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Stress Reactivity Speeds Basic Encoding Processes in Infants

ABSTRACT: Acute stress attenuates frontal lobe functioning and increases distractibility while enhancing subcortical processes in both human and nonhuman animals (reviewed by Arnsten [2009] *Nature Reviews Neuroscience*, 10(6):410–422). To date however these relations have not been examined for their potential effects in developing populations. Here, we examined the relationship between stress reactivity (infants' heart rate response to watching videos of another child crying) and infant performance on measures of looking duration and visual recognition memory. Our findings indicate that infants with increased stress reactivity showed shorter look durations and more novelty preference. Thus, stress appears to lead to a faster, more stimulus-ready attentional profile in infants. Additional work is required to assess potential negative consequences of stimulus-responsivity, such as decreased focus or distractibility. © 2016 Wiley Periodicals, Inc. *Dev Psychobiol* 58:546–555, 2016.

Keywords: attention; recognition memory; stress; stress reactivity; human infant; physiology; locus coeruleus

INTRODUCTION

Animal studies indicate that acute stress is associated with a cascade of changes in the brain, thought to mobilize the organism for fast action (Arnsten, 1998; Arnsten, 2009). This shift downregulates complex flexible thinking, dependent on frontal lobes, while facilitating more rapid responses dependent on subcortical networks (Arnsten, 2009).

In animals, elevated stress is associated with impaired selective attention (Minor, Jackson, & Maier, 1984), and a perseverative pattern of response that is consistent with prefrontal cortex dysfunction (Arnsten & Goldman-Rakic, 1998). In adults, exposure to psychosocial stress leads to worse performance on attentional set-shifting, together with concomitant decreases in fronto-parietal connectivity (Liston, McEwen, & Casey, 2009). These changes are mediated by catecholamines such as dopa-

mine and norepinephrine, released at the time of stress by brainstem sympathetic nuclei (Joëls & Baram, 2009). The sympathetic nervous system is known as the “fast-acting” arm of the organism’s response to stress and novelty, well-known for its parallel “fight-or-flight” effects on the body (McEwen & Sapolsky, 1995).

While stress downregulates the frontal lobes, it simultaneously *enhances* processes dependent on *subcortical* structures, such as basic memory consolidation, habit formation and fear conditioning (Cahill & McGaugh, 1998; Luethi, Meier, & Sandi, 2008). Additionally, catecholamine release associated with stress increases signal-to-noise ratios within primary sensory cortices (Foote, Freedman, & Oliver, 1975) and leads to more vigilant or bottom-up, stimulus-driven, attention (Buschman & Miller, 2007). Vigilant animals make faster responses to targets (Rajkowski, Kubiak, & Aston-Jones, 1994). However, they are also more distracted by non-target stimuli (Rajkowski et al., 1994), increasing false alarm errors.

Overall, downregulated frontal activity and upregulated subcortical activity during periods of acute stress are thought to allow animals to more rapidly ascertain potential risks and respond to uncertainties in the environment with learned or pre-potent actions (Aston-Jones & Cohen, 2005; Yu & Dayan, 2003).

Manuscript Received: 6 October 2015

Manuscript Accepted: 8 February 2016

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Contract grant sponsor: British Academy Postdoctoral Fellowship

Contract grant sponsor: Medical Research Council

Article first published online in Wiley Online Library (wileyonlinelibrary.com): 18 March 2016

DOI 10.1002/dev.21399 • © 2016 Wiley Periodicals, Inc.

Although the effects of acute stress on adult cognitive performance are relatively well known, similar relationships within infants are only beginning to be explored (e.g., de Barbaro, Chiba, & Deák, 2011). In infants, at birth, neuroimaging evidence suggests that subcortical structures such as the brainstem and hypothalamus are relatively mature, whereas higher-order cortical structures are relatively immature (Paus et al., 2001). Behaviorally, the capacity for endogenous (voluntary) control of attention is thought to begin to emerge at the end of the first year (Colombo & Cheatham, 2006).

Two tasks widely used to measure developing attentional processes in infants are peak look during habituation and the visual paired comparison task. During habituation an image is presented repeatedly, contingent on the infant's looks to and away from the screen. One common measure is the duration of the infant's peak, or longest, look (Colombo & Mitchell, 2009), although other studies have used other measures (Bornstein, Hahn, & Wolke, 2013). Behavioral studies with human infants indicate that looking times to both simple and complex stimuli decrease with age until about 6 months, whereas look durations to more complex stimuli, such as videos and picture of faces, starts to increase starting at around 6 months (Courage, Reynolds, & Richards, 2006). Comparing differences between simple and more complex stimuli, Courage et al. suggested that look duration depends on an interaction of two factors: the decline in look duration for all stimuli from 3- to 6-months was attributed to improvements in the ability to encode stimulus details and disengage from a stimulus; the selective increase in look duration for interesting stimuli was attributed to the emergence of an endogenous capacity to direct visual attention, thought to be dependent on the frontal lobes (Courage et al., 2006). Thus, peak look is thought to be an index of rapid information processing in early infancy, and shorter peak looks have been associated with better performance on later IQ and language measures (Colombo, 1993). Later in infancy when looks are thought to index sustained attention, the direction reverses and longer looks are generally associated with better cognitive outcomes, (Colombo & Cheatham, 2006; Ruff, Capozzoli, & Saltarelli, 1996), although some studies indicate conflicting results (Rose, Feldman, Jankowski, & Van Rossem, 2012).

In the visual paired comparison (VPC) task, a previously familiarized image is presented side-by-side with a novel image, and looking times to the two images are measured. More looking to the novel image, or novelty preference, is considered to be an index of memory for the familiarized image. The proportion of time spent looking to the novel object relates positively to working memory abilities at 11 years (Rose et al., 2012), as well as to later IQ (Colombo, 1993), spatial

memory (Colombo, Mitchell, Dodd, Coldren, & Horowitz, 1989) and language outcomes (McCall & Carriger, 1993).

