONTROL

There was a trend for a main effect of condition with lower error rates in the UP condition ($F_{(1,40)} = 3.233$, $p = .080$), despite predictions that error rates would be higher in this condition. AS latencies on correct trials were unaffected by condition ($F_{(1,40)} = .380$, $p = .541$).

Simple effects of condition within each age group (see Figure 5) revealed that the manipulation did not produce differences in error rates for adolescents ($F_{(1,21)} = 2.125$, $p = .160$) or adults ($F_{1,19)} = 1.193$, $p = .288$). Similarly, there were no effects of condition on response latencies for either adolescents ($F_{(1,21)} = .294$, $p = .594$) or adults ($F_{(1,21)} = .529$, $p = .475$).

There were no developmental differences in error rates in either the UP ($t_{(45)} = -.346$, $p = .731$) or the P condition ($t_{(43)} = .130$, $p = .897$). There was also a lack of developmental differences in AS latencies in both the UP ($t_{(45)} = .034$, $p = .973$) and the P conditions ($t_{(43)} =$

.295, p = .770). Consistent with this, there was no interaction of age group and condition for error rates ($F_{(1,40)}$ = .057, p = .812) or response latencies ($F_{(1,40)}$ = .062, p = .805).

In light of a lack of differences in AS performance across conditions in all age groups, it is therefore not surprising that the relationship between arousal *reactivity* (pupil diameter in UP minus pupil diameter in P) and inhibitory control *sensitivity* to arousal (AS error rate in UP minus AS error rate in P) was not significant for adolescents or adults when using linear models (teens: R^2 = .010, $F_{(1,22)}$ = .212, p = .650; adults: R^2 = .043, $F_{(1,20)}$ = .905, p = .353) or quadratic models (teens: R^2 = .010, $F_{(2,21)}$ = .103, p = .903; adults: R^2 = .091, $F_{(2,19)}$ = .951, p = .404). The relationship was also not significant for response latencies when using linear (teens: R^2 = .154, $F_{(1,22)}$ = 4.016, p = .058; adults: R^2 = .133, $F_{(1,20)}$ = 3.061, p = .096) or quadratic models (teens: R^2 = .160, $F_{(2,21)}$ = 2.002, p = .160; adults: R^2 = .237, $F_{(2,19)}$ = 2.946, p = .077).

Regressions of AS performance on pupillary dilation in the UP condition were not significant for error rates (R^2 = .052, $F_{(3,43)}$ = .783, p = .510) or response latencies (R^2 = .082, $F_{(3,43)}$ = 1.278, p = .294) when using the best-fitting, quadratic model. However, the relationship for error rates was significantly moderated by age group (ΔR^2 = .157, $\Delta F_{(2,41)}$ = 4.066, p = .025) (see Figure 6a). This effect was driven by a significant quadratic model fit in adolescents (R^2 = .273, $F_{(2,21)}$ = 3.945, p = .035) but not adults (R^2 = .138, $F_{(2,20)}$ = 1.608, p = .225). Adolescents' performance modeled an inverted U, with the greatest AS error rate at intermediate levels of arousal. The regression of response latencies on pupillary dilation was not moderated by age group (ΔR^2 = .078, $\Delta F_{(2,41)}$ = 1.916, p = .160).

Regressions of AS performance on pupillary dilation in the P condition were not significant for error rates (R^2 = .073, $F_{(3,42)}$ = 1.099, p = .360) or response latencies (R^2 = .052, $F_{(3,42)}$ = .768, p = .518) when using the better-fitting quadratic model. This relationship was not

moderated by age group for error rates ($\Delta R^2 = .001$, $\Delta F_{(2,40)} = .021$, $p = .979$) or response latencies ($\Delta R^2 = .053$, $\Delta F_{(2,40)} = .019$, $p = .981$). These non-significant findings highlight the specificity of the age-modulated relationship between arousal and performance to the stressor condition.

In light of the limited number of data points used to estimate regression lines for each age group, a categorical variable was created for arousal to better understand the nature of the relationship between arousal levels and AS performance in the UP condition. A three-level variable was created to reflect the quadratic nature of the relationship, and results revealed that adults performed equally in low, medium, and high arousal conditions ($F_{(2,20)} = .788$, $p = .468$). There was a trend indicating teens performed differently across arousal levels ($F_{(2,21)} = 3.048$, $p = .069$). Due to low power resulting from the small number of teens categorized in the low and medium levels of arousal, ANOVAs were re-run collapsing low and medium arousal groups into a single category (see Figure 6b). Results revealed that teens performed best at high as opposed to medium/low arousal ($F_{(1,22)} = 6.373$, $p = .019$), while adults' performance did not differ between high and medium/low arousal groups ($F_{(1,21)} = .862$, $p = .364$). Consistent with this, there was a significant interaction of age group by arousal group ($F_{(1,43)} = 5.198$, $p = .028$).

Adolescents with high arousal performed comparably to adults with low/medium arousal ($t_{(30)} = .836$, $p = .410$), suggesting that adolescents' higher levels of arousal may allow them to perform like adults with typical levels of arousal for their age group.

3.3 RELATIONSHIP TO BEHAVIOR TRAITS

In order to assess the association between arousal, inhibitory control, and behavior traits reflecting cognitive control over behavior, the relationship between pupil dilation, AS performance, and behavioral reports of dysregulation (ADI, SSS-DI, ATQ-EC) were examined using correlations within each age group. As these analyses were exploratory, questionnaires were correlated with arousal *levels* (pupil diameter in UP condition), arousal *reactivity* (pupil diameter in UP minus pupil diameter in P), inhibitory control under arousal (AS error rates in UP condition), and sensitivity of IC to arousal (AS error rate in UP minus AS error rate in P).

