The origins of effortful control: how early development within arousal/regulatory systems influences attentional and affective control.

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Abstract

In this review, I consider the developmental interactions between two domains sometimes characterised as at opposite ends of the human spectrum: early-developing arousal/regulatory domains, that subserve basic mechanisms of survival and homeostasis; and the later-developing 'higher-order' cognitive domain of effortful control. First, I examine how short-term fluctuations within arousal/regulatory systems associate with fluctuations in effortful control during early childhood. I present evidence suggesting that both hyper- and hypo-arousal are associated with immediate reductions in attentional and affective control; but that hyper-aroused individuals can show cognitive strengths (faster learning speeds) as well as weaknesses (reduced attentional control). I also present evidence that, in infancy, both hyper- and hypo-aroused states may be dynamically amplified through interactions with the child's social and physical environment. Second, I examine long-term interactions between arousal/regulatory systems and effortful control. I present evidence that atypical early arousal/regulatory development predicts poorer attentional and affective control during later development. And I consider moderating influences of the environment, such that elevated early arousal/regulatory system reactivity may confer both cognitive advantages in a supportive environment, and disadvantages in an unsupportive one. We discuss how future research can further our understanding of these close associations between attentional and affective domains during early development.

Keywords: effortful control, arousal, physiological stress, attention control, emotion regulation, self regulation, autonomic arousal

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1 Introduction

The transition from a ‘mewling and puking’ bundle to an adult ‘full of wise saws and modern instances’ (Shakespeare, 1623) is sometimes viewed as a process in which different cognitive functions come online one by one according to a predetermined maturational timetable, as an adult is built from a genetic blueprint like a mosaic (Karmiloff-Smith, 2007). In fact, an overwhelming body of evidence now suggests that this is not how development operates (Johnson, 2015). Instead, development is achieved as a consequence of complex, ongoing and dynamic interactions between developmental domains over time (Geva & Feldman, 2008; Karmiloff-Smith, 1992, 1998; S. W. Porges & Furman, 2011; Thelen & Smith, 1994). Neuroimaging evidence suggests that, during early development, a wider number of different brain regions are active while performing a particular processing task (Johnson, 2015). Over time, interactive dynamics (Oliver, Johnson, Karmiloff-Smith, & Pennington, 2000) lead to different brain regions becoming more specialised, and to functional activation patterns becoming more localised (Johnson, 2000; Johnson, Grossmann, & Kadosh, 2009; Mareschal, 2007).

The aim of this review is to consider the early developmental interactions between two domains sometimes characterised as at opposite ends of the human spectrum: arousal/regulatory domains, that subserve basic mechanisms of survival and homeostasis; and the ‘higher-order’ cognitive domain of effortful control, which includes both attentional and affective control. During early development, as we shall see, the neural circuits involved in arousal/regulatory function are relatively mature, at a time when cortical (in particular pre-frontal cortical) function is still immature. Possibly due to this, as I shall argue, research suggests that, during early development, arousal/regulatory systems are heavily involved in tasks traditionally thought of as ‘higher-order’ cognitive functions. This, I argue, is important as it implies that, during early development, attentional and affective domains are closely inter-related.

First, in the remainder of section 1, I define our terms and describe how arousal/regulatory function and effortful control are measured during early childhood. Then, in sections 2-4, I consider short-term interactions between arousal/regulatory systems and effortful control. In section 2 I discuss the Aston-Jones framework, and examine how both hyper- and hypo-arousal is associated with immediate reductions in two types of effortful control: attentional, and affective. In section 3 I consider the Arnsten framework, and examine how hyper-arousal is associated with superior performance at some types of tasks, and worse performance at others. In section 4 I consider dynamical approaches, contrasting allostatic processes (through which small increases and decreases in arousal are effortfully corrected for over time, to maintain homeostasis) with metastatic processes (through which increases and decreases become amplified over time, leading to chain reaction cascades).

In sections 5-6, I consider long-term interactions between arousal/regulatory systems and effortful control. In section 5 I consider long-term correlations between arousal/regulatory systems and effortful control. In section 6 I consider how these relationships may be moderated by long-term interactive influences of the environment, contrasting two theoretical perspectives: diathesis-stress and Differential Susceptibility Theory. Finally, in section 7, I summarise the main findings and discuss directions for future work.