In previous research we have used time-series analyses to examine covariation between continuously measured arousal and continuously measured look duration while a stream of novel static and dynamic visual stimuli are presented. We found that acute fluctuations in arousal associate with changes in look duration (de Barbaro, Wass, & Clackson, in press), such that higher periods of arousal are associated with *shorter* looks. Short-term changes in arousal were found to precede changes in look duration. In terms of the Arnsten model, this finding can be understood two ways. In older infants, shorter looks may reflect decreases in sustained attention. Alternatively, short looks may reflect faster stimulus encoding. However, the implications of these two alternatives on learning are unclear.

Namely, short looking may reflect difficulties sustaining attention, as sustained attention is predicted to be down-regulated during periods of acute stress. This interpretation also predicts that acute increases in stress could *negatively* affect infants' performance on the VPC. Namely, if stress decreases sustained attention, it could also negatively affect stimulus encoding. This could be reflected in familiarity preferences or less discrimination between the two stimuli in the paired comparison task, both indices of a lack of habituation to the original stimulus (Fagan, 1974). Consistent with this, Geva, Gardner, and Karmel, 1999 found that in low arousal states after feeding, infants showed a novelty preference, whereas before feeding, in high arousal states, they showed a familiarity preference, thought to indicate that the infant had not yet habituated to the original stimulus. Similarly, in a paradigm with 6–7 month old infants, de Barbaro et al. (2011) found that infants who showed faster responses to brightly-colored videos were more distracted by peripheral stimuli and also showed more perseveration to the videos stimuli over the course of multiple trials, also suggesting a lack of habituation. While they did not measure or manipulate arousal levels, their measures of responsiveness were based on measures shown in monkeys to correspond with a continuum of brainstem arousal activity (Aston-Jones, Rajkowski, & Cohen, 1999). Thus, if increases in arousal increase vigilance, they may also lead to perseverative looking to familiar stimuli, or reductions in stimulus discrimination in the VPC.

However, there is an alternative possible explanation for our finding that acute increases in arousal associate with decreases in look duration. Look duration might depend on subcortical mechanisms related to stimulus encoding, as has been suggested for example, by Sirois and Mareschal (2002). Therefore, a finding that acute

increases in arousal are associated with shorter look durations might reflect the fact that stress upregulates subcortical processing, also predicted by the Arnsten model. Under this interpretation, the model makes opposite predictions. Acute increases in stress may speed infants' encoding of basic stimulus features and increase their readiness for novel stimuli, leading to enhanced discrimination on the paired comparison task. Some animal models indicate that recognition memory tasks are subcortically mediated (Alvarez, Zola-Morgan, & Squire, 1995). In infants, increased cortisol reactivity (a hormonal marker of stress system functioning) during a mobile-kicking motor learning task predicted better performance and subsequent retention on a next-day repetition of the task in 3-month-old infants (Haley, Weinberg, & Grunau, 2006). In another study, cortisol baselines were positively correlated with performance on a (land-only) version of the Morris Water Maze task created for toddlers (Stansbury, Haley, & Koenecker, 2000). Thus, infant memory tasks thought to be dependent on subcortical structures have previously been shown to be facilitated under conditions of stress, in accordance with this second interpretation.

The present study was intended to address this ambiguity. In typical 12-month-old infants we assessed visual recognition memory and peak look during habituation. In the same session, we also measured infants' physiological reactivity, indexed as heart rate acceleration while infants watched a video of another infant crying. In previous research we have shown that heart rate shows strong patterns of phasic covariation with other widely used measures of arousal such as electrodermal activity and movement patterns (Wass, Clackson, & de Barbaro, 2015), validating its use as a single measure to index arousal.

We predicted that increases in arousal over baselines would be associated with shorter looking times (Analysis 1), but that they may be associated with either better or worse discrimination between the stimuli (Analysis 2). Finally, we hypothesized that the effects of arousal on attention would moderate the effects on discrimination, as previous studies have shown that peak look correlates with discrimination (e.g., Colombo, Richman, Shaddy, Follmer Greenhoot, & Maikranz, 2001a). To examine this we tested whether reactivity predicted shared variance across the two measures (Analysis 3).

METHODS

Participants

We report data from 51 typically developing 12-month-old infants (27 female; mean age in days: 381, SD: 40.63). A

further two infants took part in the study but contributed no data due to recording errors. Parents were recruited through a database of interested participants created by a group of researchers interested in infant development. Volunteers contacted the database organizers after viewing flyers left at local playgroups or following radio advertisements in a small university town in the UK. Reimbursement for participation in the study included a T-shirt for the infant and travel reimbursement. All families who visited us at the lab elected to participate in the full session presented below.

Materials and Procedures

The two tasks and the reactivity challenge were presented as part of a testing battery that lasted approximately 20 min in total. All three were presented in separate blocks in a pseudo-randomised order, with no two blocks of the same task presented consecutively. The order was identical across all infants, with a baseline followed by 17 testing blocks, including three separate tasks (featuring animations and TV clips) that are being written up elsewhere. The habituation and visual paired comparison task were always paired into a single consecutive block, presented in blocks 2, 6, and 13. The reactivity challenge (a video of another baby crying) was presented in blocks 4 and 14. The battery was presented unbroken in one block unless the infant became distressed during testing, in which case a break was taken before continuing.

Viewing materials were presented using a Tobii TX300 eyetracker subtending approximately 30° of visual angle. Infants were seated on their caregiver's lap. Stimulus presentation was performed using Matlab, Psychtoolbox and the Matlab Tobii SDK. Electro-cardiogram (ECG) was recorded using a BioPac™ (Santa Barbara, CA) recording at 1,000 Hz. ECG was recorded using disposable Ag-Cl electrodes placed in a modified lead II position.