Results indicated no significant correlations between pupil diameter in the UP condition and any of the questionnaire measures among adults (ADI: $r(24) = .177$, $p = .409$, SSS-DI: $r(24) = .309$, $p = .141$, ATQ-EC: $r(24) = -.118$, $p = .584$) nor among teens (ADI: $r(24) = .151$, $p = .481$, SSS-DI: $r(24) = .062$, $p = .773$, ATQ-EC: $r(24) = -.076$, $p = .724$), indicating that dysregulated behavior does not relate to arousal levels at either point in development. Results also indicated no relationship between difference in pupil diameter between conditions and questionnaire measures among adults (ADI: $r(23) = .102$, $p = .643$, SSS-DI: $r(23) = -.075$, $p = .735$, ATQ-EC: $r(23) = -.035$, $p = .875$) nor among teens (ADI: $r(24) = -.125$, $p = .560$, SSS-DI: $r(24) = .013$, $p = .953$, ATQ-EC: $r(24) = .221$, $p = .300$), showing that dysregulated behavior does not relate to measures of arousal reactivity at either point in development.

AS error rates in the UP condition was not correlated with questionnaires among adults (ADI: $r(23) = -.035$, $p = .876$, SSS-DI: $r(23) = -.020$, $p = .928$, ATQ-EC: $r(23) = -.333$, $p = .121$) nor among teens (ADI: $r(24) = -.123$, $p = .566$, SSS-DI: $r(24) = -.160$, $p = .455$, ATQ-EC: $r(24) = .160$, $p = .456$), indicating that dysregulated behavior does not relate to measures of inhibitory control under states of arousal.

Difference in AS error rates was not correlated with any of the questionnaires among adults (ADI: $r(22) = -.219$, $p = .327$, SSS-DI: $r(22) = -.068$, $p = .765$, ATQ-EC: $r(22) = .039$, $p = .862$), but there was a significant relationship among teens for all questionnaires (ADI: $r(24) = -.649$, $p = .001$, SSS-DI: $r(24) = -.452$, $p = .027$, ATQ-EC: $r(24) = .491$, $p = .015$) (see Figure 7), indicating that dysregulated behavior is related to *sensitivity* of IC to manipulations of arousal. Directionality was consistent, with more dysregulated behavior, more impulsive symptoms, and less effortful control correlated with better performance in the UP relative to P condition. Since some individuals made fewer errors in the UP condition compared to the P condition while others made fewer errors in the P condition, measures of dysregulation were correlated with the absolute value of AS error rates to determine whether behavioral dysregulation is related to the *variability* of inhibitory control under different arousal conditions. Results indicated no significant relationship among teens for all questionnaires (ADI: $r(24) = .088$, $p = .681$, SSS –DI: $r(24) = .156$, $p = .467$, ATQ-EC: $r(24) = .020$, $p = .927$), indicating that behavioral dysregulation is not related to the variability of between arousal conditions but rather the directionality. That is, teens with more dysregulated behavior do not show more variability in error rates across conditions. Instead they show increasingly better performance in the UP condition relative to the P condition.

Developmental comparisons revealed no differences between adolescents and adults in mean ADI score ($t_{(38.307)} = 1.395$, $p = .171$) or ATQ-EC score ($t_{(39.879)} = -.660$, $p = .513$). Adolescents' mean SSS-DI scores were higher than adults' ($t_{(46)} = 2.909$, $p = .006$), indicating higher levels of impulsive, disinhibited sensation seeking.

3.4 PARTICIPANT REPORTS ABOUT TONE STIMULI

In interviews at the end of the experiment, more than half of participants (56%) noted that the tones they heard (referring to the UP and P tones collectively) were “annoying” or “irritating”. Almost all (96%) were also able to distinguish that not all tone sequences were the same, but less than half of participants (39%) were able to identify the unpredictable nature of the tone presentation (via reports of different rhythms, beats, etc.) as the source of the difference. Similarly, most participants could not identify the additional manipulations; less than half (43% percent) could identify the differences in the sound frequencies across conditions, and only 27% noticed differences in the quality (sine wave versus saw tooth wave) of the tone being played. Multiple participants reported noticing differences in tempo or volume of tone sequences which were not actually manipulated. These results indicate that the tone manipulation was not clearly identifiable to the majority of participants, and supports claims that the unpredictable stimuli can elicit effects without placing any more demands for top-down allocation of attention than predictable tones.

Developmental comparisons indicated that teens were less able to identify that tone sequences differed according to unpredictability ($\chi^2(1) = 6.875$, $p = .009$), which may contribute to their less differentiated subjective reports of arousal across conditions. Teens and adults did not differ in their ability to recognize the sound frequency ($\chi^2(1) = .762$, $p = .383$) and tone quality manipulations ($\chi^2(1) = .105$, $p = .745$).

4.0 DISCUSSION

This study explored developmental differences between adolescents and adults in autonomic arousal, its effects on inhibitory control, and its relationship with behavior. Results indicate that adolescents have higher levels of autonomic arousal and reactivity, and unlike adults, their inhibitory control is susceptible to the effects of arousal in a manner relevant to behavioral traits. More broadly, these results suggest that adolescents' emotional and cognitive control processes are more susceptible to external stressors and expands upon prior research showing that cognitive control has yet to reach adult levels of stability during this developmental period (Luna et al., 2008).

4.1 AUTONOMIC AROUSAL

Results indicated that compared to adults, adolescents have higher levels of arousal that remained elevated throughout the experiment. Adults, on the other hand, showed overall less arousal and arousal levels were was stable over the course of a task and across different conditions. These data indicate that adolescents have higher levels of baseline arousal as well as arousal reactivity than adults. This extends prior work showing that adolescents show greater pupillary reactivity to emotional stimuli relative to children (Silk et al., 2009), suggesting that adolescence may be a unique period marked by an increased autonomic responsivity to stressors.

Higher arousal in adolescence may contribute to their known immaturities in emotional processing and may also underlie their vulnerabilities to anxiety and mood disorders (Dahl, 2004; Spear, 2009) as well as predisposition for risk taking behavior (Somerville, Jones, & Casey, 2009; Steinberg, 2004).

However, despite adolescents' physiological evidence of higher levels of arousal, they did not show awareness of their arousal levels nor did they show awareness of changes in arousal due to the stressor. This dissociation is consistent with a findings by (Stroud et al., 2009) and (Gunnar et al., 2009) showing that physiological stress responses are dissociated from subjective reporting of the physiological affective response in the teenage years. Adolescents' poor reporting of subjective arousal may go hand in hand with their elevated levels of physiological arousal. That is, limitations in explicit awareness of their levels of arousal may undermine efforts to engage modulatory processes.