Task 1: Habituation Task. This task was presented in three blocks at different stages of the testing protocol. Each block featured a novel image (a picture of a child's face). Trials commenced with a small (3°) fixation target, presented concurrently with an attention-getter sound; once the infant had looked to this target, the image (subtending c.10°) was presented. An experimenter, behind a curtain, viewed a live video feed and a feed showing live eye-tracking data. When the eyetracker indicated that the infant had looked away from the screen, the experimenter visually confirmed this from the video feed and pressed a key to signal the end of a trial. (This manual check was incorporated into the procedure during piloting because occasionally the eyetracker failed to detect the child's gaze, even while they were looking at the screen.) The same image was re-presented until two consecutive looks had taken place that were less than 50% of the longest look recorded that block (following Colombo & Mitchell, 2009). The block also ended if the child had accumulated either 12 looks or 120 s looking time without reaching habituation criteria. The main dependent variable was Peak Look

duration, calculated as the mean of the peak looks observed across the three trials. Previous research suggests that peak look tends to relate closely to other typical measures in this task (Colombo & Mitchell, 1990). Our own data confirmed this, and suggested that peak look duration is also closely associated with mean look duration $r^2(51) = .83, p < .001$. All infants completed all three trials with the exception of three, who each missed one trial.

Task 2: Visual Recognition Memory Task. This task was presented immediately following the habituation task. A different (novel) attention-getter sound was presented, together with a fixation target. Once the infant had looked to this target, the previously habituated image was presented alongside a previously unseen image (both subtending 10°). The two images were presented concurrently for 8 s, then the fixation target was presented again and the two images were re-presented for a further 8 s with the left/right order reversed. The dependent variable was the proportion looking time to the novel target (PTN). This was defined as the proportion of total eyetracker data available during the 16 s trial duration spent looking at the novel vs. the familiar image.

Only those trials in which valid eyetracker data were available for at least 45% of the trial were included. Two infants were excluded for failing to provide at least one valid trial. All other infants provided at least one valid trial. Of note, data pre- and post- these exclusions were highly correlated, $r^2(49) = .84, p < .001$, suggesting that removing cases with missing data values did not substantially impact our findings.

Stress Reactivity. Baseline HR was recorded during two child-friendly videos that were presented at the start of the session. These lasted 70 s in total. Qualitative observations indicated that infants were relatively calm and still during these videos. In addition, two 30-s long “stressor” videos were interspersed within the testing protocol. These videos, which were presented with sound, showed young infants crying intensely (see Fig. 1). Parents were warned that these videos would be presented before the start of the experiment. If infants showed strong or persistent negative affect (such as crying), the presentation of the videos the experiment was curtailed. This occurred less than 5% of the time; the vast majority of the infants observed both videos in full.

Heart rate data was unavailable for five babies: two because the recording electrodes became dislodged during the testing session, and three due to an equipment error which led to inaccurate time-synching between Matlab and the heart rate recording software.

Automatic identification of heart beats from all HR data was performed by the commercial software package Acknowledge R-peak identification function. Artefact rejection was then performed by excluding those beats showing an inter-beat interval of <330 or <750 ms, and by excluding those samples showing a rate of change of inter-beat interval of greater than 80 ms between samples (see Wass, de Barbaro, & Clackson, 2015). Average HR (in beats per minute (BPM)

was calculated during the stressor videos, and during the baseline videos. Stress reactivity was indexed as: (HR during stressor videos) – (HR during baseline videos). A *t*-test confirmed that as a group, infants had higher BPM during the stressor than the baseline videos $t(45) = -4.75, p < .001$, confirming the validity of this as a stressor measure.

Richards (1980) discussed how reactivity data may be susceptible to the Law of Initial Values (LoIV; Richards, 1980). LoIV states that the reactivity values may be partially determined by the baseline values, insofar as high baseline values are less likely to increase and low baseline values are less likely to decrease. According to standard tests, we assessed for LoIV effects by testing for a negative correlation between baseline and reactivity measures (Richards, 1980). The correlation coefficient was found to be negative but not significant: $r^2 = -.124, p = .410$, indicating that baseline values showed minimal associations with reactivity scores. Nevertheless relationships with baseline HR have been tested for in the analyses below.

RESULTS

Analytical Approach

Our planned analysis was to evaluate how stress reactivity relates to peak look during habituation and novelty preference (Analyses 1 and 2). Additionally, we wanted to assess whether the looking time measure moderated the effects of arousal on discrimination. Thus we examined the correlation between these two measures and also ran an additional regression model to test whether they were independently associated with physiological reactivity (Analysis 3).

Descriptive Statistics

As seen in Figure 2, scatterplots show that increased stress reactivity is associated with shorter peak looks during the habituation task and a greater proportion of time spent looking at the novel target in the visual recognition memory task.

Tests of Statistical Assumptions

First, a Shapiro–Wilk test was conducted to ensure that variables were normally distributed. For Task 1, peak look contained one outlier (value = 72.74; $5.43 \text{ SD} > M$), which was removed. Even following the removal of this outlier, peak look was found to be skewed $W(52) = .721, p < .001$, as is typical for look duration data (Frick, Colombo, & Saxon, 1999). Therefore a log transformation was performed, after which the data were statistically equivalent to a normal distribution: $D(51) = .973, p = .307$. Task 2 contained one outlier