Adolescents reported feeling less arousal than adults despite evidence that they have higher levels of arousal than adults. On the other hand, adults, who did not show physiological evidence for arousal differences by condition, rated feeling differentially aroused across the conditions. Results characterizing the time course of arousal throughout the experiment showed that adults did not change arousal levels, which were constantly low, while adolescents lowered their high arousal over the course of the trial. Adult's awareness of arousal may trigger specialized top-down regulatory processes that serve to stabilize pupil dilation, which has been shown to reflect task-related neural activity (Siegle, Steinhauer, Stenger, Konecky, & Carter, 2003). This adult manner to regulate arousal appears to have unique components: it is automatic as it is evident immediately at the start of the study, it is sustained as it maintains a regulated level throughout a trial, and it is independent from processes that support awareness of arousal as

they don't fluctuate with changes in reports of arousal. The finding that adolescents do eventually lower their arousal at the end of the trial suggests that they are able to regulate although it is not automatic like adults and may be supported by a different system. These results fit well with the literature indicating immaturities in top down regulation of behavior in adolescence (Luna et al., 2008). This disconnect is important because it is the subjective experience of arousal rather than objective levels of arousal that define anxiety disorders and cause impairment in everyday functioning. Therefore, immaturities in the ability to readily engage automatic process of top down regulation of arousal in adolescence may underlie susceptibility to unregulated emotional reactivity that underlies risk taking behavior and the emergence of psychopathology. Importantly, these results delineate that what matures from adolescence to adulthood is the efficiency to engage regulatory processes which are available but still slow to come on line.

4.2 AROUSAL AND INHIBITORY CONTROL

This study sought to push inhibitory control systems using an emotion manipulation paradigm that has been shown to activate amygdala activity (Herry et al., 2007). Even though the manipulation elicited increased autonomic arousal reactivity, adolescents' inhibitory control was comparable to adults' inhibitory control even under arousal conditions. This was surprising in light of predictions that adolescents' inhibitory control would be differentially susceptible to the effects of emotion. Instead, these results indicate that even in emotionally-modulated circumstances, adolescents can demonstrate adult levels of inhibitory control.

While the effects of different levels of arousal on inhibitory control were minimal, an interesting age-modulated effect emerged when we explored how arousal was associated with inhibitory control. Teens but not adults showed a significant relationship between arousal levels and inhibitory control, with higher levels of arousal facilitating improved inhibitory control in this age group. These results suggest that while adolescents do have the ability to perform comparably to adults, there are still immaturities in their systems that makes their cognitive control vulnerable to being influenced by external variables such as arousal. That they showed optimal performance at higher arousal suggests that they may need elevated levels of arousal to perform like adults. Alternatively, higher arousal during optimal performance could suggest that adolescents may require greater attention and effort to exert cognitive control at adult levels.

4.3 RELATIONSHIP TO BEHAVIOR TRAITS

We also investigated the association between inhibitory control under different arousal conditions and behavioral traits of dysregulation, which has been explored using measures of temperament in early development (Posner & Rothbart, 1998, 2007; Rueda, Posner, & Rothbart, 2005), but remains to be understood in adolescence (Galvan, Hare, Voss, Glover, & Casey, 2007; Somerville et al., 2009). When we associated inhibitory control with assessments of affective and behavioral dysregulation, impulsive sensation seeking, and effortful control of behavior, we found that adolescents but not adults showed a significant association with inhibitory control. A consistent relationship emerged across measures, with adolescents who were more dysregulated,

impulsive, and with less effortful control over their behavior showing greater sensitivity of inhibitory control to elevated arousal conditions, performing best in the unpredictable condition.

Importantly, the relationship that emerged was specific. None of the various measures of behavioral dysregulation were correlated with measures of autonomic arousal levels or reactivity. Instead, they were related to emotionally-modulated inhibitory control performance, and importantly the directionality of the inhibitory control under different emotional arousal states mattered. The *sensitivity* of inhibitory control to high versus low arousal conditions is what is relevant to behavioral dysregulation, not the susceptibility of inhibitory control to high arousal states irrespective of inhibitory control in other conditions or the degree of variability of inhibitory control across different arousal conditions. Specifically, it is the teens whose inhibitory control was best in the unpredictable condition (under high arousal) who plan ahead less than their peers, who lose their temper or become emotional seemingly with no warning, who cannot follow through with their plans, and who impulsively seek out exciting, novel experiences. Our results suggest that these dysregulated teens operate optimally at higher arousal levels, and their behaviors may reflect a trait where higher arousal is needed for behavior to be cognitively controlled.

These findings also highlight important developmental transitions from adolescence to adulthood. We found that in adolescence, individual differences in behavior are relevant to arousal-modulated inhibitory control, whereas in adulthood, behavior does not show an association with emotionally-modulated control abilities. This finding suggests that dysregulation in adulthood may be qualitatively different from adolescence, be it from developmental changes in the factors that drive dysregulated behavior or maladaptive compensatory mechanisms that emerge from experience. Secondly, we found that adolescents

reported specific regulatory deficits which may reflect their specific behavioral susceptibilities to modulation. That is, teens and adults did not differ in their reports of effortful control over behavior or their ability to regulate their own cognitions and emotions in situations that do *not* involve incentives or a peer group. Rather, they reported immaturities in regulation when cognitive control is required in the context of both emotional arousal and potential social rewards. This is consistent with evidence that adolescents' limited control over behavior emerges in social contexts (Steinberg, 2004), and this may reflect behavioral control systems that are more sensitive to both heightened emotionality *and* increased sensitivity to rewards (Nelson et al., 2005; Somerville et al., 2009).