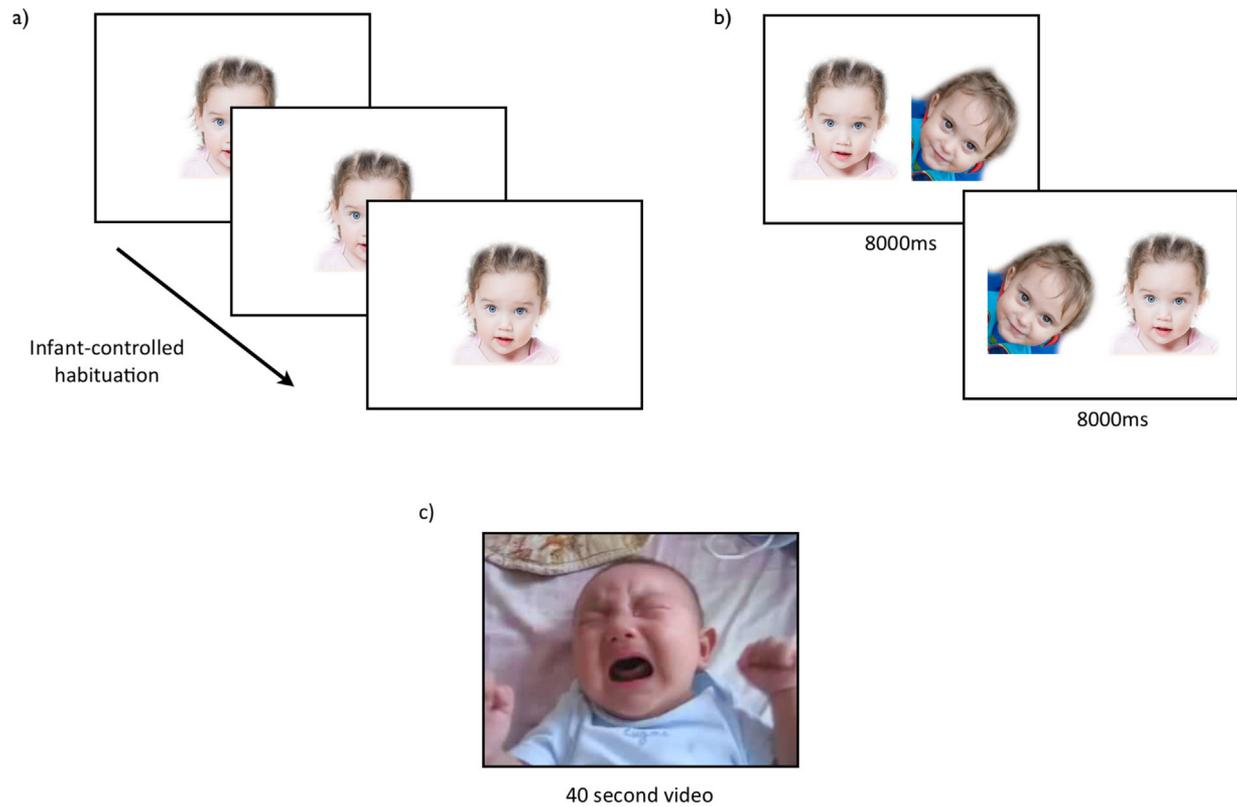


FIGURE 1 Schematics showing the three tasks administered. (a) Habituation task. (b) Visual recognition memory task. (c) Stress reactivity task.

greater than three standard deviations below the mean (PTN outlier value = .19; $4.45 \text{ SD} < M$). After this outlier was removed, PTN was normally distributed: $W(49) = .983, p = .702$. For Task 3, baseline and stressor reactivity variables were normally distributed with no outliers: baseline HR: $W(46) = .982, p = .681$; stress reactivity: $W(46) = .966, p = .195$. Table 1 shows descriptive statistics for main variables across the study prior to transformation and with outliers removed.

Analysis 1: Does Stress Reactivity Relate to Peak Look Duration?

Confirming the trends seen in Figure 2, statistical analysis shows a significant correlation between stress reactivity and peak look durations ($R = -.296, p = .048$), with higher stress reactivity being associated with shorter peak look durations. In contrast, baseline HR does not correlate with peak look ($R = -.199,$

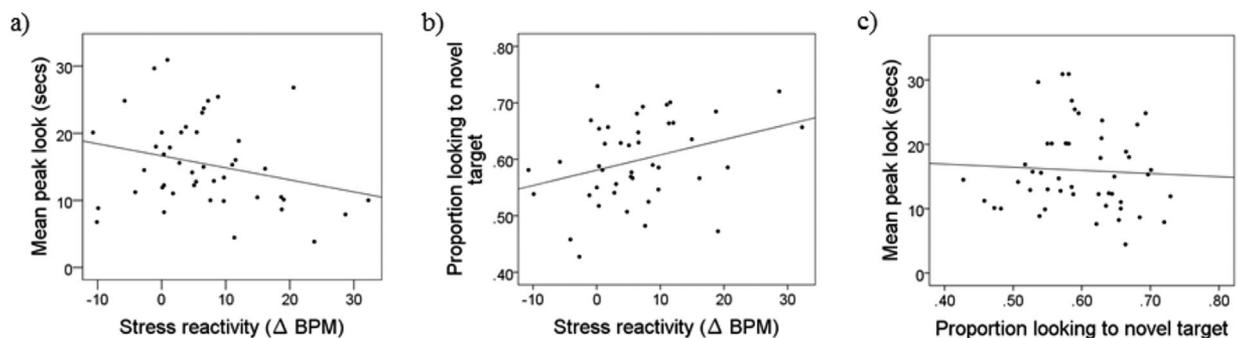


FIGURE 2 Scatterplots showing infants' performance on attentional measures plotted against stress reactivity (a and b), and the attentional measures plotted against each other (c). Stress reactivity is defined as the BPM change between heart rate during stressor video and baseline heart rate, with positive values indicating increased BPM during stressor video.