4.4 IMPLICATIONS FOR BRAIN MATURATION AND THE EMERGENCE OF PSYCHOPATHOLOGY

Overall, these findings indicate that affective and cognitive control systems become more solidified from adolescence into adulthood, with affective and inhibitory systems becoming more stable and less amenable to disruption by external factors. From adolescence to adulthood, what develops is an increasing robustness of the adolescent affective and inhibitory control systems to interference. There is a developmental decrease in arousal levels and reactivity with a concomitant increase in self-awareness of arousal. Similarly, cognitive control becomes less influenced by arousal with age, though in adolescence cognitive control is best at the high levels of arousal characteristic of the teen years. Lastly, with age, the sensitivity of cognitive control to arousal becomes less relevant to dysregulated behavior. Adolescents' behavior is more sensitive to their variability in their arousal states, with those having more susceptible systems demonstrating

greater difficulty regulating their emotions, persisting on goal-directed tasks in light of their emotions, and engaging in impulsive sensation-seeking activities.

Neurobiological models of adolescent emotional and cognitive behavior posit that behavioral changes are supported by an imbalance between the developmental maturity of cortical and subcortical circuitries (Casey, Jones, & Hare, 2008; Dahl & Gunnar, 2009; Somerville et al., 2009; Spear, 2000). Specifically they posit that the relative maturity of limbic structures compared to the ongoing maturation of cortical circuitries results in variable adolescent cognitive control of behavior. Given the continued maturation of the brain that has been found to underlie age related improvements in behavior, it is important to consider possible links between our results and what is known regarding specifics of age related brain changes. This experiment utilized a tone paradigm with known mechanisms for eliciting arousal and an inhibitory control task with well-delineated neural correlates. Adolescents' elevated pupillary reactivity to the tones was likely a reflection of increased amygdala activity, as pupillary dilation is supported by activity in corticolimbic and midbrain circuitries (Sah et al., 2003; Siegle et al., 2003; Silk et al., 2009), and there is evidence that the unpredictable tones elicit neural activity in the amygdala in particular (Herry et al., 2007). Consistent with this, functional imaging studies have reported increased amygdala activity to emotional stimuli in adolescence (Ernst et al., 2005; Guyer et al., 2008; Hare et al., 2008; Monk, McClure et al., 2003) and increases in amygdala structural volumes in adolescence (Sowell, Trauner, Garmst, & Jernigan, 2002). Increased amygdala activity may contribute to differing inhibitory control abilities in adolescence but not adulthood because of differential connectivity between cortical and subcortical regions across development.

The neural circuitry implicated in the inhibitory control required by the antisaccade task canonically involves a network involving the dorsolateral prefrontal cortex (DLPFC),

supplementary eye fields (SEF), and intraparietal sulcus (IPS). While anatomical connectivity studies have failed to find direct connections between the amygdala and any of these regions (DLPFC: (Barbas, 2000; McDonald, Mascagni, & Guo, 1996; Stefanacci & Amaral, 2002), there is evidence for indirect connections via ventral and medial PFC regions (Amaral, 2002; Groenewegen, Wright, & Uylings, 1997; McDonald et al., 1996; Sah et al., 2003), which have been implicated in emotion regulation (Delgado, Nearing, Ledoux, & Phelps, 2008) and are responsive to stressors (Liston et al., 2006). It is possible that the relative strength of afferent input to the ventromedial PFC and its afferents to the DLPFC are stronger in adolescence, and into adulthood there is a shift to greater DLPFC control, with stronger efferent inputs to the ventromedial PFC that serve to minimize amygdala activity and its effects on inhibitory control and behavior (Sowell, Thompson, & Toga, 2007).

A dynamic shift in the balance between cortical and limbic structures during adolescence could potentially represent a period where vulnerability to the development of mood and anxiety disorders may be particularly high (Casey et al., 2008; Dahl & Gunnar, 2009; Nelson et al., 2005; Spear, 2000). There is much support for theories that the pathology of affective disorders represents an imbalance between bottom-up attention to threat and top-down control mechanisms (for reviews, see Bishop (2009) and Quirk & Gehlert (2003). If adolescence is indeed a time of shifting balances between these two modulating circuits – where subcortical systems are already mature but cortical control circuitries are still maturing – then this may be the time when the shift in the balance could potentially go awry for a subset of individuals with certain risk characteristics.

4.5 LIMITATIONS

We expected that the manipulation (a stressor) would lead to differences in emotion that would in turn contribute to differential effects on cognition. While the stressor elicited emotional reactivity in adolescents, data indicate that adults' pupil dilation did not differ between task-conditions, which limits our ability to draw conclusions about how autonomic arousal differentially affect cognitive control over development. Instead, these results indicate that the same stressor manipulation elicited a different response in adolescents (differential pupillary dilation) and adults (differential subjective reports), highlighting how the same stressor can initiate different emotional pathways across different points in development. How pupillary dilation in the teen years maps onto subjective reports of arousal in adulthood and whether they represent an overlapping construct of emotion across time is unclear. Future studies may seek to find a stimulus that can equate levels of arousal or subjective ratings in order to examine the effects of emotion on cognitive control in a more controlled manner, but this raises the question of whether such a manipulation has any ecological validity (that is, does one equate the stressor and look at how it affects emotion and cognition or vary the stressor to equate emotion so that one can examine how it affects cognition?). Though we can broadly draw conclusions about how emotion affects cognitive control, it is important to highlight that there are developmental differences in emotion elicitation processes which need to be acknowledged when interpreting findings.

4.6 FUTURE STUDIES

Future studies are necessary to validate that adolescents' higher arousal corresponds to increased amygdala activity, and to explore how this activity may alter patterns of neural activity associated with the antisaccade task. Given our finding that teens perform equivalently to adults in the emotion-modulated AS task, findings from fMRI studies would not be confounded by developmental differences in performance. As compared to adults, adolescents may show increased activity in ventromedial prefrontal and orbitofrontal cortical regions due to an increased need for emotion regulation due to heightened emotional reactivity. Would an increase in activity associated with emotion regulation be related to changes in cognitive control circuitries? Prior research examining reward-modulated inhibitory control suggests that the reward motivation system may be sluggish but overactive in the presence of reward contingencies (Geier et al., 2009). fMRI studies characterizing the ability to recruit top down modulation of arousal may show a similar pattern of less efficient recruitment of top down circuitries needed for adult level controlled behavior. Comparisons of neural correlates of inhibitory control of teens at "typical" high levels of arousal with adults at "typical" lower levels of arousal could provide a clearer picture of representative arousal-inhibitory control interactions. Ideally, longitudinal studies could provide more sensitive information about the nature of developmental change in the brain and its relationship to behavior.