Table 1. Descriptive Statistics for Key Variables

	Mean	S.D	Range	<i>N</i>
Task 1: Habituation—peak look duration (secs)	15.43	6.68	3.84–30.93	51
Task 2: Visual recognition memory—proportion to novel	.60	.07	.43–.73	49
Task 3: Stress reactivity—HR change to stressor (BPM)	6.63	9.46	–10.7 to 32.26	46
Baseline HR (BPM)	122.83	10.96	98.65–144.99	46

$p = .189$) showing that the relationship between stress reactivity and peak look durations is not influenced by baseline HR.

Analysis 2: Does Stress Reactivity Relate to Increased Discrimination on the VPC?

Stress reactivity also significantly correlates with the proportion of time looking to the novel picture in the visual recognition memory task ($R = .326$, $p = .033$), with higher stress reactivity being associated with a higher proportion of time spent looking at the novel image. Again, baseline HR does not correlate with the proportion of time spent looking at the novel image ($R = -.180$, $p = .248$).

Analysis 3: Do the Effects of Arousal on Looking Account for the Effects on Discrimination?

Peak look durations and the proportion of time looking to the novel target are not correlated ($R = -.089$, $p = .547$; see Fig. 2), but both peak look durations and novelty preference scores relate to stress reactivity. Analysis 3 sought to further investigate the extent to which these changes in looking duration related to arousal might moderate the effects on discrimination. If this were the case, once we controlled for the relationship between arousal and looking duration, there should no longer exist a relationship between arousal and discrimination. To test this we used a regression model with peak look and novelty preference scores as predictors, and stress reactivity as the dependent variable. This is equivalent to calculating a partial correlation between novelty preference and stress reactivity, controlling for peak look. The analysis showed that when values for peak look are held constant, stress reactivity and novelty preference are still significantly associated ($\beta = .301$, $t = 2.131$, $p = .039$), indicating a significant amount of unshared variance between the two attentional variables. However, when novelty preference scores are controlled for, peak look and reactivity only show a marginally significant association ($\beta = -.268$, $t = -1.841$, $p = .073$), indicating some degree of shared variance between these same variables. The two-factor model

suggests that 9.6% of the variance in stress reactivity is explained by novelty preference scores alone, 7.1% is explained by peak look alone, and 1.1% is shared.

DISCUSSION

We examined the relationship between stress reactivity, indexed as infants' HR response to an external behavioral stressor, and two tasks that are commonly used to assess infant attention and learning. We found that higher stress reactivity associated with shorter peak look in a habituation task (Analysis 1) and with novelty preferences in a visual paired comparison task (Analysis 2). Analysis 3 suggested that these relationships were largely, but not entirely, independent of one another. Thus, *higher* stress reactivity was associated with behaviors consistent with a more vigilant, stimulus-ready profile and rapid encoding of basic stimulus features.

There are a number of possible challenges to this interpretation of the results. First, according to the Law of Initial Values, stress reactivity might be confounded by the pre-stimulus heart rate (Richards, 1980). Thus, children with a higher baseline HR might show lower HR change to stressor, suggesting the opposite relationship between HR measures and behavior. However we found no relationship between baseline HR and cognitive performance. Second, we considered that differences in eyetracking or cardiac recording data quality might explain our results. However, we found no systematic differences in data quality contingent on HR changes, and one of our measures (peak look) was derived from hand-coding.

Analysis three indicated a lack of correlation between shorter looks and more novelty performance in the VPC, in contrast to previous work on these measures (Colombo, Richman, Shaddy, Follmer Greenhoot, & Maikranz, 2001b; Jankowski, Rose, & Feldman, 2001). This may have been due to the fact that the overall mean of our novelty preference scores ($M = 0.60$; $SD = 0.07$) was significantly higher than typically reported for this task (e.g., Colombo et al. [2001a] report overall $M = 55.2$ and $SD = 13.7$), suggesting a possible ceiling effect in this measure. We

note also that a number of previous reports (e.g., Rose, Feldman, & Jankowski, 2004) have also failed to replicate the original correlations between these measures, even in infants younger than those we tested. For the purposes of our questions this is not significant as both measures show independent modulation by stress.

A number of past studies indicate that cardiac indices of parasympathetic tone are associated with enhanced learning and sustained attention. In particular, higher variability in resting heart rate (known as vagal tone or resting respiratory sinus arrhythmia) has been associated with shorter looks and more novelty preference in habituation and paired comparison tasks similar to those used in this study (Linnemeyer & Porges, 1986; Richards, 1985). Additionally, another parasympathetic index, HR *decelerations* in response to stimulus presentation, have also been associated with enhanced discriminations (Richards, 1997), and are more broadly considered an index of sustained attention (Lansink & Richards, 1997). However, it is unlikely that heightened parasympathetic activity can account for the findings presented here. We found that shorter looks and more novelty preference were associated with *accelerated* HR to a challenge, which is typically *negatively* associated with parasympathetic indices such as vagal tone (e.g., Kagan, Reznick, & Snidman, 1988). Thus, we saw an opposite pattern of effects than that predicted by heightened parasympathetic activity. One possibility is that both high parasympathetic tone and sympathetic reactivity may confer advantages for these tasks via different mechanisms. For example, parasympathetic activity may focus attention while sympathetic activity may increase vigilance, thought to reflect two ends of an attentional spectrum (Aston-Jones et al., 1999). Below, we further interpret our results, providing detail as to the conditions under which these mechanisms could show diverging performance.

In the introduction we considered two possible explanations for our finding that increased stress associates with decreases in look duration. The first is that reactivity would be associated both with faster looks and with reduced discrimination in the VPC. If stress downregulates frontal activity, it could reduce sustained attention and reduce infants' stimulus learning, leading to both shorter looks and reduced discrimination. Our results suggest that this is not the case: as stress reactivity increases, infants showed shorter looks, but they also showed more novelty preference in the VPC.