The findings that certain adolescents are more susceptible to external modulations highlights the value of exploring how individual differences contribute to emotion and emotion-modulated inhibitory control at this time. Such factors may include gender, pubertal timing, genotype for genes expressed in corticolimbic circuits, exposure to stressors, peer group status, quality of friendships, and parenting. fMRI investigations comparing teens with high arousal/good

inhibitory control with those with lower arousal/worse inhibitory control could clarify what neural mechanisms facilitate some adolescents to perform better than others. Comparisons of adolescents varying in dysregulation (according to questionnaire-based reports or observations) could provide insight into individual differences in neural correlates behavior. Ideally, group-based longitudinal analyses (Nagin, 2005) could identify subgroups on the basis of behavioral subgroups, gender, pubertal status, etc. that may follow different trajectories, and specify more clearly the nature of developmental change of emotion-modulated cognitive control and its neural correlates.

Table 1. Participant characteristics.

	Adolescents (n = 24)	Adults (n = 24)	Test statistic	p
Demographics				
Age				
M	15.9	27.2		
SD	0.6	1.8		
Sex (% Female)	50	50	$\chi^2(1) = 1.000$	1.000
Race (% White)	80	83	$\chi^2(1) = 0.137$	0.712
Ethnicity (% Non-Hispanic)	88	92	$\chi^2(2) = 0.357$	0.837
Socioeconomic status				
Parental education (mean rank)	23.1	25.9	U = 255‡	0.464
Personality Traits				
Negative Affectivity - Auditory Discomfort				
M	11.2	11.8	t(40) = -0.486	0.630
SD	3.0	4.6		
Orienting Sensitivity - Auditory				
M	14.5	15.9	t(40) = -1.229	0.226
SD	3.5	3.4		
Trait Anxiety				
M	33.5	32.0	t(46) = 0.587	0.560
SD	9.1	8.3		
Sleep Status				
Sleep				
Hours - previous night				
M	8.0	7.2	t(46) = 1.948	0.058†
SD	1.3	1.5		
Adequate amount of sleep? - previous night (% Yes)	80	83	$\chi^2(1) = 0.137$	0.712
Recent changes to sleep? (% Yes)	21	21	$\chi^2(2) = 1.413$	0.598

‡ $n_1 = 24$, $n_2 = 24$

† Significant at trend level

Table 2. Sensation Seeking Scale – Disinhibition/Impulsiveness subscale (Zuckerman, 1979).

Instructions: Please indicate which of the choices most describes your likes or the way you feel.

I like "wild" uninhibited parties (r)
I prefer quiet parties with good conversation. (r)

I keep track of where my things are.
I don't keep very close track of where my things are.

I rarely, if ever, do anything crazy.
I enjoy doing things that others might find crazy.

I am not interested in experience for its own sake.
I like to have new and exciting experiences and sensations even if they are a little frightening, unconventional or illegal.

I like to date people who are physically exciting. (r)
I like to date people who share my values. (r)

Before I make a decision I usually try to consider all sides of the issue.
I like to make decisions based on a 'gut feeling'.

I prefer to spend my money right away rather than save it. (r)
I prefer to save my money and think about what I really want to purchase. (r)

Even if I had the money, I would not want to associate with flighty rich people who fly from one place to another to attend high society events.
I could see of myself looking for pleasures around the world with the "jet set".

I try to be fully prepared before I being working on anything.
If I get the chance to do something fun, I do it no matter what I had been doing before.

I consider myself as a pretty impulsive person. (r)
I am a cautious person. (r)

(r) reverse scored

Table 3. Abbreviated Dysregulation Inventory (Mezzich et al., 1997)

Instructions: Below is a series of statements. Indicate how often they are true of you by circling the number that best describes you.

Response options: never true, occasionally true, mostly true, always true

Behavioral Dysregulation
I have difficulty remaining seated at school or at home during dinner.
I get very fidgety after a few minutes if I am supposed to sit still.
I have difficulty keeping attention on tasks.
I get into arguments when people disagree with me.
Little things or distractions throw me off.
I can't seem to stop moving.
Most of the time I don't pay attention to what I am doing.
I get bored easily.
I am easily distracted.
I spend money without thinking about it first.

Cognitive Dysregulation (all items are reverse scored)
I develop a plan for all my important goals.
I put my plans into action.
I think about the future consequences of my actions.
Once I have a goal I make a plan to reach it.
As soon as I see things are not working, I do something about it.
I consider what will happen before I make a plan.
I think about my mistakes to make sure they don't happen again.
I spend time thinking about how to reach my goals.
Failure at a task or in school makes me work harder.
I stick to a task until it is finished.

Emotional Dysregulation
I have trouble controlling my temper.
I lose sleep because I worry.
When I am angry I lose control over my actions.
I get so frustrated that I often feel like a bomb ready to explode.
I fly off the handle for no good reason.
There are days when I'm "on edge" all the time.
I easily become emotionally upset when I am tired.
Often I am afraid I will lose control of my feelings
I slam doors when I am mad.
My mood goes up and down without reason.

Table 4. Adult Temperament Questionnaire – Effortful Control (Derryberry & Rothbart, 1998 ; Rothbart, Ahadi, & Evans, 2000)

Instructions: Please read each statement carefully and give your best estimate of how well it describes you. Circle the appropriate number below to indicate how well a given statement describes you.

Response options: extremely untrue, quite untrue, slightly untrue, neither true nor false, slightly true, quite true, extremely true, not applicable

Inhibitory Control

If I want to, it is usually easy for me to keep a secret.
It is easy for me to hold back my laughter in a situation when laughter wouldn't be appropriate.
When I see an attractive item in a store, it's usually very hard for me to resist buying it. (r)
I can easily resist talking out of turn, even when I'm excited and want to express an idea.
When I decide to quit a habitual behavioral pattern that I believe to be undesirable, I am usually successful.
When I'm excited about something, it's usually hard for me to resist jumping right into it before I've considered the possible consequences. (r)
Even when I feel energized, I can usually sit still without much trouble if it's necessary.
I often avoid taking care of responsibilities by indulging in pleasurable activities. (r)
At times, it seems the more I try to restrain a pleasurable impulse (e.g., eating candy), the more likely I am to act on it. (r)
I usually have trouble resisting my cravings for food drink, etc. (r)
It is easy for me to inhibit fun behavior that would be inappropriate.