This pattern of results confirms our second hypothesis, namely, that stress reactivity would be associated shorter looks as well as more discrimination. This is consistent with the literature indicating the facilitative

effects of acute stress on subcortical structures. Visual recognition memory has been proposed to be substantiated primarily by medial temporal lobe structures including the hippocampus (Alvarez et al., 1995). These are among the subcortical structures postulated to be upregulated under conditions of acutely heightened stress (Arnsten, 2009). Consistent with this, investigations into cortisol reactivity, a marker of HPA axis function, have also noted positive associations between physiological reactivity and some memory tasks developed for infants and toddlers (Haley et al., 2006; Stansbury et al., 2000).

Consistent with hypothesis two, more reactive infants showed faster looks and more discrimination in the VPC. This profile is thought to be the hallmark of superior early infant cognition, thought to reflect faster processing speed and be predictive of superior cognitive performance in later childhood (Colombo, 1993; Colombo & Mitchell, 1990). However, it would be premature to conclude that more reactive infants "learn better" across all types of tasks, or that there were no effects of increased HR on sustained attention, as proposed in hypothesis one. In particular, it is possible that at 12 months, short looks and novelty preferences do not require sustained attentional focus, as we elaborate below.

Traditional information processing theories (Colombo & Mitchell, 1990; Sokolov, 1963) posit that any given stimulus contains a discrete amount of "information," like the bits used to store a file on a computer. Accordingly, they posit infants who show shorter looks to a stimulus have encoded it faster due to superior information processing abilities. By contrast, more enactive and ecological theories of perception (Churchland, Ramachandran, & Sejnowski, 1994; Hayhoe & Ballard, 2005) suggest that visual attention and discrimination are active sensory processes more akin to active probing, such as when a blind person uses a cane. From this perspective, the duration of time spent looking reflects active elaboration of stimulus features, with no clear "limit" to the information that can be gleaned from a stimulus. Active elaboration is thought to be an increasingly important cognitive process in the second half of the first year, when infants' look durations to complex objects begin to increase (Courage et al., 2006). Considering this, we cannot assume that more and less reactive infants encode equivalent detail from each image.

The Arnsten model predicts that stress will shift infants into a more vigilant, stimulus-ready profile. This could account for the shorter looks and heightened novelty preferences we observed in stressed infants. For example, during periods of increased arousal, infants may spend less time elaborating image details

and instead attend to global features of an image, allowing them to rapidly encode discriminative features. By contrast, infants with longer looks and more baseline arousal levels may be elaborating additional details from each image, and may thus show reduced propensity to examine the paired comparison image (see, e.g. Colombo, Mitchell, Coldren, & Freese, 1991; Jankowski et al., 2001). In this way reactive infants may show more discrimination between pairs of stimuli.

Animal models indicate that a vigilant or stimulus-ready attentional profile is associated with decreases in sustained attention (Aston-Jones & Cohen, 2005). We did not find evidence that stress impaired discrimination, which we hypothesized may occur if stress decreased sustained attention. However, this does not preclude effects of distractibility could be observed in other tasks. One possibility is that increased distractibility is masked by the typical laboratory testing situation, in which attentional competition is purposefully minimized. By contrast, in naturalistic environments filled with dynamic multimodal stimuli, the very same stimulus readiness that leads to faster looking and novelty preferences in the laboratory may contribute to distractibility. Directly examining the relations between arousal and attention in more varied contexts, including naturalistic contexts with attentional competition is necessary to investigate this possibility and thus understand how our results might generalize to other types of learning contexts (see e.g., Wass, 2014).

Another important limitation to our study was the narrow age range we tested. Future work should investigate how the relationships shown here evolve over development. For example, if reactivity reflects a stable feature of individuals (e.g., Kagan, Snidman, & Arcus, 1998), our data may indicate a mechanism by which more reactive infants are more sensitive to their environments, as is theorized in a number of influential accounts (Belsky, Bakermans-Kranenburg, & Van IJzendoorn, 2007; Boyce & Ellis, 2005; Obradovic, 2016). In particular, our findings indicate that infants who show more physiological reactivity show more attentional vigilance and make rapid discriminations. Over the long-term, this may lead them to be more impressionable to the impacts of both adverse and positive environments.

Finally, previous literature indicates that our measures of basic information processing are related to later individual differences in higher-order cognitive functions. As we detailed in the introduction, there is conflicting evidence as to the longitudinal outcomes of “faster” looking durations at the end of the first year. Within the framework of sustained attention, studies have indicated that longer bouts of looking in

naturalistic free-play interactions at 12 months are associated with higher IQ and less hyperactivity at 3 years (Lawson & Ruff, 2004; Ruff & Saltarelli, 1993). This is consistent with the biological literature on the effects of acute stress on cognition: where stress increases vigilance and subcortical encoding processes while downregulating frontal networks supporting IQ and top-down attention (Arnsten, 1998). However, other studies indicate that short looking and novelty preference in the VPC are *positively* associated with later working memory and IQ, even at the end of the first year (Fagan, Holland, & Wheeler, 2007; Rose et al., 2012), as has been repeatedly observed in studies with younger infants (Colombo, 1993). This is particularly perplexing as both working memory and IQ measures are subserved by frontal brain regions known to be *negatively* affected by stress (Arnsten, 2009). Thus, additional studies are needed to assess the relations between arousal and tasks that can tease apart cortical and subcortical networks in a single developmental sample.

Our present findings suggest that higher stress reactivity, measured by accelerated heart rate to challenge, is associated with a stimulus-ready attentional profile, indexed by both faster look durations and more novelty preference. This is consistent with work showing facilitation of tasks dependent on subcortical lobes following acute increases in sympathetic activity following stress. Possible directions for future work include: a) the use of naturalistic contexts to examine the relations between attentional speed and distractibility, and b) longitudinal studies to examine how arousal-cognition relations evolve over development and specifically with respect to tasks dependent on emerging cortical networks.

NOTES

This work was supported by a British Academy Postdoctoral Fellowship to S.V.W. and by Medical Research Council intramural funding for K.B. Thanks to Duncan Astle and Emily Jones for useful discussions, and to Peter Watson for advice on statistics.

REFERENCES

- Alvarez, P., Zola-Morgan, S., & Squire, L. R. (1995). Damage limited to the hippocampal region produces long-lasting memory impairment in monkeys. *The Journal of neuroscience*, 15(5), 3796–3807.
- Arnsten, A., & Goldman-Rakic, P. (1998). Noise stress impairs prefrontal cortical cognitive function in monkeys: Evidence for a hyperdopaminergic mechanism. *Archives*

- of General Psychiatry, 55(4), 362–368. DOI: 10.1001/archpsyc.55.4.362
- Arnsten, A. F. (2009). Stress signaling pathways that impair prefrontal cortex structure and function. *Nature Reviews Neuroscience*, 10(6), 410–422.
- Arnsten, A. F. T. (1998). Neuroscience: Enhanced: The biology of being frazzled. *Science*, 280(5370), 1711.
- Aston-Jones, G., & Cohen, J. D. (2005). An integrative theory of locus coeruleus-norepinephrine function: Adaptive gain and optimal performance. *Annual Review of Neuroscience*, 28(1), 403–450.
- Aston-Jones, G., Rajkowski, J., & Cohen, J. (1999). Role of locus coeruleus in attention and behavioral flexibility. *Biological Psychiatry*, 46(9), 1309–1320.
- Belsky, J., Bakermans-Kranenburg, M. J., & Van IJzendoorn, M. H. (2007). For better and for worse differential susceptibility to environmental influences. *Current Directions in Psychological Science*, 16(6), 300–304.
- Bornstein, M. H., Hahn, C.-S., & Wolke, D. (2013). Systems and cascades in cognitive development and academic achievement. *Child Development*, 84(1), 154–162. DOI: 10.1111/j.1467-8624.2012.01849.x
- Boyce, W. T., & Ellis, B. J. (2005). Biological sensitivity to context: I. An evolutionary-developmental theory of the origins and functions of stress reactivity. *Development and Psychopathology*, 17(2), 271–301.
- Buschman, T. J., & Miller, E. K. (2007). Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science*, 315(5820), 1860–1862.
- Cahill, L., & McGaugh, J. L. (1998). Mechanisms of emotional arousal and lasting declarative memory. *Trends in Neurosciences*, 21(7), 294–299.
- Churchland, P. S., Ramachandran, V., & Sejnowski, T. J. (Eds.). (1994). *A Critique of pure vision* (pp 23–60). Cambridge, MA: MIT Press.
- Colombo, J. (1993). *Infant cognition: Predicting later intellectual functioning* (Vol. 5). Newbury Park, CA: Sage Publications.
- Colombo, J., & Cheatham, C. L. (2006). The emergence and basis of endogenous attention in infancy and early childhood. *Advances in Child Development and Behavior*, 34, 283–322.
- Colombo, J., & Mitchell, D. W. (1990). Individual differences in early visual attention: Fixation time and information processing. *Individual Differences in Infancy: Reliability, Stability, Prediction*, 193–227.
- Colombo, J., Mitchell, D. W., Coldren, J. T., & Freese, L. J. (1991). Individual differences in infant visual attention: Are short lookers faster processors or feature processors? *Child Development*, 62(6), 1247–1257.
- Colombo, J., Richman, W. A., Shaddy, D. J., Follmer Greenhoot, A., & Maikranz, J. M. (2001a). Heart rate-defined phases of attention, look duration, and infant performance in the paired-comparison paradigm. *Child Development*, 72(6), 1605–1616.
- Colombo, J., Richman, W. A., Shaddy, D. J., Follmer Greenhoot, A., & Maikranz, J. M. (2001b). Heart rate defined phases of attention, look duration, and infant performance in the paired comparison paradigm. *Child Development*, 72(6), 1605–1616.
- Colombo, J., Mitchell, D., Dodd, J., Coldren, J. T., & Horowitz, F. D. (1989). Longitudinal correlates of infant attention in the paired-comparison paradigm. *Intelligence*, 13(1), 33–42.
- Colombo, J., & Mitchell, D. W. (2009). Infant visual habituation. *Neurobiology of Learning and Memory*, 92(2), 225–234.
- Courage, M., Reynolds, G., & Richards, J. (2006). Infants' attention to patterned stimuli: Developmental change from 3 to 12 months of age. *Child Development*, 77(3), 680–695.
- de Barbaro, K., Chiba, A., & Deák, G. O. (2011). Micro-analysis of infant looking in a naturalistic social setting: Insights from biologically based models of attention. *Developmental Science*, 14(5), 1150–1160.
- de Barbaro, K., Wass, S., & Clackson, K. (in press, *Child Development*). Infant attention is dynamically modulated with changing arousal levels.
- Fagan, J. F. (1974). Infant recognition memory: The effects of length of familiarization and type of discrimination task. *Child Development*, 351–356.
- Fagan, J. F., Holland, C. R., & Wheeler, K. (2007). The prediction, from infancy, of adult IQ and achievement. *Intelligence*, 35(3), 225–231.
- Foote, S. L., Freedman, R., & Oliver, A. P. (1975). Effects of putative neurotransmitters on neuronal activity in monkey auditory cortex. *Brain Research*, 86(2), 229–242.
- Frick, J. E., Colombo, J., & Saxon, T. F. (1999). Individual and developmental differences in disengagement of fixation in early infancy. *Child Development*, 70(3), 537–548.
- Geva, R., Gardner, J. M., & Karmel, B. Z. (1999). Feeding-based arousal effects on visual recognition memory in early infancy. *Developmental Psychology*, 35(3), 640.
- Haley, D. W., Weinberg, J., & Grunau, R. E. (2006). Cortisol, contingency learning, and memory in preterm and full-term infants. *Psychoneuroendocrinology*, 31(1), 108–117.
- Hayhoe, M., & Ballard, D. (2005). Eye movements in natural behavior. *Trends in Cognitive Sciences*, 9(4), 188–194.
- Jankowski, J. J., Rose, S. A., & Feldman, J. F. (2001). Modifying the distribution of attention in infants. *Child Development*, 72(2), 339–351.
- Joëls, M., & Baram, T. Z. (2009). The neuro-symphony of stress. *Nature Reviews Neuroscience*, 10(6), 459–466.
- Kagan, J., Reznick, J. S., & Snidman, N. (1988). Biological bases of childhood shyness. *Science*, 240(4849), 167–171.
- Kagan, J., Snidman, N., & Arcus, D. (1998). Childhood derivatives of high and low reactivity in infancy. *Child Development*, 69(6), 1483–1493.
- Lansink, J. M., & Richards, J. E. (1997). Heart rate and behavioral measures of attention in 6, 9, and 12 month old infants during object exploration. *Child Development*, 68(4), 610–620.
- Lawson, K. R., & Ruff, H. A. (2004). Early focused attention predicts outcome for children born prematurely. *Journal of Developmental and Behavioral Pediatrics*, 25(6), 399.