Activation Control

I usually finish doing things before they are actually due (e.g., paying bills, finishing homework, etc.).
I am often late for appointments. (r)
I often make plans that I do not follow through with. (r)
As soon as I have decided upon a difficult plan of action, I begin to carry it out.
If I think of something that needs to be done, I usually get right to work on it.
I can make myself work on a difficult task even when I don't feel like trying.
Even when I have enough time to complete an activity today, I often tell myself that I will do it tomorrow. (r)
If I notice I need to clean or wash something (e.g., car, apartment, laundry, etc.), I often put it off until tomorrow. (r)
I hardly ever finish things on time(r)
I usually get my responsibilities taken care of as soon as possible.
When I am afraid of how a situation might turn out, I usually avoid dealing with it. (r)
I can keep performing a task even when I would rather not do it.

Attentional Control

When I am sad about something, it is hard for me to keep my attention focused on a task. (r)

When I am anxious about the outcome of something, I have a hard time keeping my attention focused on a task. (r)

It is very hard for me to focus my attention when I am distressed. (r)

When I am happy and excited about an upcoming event, I have a hard time focusing my attention on tasks that require concentration. (r)

When I am especially happy, I sometimes have a hard time concentrating on tasks that require me to keep track of several things at once. (r)

When I hear good news, my ability to concentrate on taking care of my responsibilities goes out the window. (r)

When I am trying to focus my attention, I am easily distracted. (r)

When trying to focus my attention on something, I have difficulty blocking out distracting thoughts. (r)

When trying to study something, I have difficulty tuning out background noise and concentrating. (r)

When interrupted or distracted, I usually can easily shift my attention back to whatever I was doing before.

I am usually pretty good at keeping track of several things that are happening around me.

It's often hard for me to alternate between two different tasks. (r)

(r) reverse scored

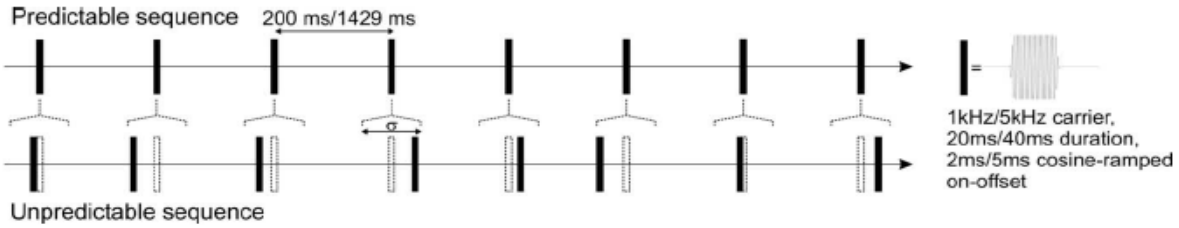


Figure 1. Predictable and unpredictable tone sequences (from Herry et al., 2007) .

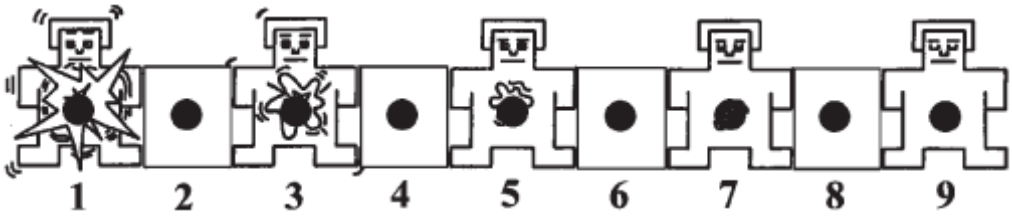


Figure 2. Self-Assessment Manikin (Backs, da Silva, & Han, 2005).

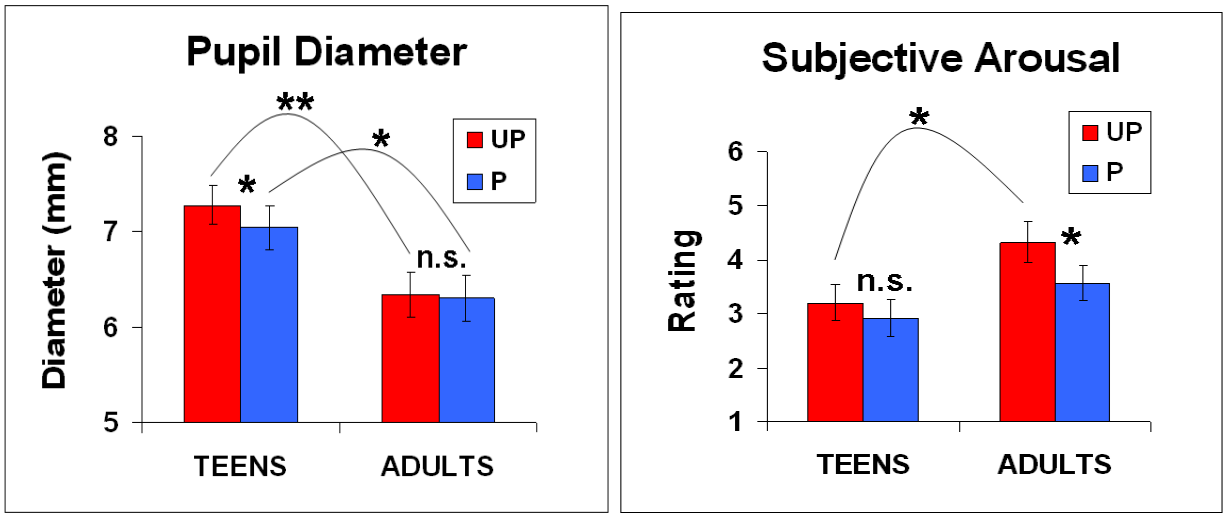
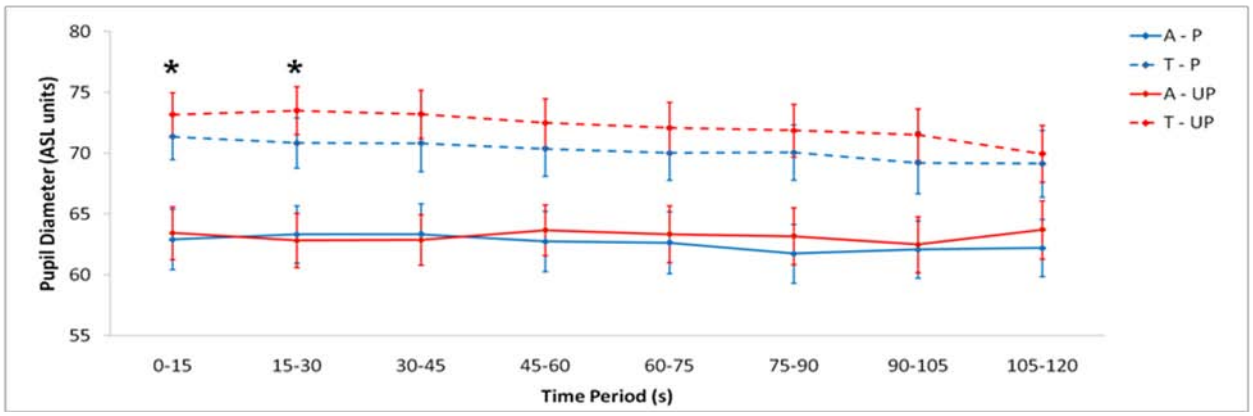