- Linnemeyer, S. A., & Porges, S. W. (1986). Recognition memory and cardiac vagal tone in 6-month-old infants. *Infant Behavior and Development*, 9(1), 43–56.
- Liston, C., McEwen, B., & Casey, B. (2009). Psychosocial stress reversibly disrupts prefrontal processing and attentional control. *Proceedings of the National Academy of Sciences*, 106(3), 912–917.
- Luethi, M., Meier, B., & Sandi, C. (2008). Stress effects on working memory, explicit memory, and implicit memory for neutral and emotional stimuli in healthy men. *Frontiers in Behavioral Neuroscience*, 2(5), 1–9.
- McCall, R. B., & Carriger, M. S. (1993). A meta-analysis of infant habituation and recognition memory performance as predictors of later IQ. *Child Development*, 64(1), 57–79.
- McEwen, B. S., & Sapolsky, R. M. (1995). Stress and cognitive function. *Current Opinion in Neurobiology*, 5(2), 205–216.
- Minor, T. R., Jackson, R. L., & Maier, S. F. (1984). Effects of task-irrelevant cues and reinforcement delay on choice-escape learning following inescapable shock: Evidence for a deficit in selective attention. *Journal of Experimental Psychology: Animal Behavior Processes*, 10(4), 543.
- Obradovic, J. (2016). Physiological responsivity and executive functioning: Implications for adaptation and resilience in early childhood. *Child Development Perspectives*, 10(1), 65–70.
- Paus, T., Collins, D., Evans, A., Leonard, G., Pike, B., & Zijdenbos, A. (2001). Maturation of white matter in the human brain: A review of magnetic resonance studies. *Brain Research Bulletin*, 54(3), 255–266.
- Rajkowski, J., Kubiak, P., & Aston-Jones, G. (1994). Locus coeruleus activity in monkey: Phasic and tonic changes are associated with altered vigilance. *Brain Research Bulletin*, 35(5–6), 607–616.
- Richards, J. E. (1980). The statistical analysis of heart rate: A review emphasizing infancy data. *Psychophysiology*, 17(2), 153–166.
- Richards, J. E. (1985). Respiratory sinus arrhythmia predicts heart rate and visual responses during visual attention in 14 and 20 week old infants. *Psychophysiology*, 22(1), 101–109.
- Richards, J. E. (1997). Effects of attention on infants' preference for briefly exposed visual stimuli in the paired-comparison recognition-memory paradigm. *Developmental Psychology*, 33(1), 22.
- Rose, S. A., Feldman, J. F., & Jankowski, J. J. (2004). Infant visual recognition memory. *Developmental Review*, 24(1), 74–100.
- Rose, S. A., Feldman, J. F., Jankowski, J. J., & Van Rossem, R. (2012). Information processing from infancy to 11 years: Continuities and prediction of IQ. *Intelligence*, 40(5), 445.
- Ruff, H., & Saltarelli, L. (1993). Exploratory play with objects: Basic cognitive processes and individual differences. *New Directions for Child and Adolescent Development*, 1993(59), 5–16.
- Ruff, H. A., Capozzoli, M., & Saltarelli, L. M. (1996). Focused visual attention and distractibility in 10-month-old infants. *Infant Behavior and Development*, 19(3), 281–293.
- Sirois, S., & Mareschal, D. (2002). Models of habituation in infancy. *Trends in Cognitive Sciences*, 6(7), 293–298.
- Sokolov E. (1963). *Perception and the conditioned reflex*. New York: MacMillan.
- Stansbury, K., Haley, D., & Koeneker, A. (2000). Higher cortisol values facilitate spatial memory in toddlers: Brief report. *Annals of the New York Academy of Sciences*, 911(1), 456–458.
- Wass, S., de Barbaro, K., & Clackson, K. (2015). Tonic and phasic co-variation of peripheral arousal indices in infants. *Biological Psychology*, 111, 26–39.
- Wass, S. V. (2014). Comparing methods for measuring peak look duration: Are individual differences observed on screen-based tasks also found in more ecologically valid contexts? *Infant Behavior and Development*, 37(3), 315–325.
- Yu, A. J., & Dayan, P. (2003). Expected and unexpected uncertainty: ACh and NE in the neocortex. *Advances in Neural Information Processing Systems*, 15, 157–164.