Figure 3. Effects of condition on arousal.



* denotes significant effect of condition within adolescent age group at each time point

Figure 4. Arousal time courses.

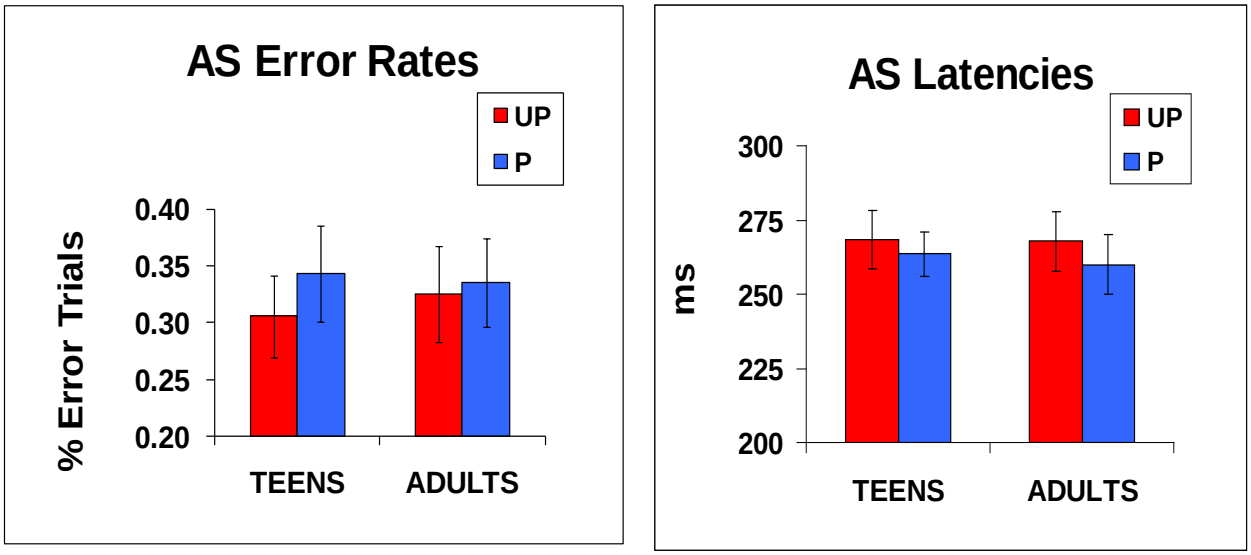


Figure 5. Effects of condition on antisaccade performance.

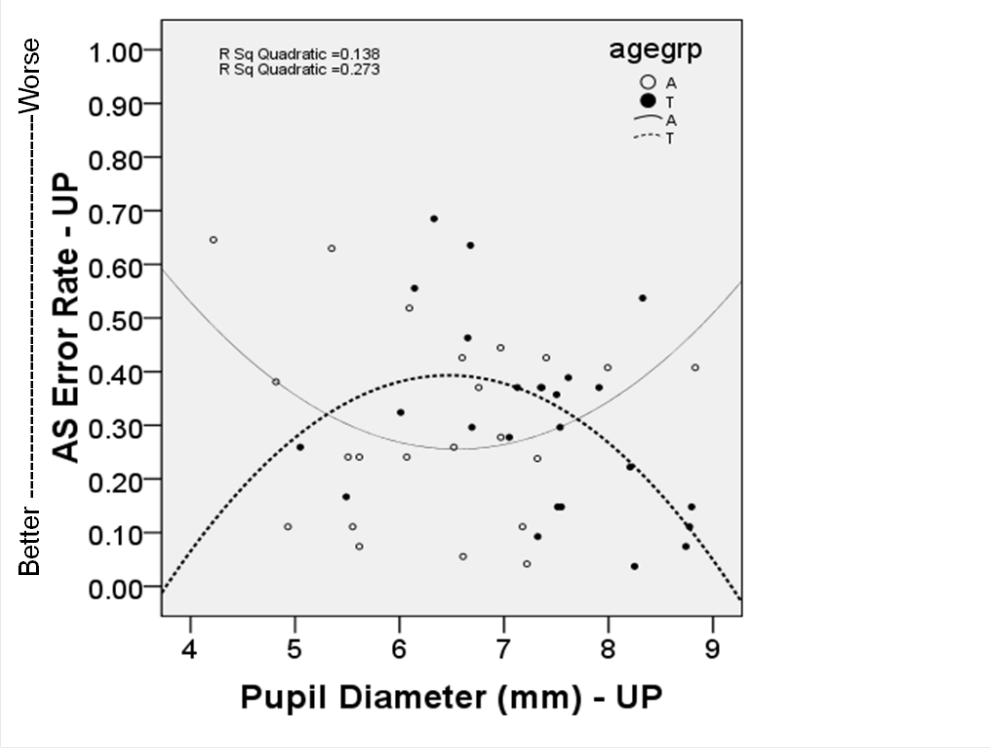


Figure 6a. Relationship of arousal and antisaccade performance in the unpredictable condition.

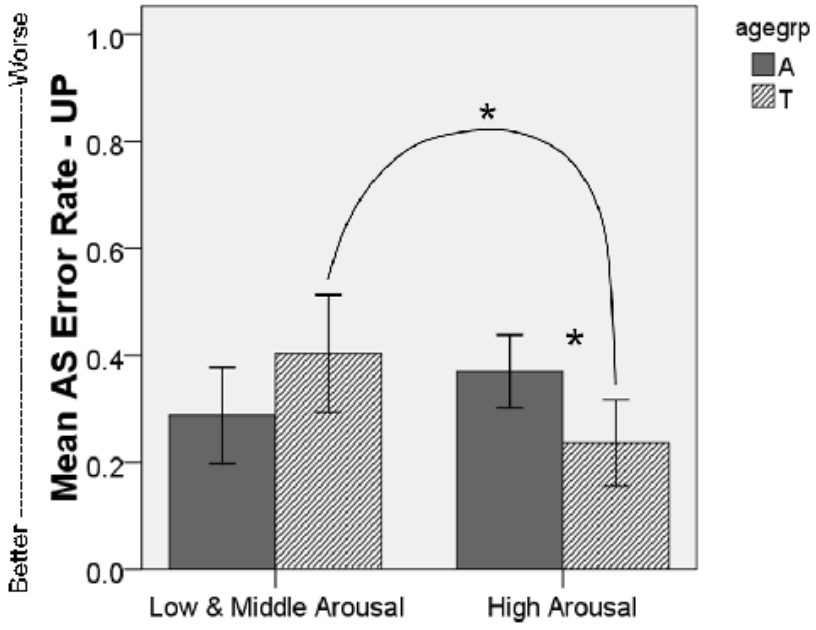


Figure 6b. Relationship of arousal and antisaccade performance in the unpredictable condition: categorical arousal variable.

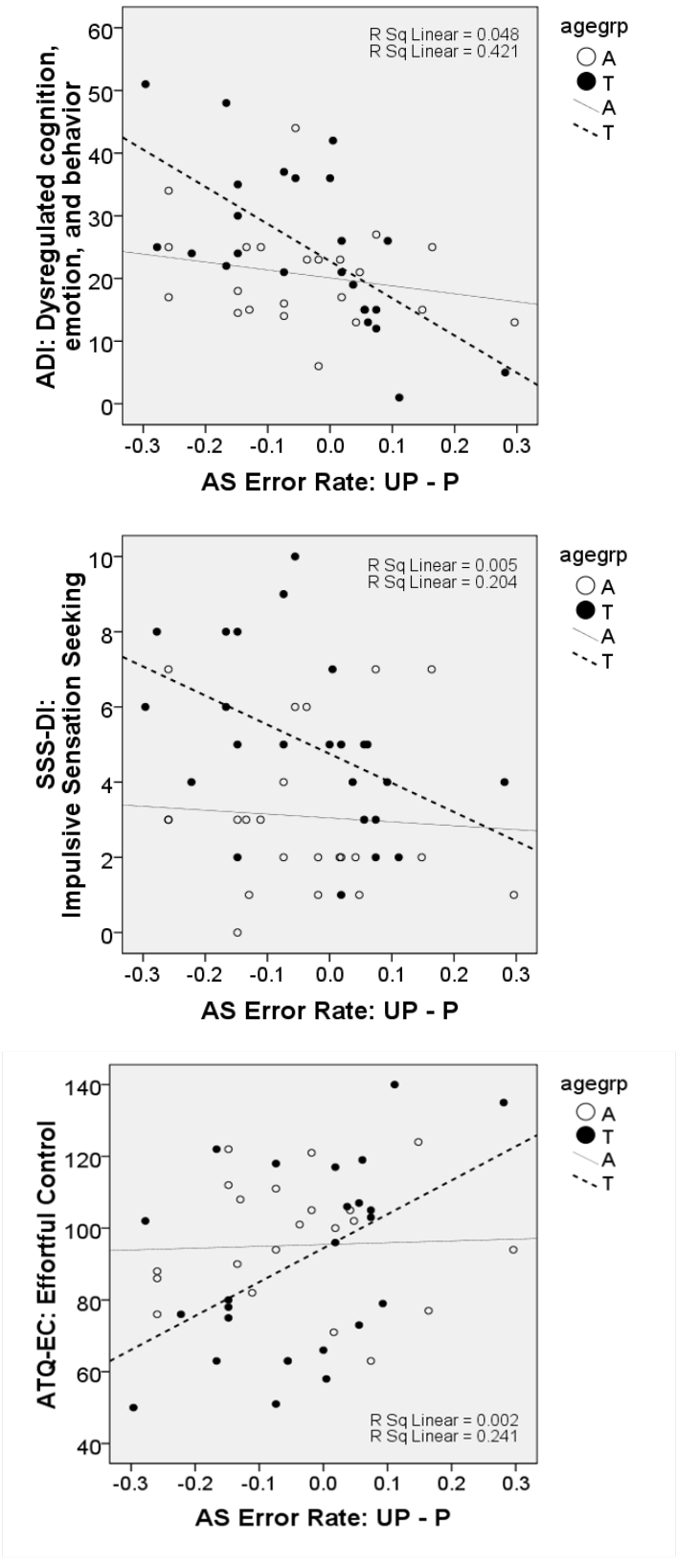


Figure 7. Relationship of questionnaire measures and differences in antisaccade performance.

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