1.1 Arousal/regulatory systems

1.1.1 Neural correlates

Our arousal/regulatory systems involve a network of brain regions from the brainstem (including the medulla, pons (locus coeruleus) and midbrain) up to the forebrain via both the hypothalamus and the thalamus (Pfaff, 2018), as well as neurotransmitter systems including noradrenaline (norepinephrine) (Aston-Jones & Bloom, 1981; Aston-Jones & Cohen, 2005; Aston-Jones, Rajkowski, & Cohen, 1999) and acetycholine (Trofimova & Robbins, 2016). These brain regions are some of the earliest to become functionally mature: even shortly after birth, axons around the cerebellum, pons, and internal capsule show myelination (Deoni et al., 2011; Paus et al., 2001).

These systems control functions including the Autonomic Nervous system, which is the fast-acting neural substrate of the body's stress response (e.g. Cacioppo, Tassinary, & Berntson, 2000; Jänig, 2008; Tsigos & Chrousos, 2002; Ulrich-Lai & Herman, 2009), as well as more slow-acting endocrine systems such as the Hypothalamic-Pituitary-Adrenal (HPA) axis (Cacioppo et al., 2000). The Autonomic Nervous System operates through two complementary systems - the sympathetic nervous system (SNS), which is involved in quick response mobilising ('fight or flight') responses, and parasympathetic (PNS) nervous system (Cacioppo et al., 2000), which is involved in more slow-acting and response-dampening ('rest or digest') responses (Ulrich-Lai & Herman, 2009).

1.1.2 Measurement in humans

In humans, Autonomic Nervous System function is measured by recording peripheral physiological indicators such as heart rate, Respiratory Sinus Arrhythmia (RSA) (which indexes the degree to which heart rate changes relative to respiratory cycles), Impedance Cardiography (which indexes the time interval between the heart beat and the outflow of blood from the aorta), Electrodermal Activity, Body Movement, and Pupil Size. Heart rate (McCabe, Schneiderman, & Field, 2000) and pupil size (Loewenfeld, 1993) are both thought to receive contributions from both the parasympathetic and sympathetic subsystems. In contrast, Respiratory Sinus Arrhythmia is thought to index mainly the parasympathetic system (Anrep, Pascual, & Rossler, 1935), whereas Impedance Cardiography (Oberlander, Grunau, Pitfield, Whitfield, & Saul, 1999) and Electrodermal Activity (Shields, Macdowell, Fairchild, & Campbell, 1987) are thought to index sympathetic nervous system activity.

The Hypothalamic-Pituitary-Adrenal axis operates via glucocorticoids (cortisol in humans, corticosterone in rodents) (de Kloet, Rots, & Cools, 1996; M. Gunnar & Quevedo, 2007). In humans, cortisol is readily detected by sampling tissue such as saliva or hair (Liu, Snidman, Leonard, Meyer, & Tronick, 2016).

1.1.3 'Splitters' vs 'lumpers'

Just as with the field of effortful control (described below), researchers studying the function arousal/regulatory function – and, in particular, the functions of the Autonomic Nervous System - tend to be divided between 'splitters', who emphasise the fractionation of different arousal/regulatory subsystems (Janig & Habler, 2000; Lacey, 1967; Schneirla, 1946; Trofimova & Robbins, 2016), and 'lumpers', who emphasise their unitary function (Calderon, Kilinc, Maritan, Banavar, & Pfaff, 2016; Pfaff, 2018). Certainly, there is evidence that both approaches are partially correct. For example, animal researchers measured three behaviours associated with arousal/regulatory systems: motor activity (distance travelled, total movement duration); sensory responses to external stimuli (e.g. auditory, vestibular, tactile and olfactory); and emotional responses (e.g. to conditioned fear paradigms) (Calderon et al., 2016; Pfaff, 2018). They applied Principle Components Analyses to high-throughput analyses of behaviour, and found that a significant Generalised Arousal component accounts for between 29 to 45%

of the variance in behaviour across studies (reviewed Calderon et al., 2016; Pfaff, 2018) – suggesting that arousal shows both one unitary factor and smaller, differentiable sub-factors.

Similarly, in physiology, it has been shown that sympathetic and parasympathetic nervous system function is non-additive (Berntson, Cacioppo, Quigley, & Fabro, 1994; Jänig, 2008; Janig & Habler, 2000). However, although different physiological markers track different subcomponent processes, research has shown that heart rate, Respiratory Sinus Arrhythmia, Electrodermal Activity, body movement and pupil size all show reasonably strong patterns of tonic and phasic covariation in infants (S. V. Wass, de Barbaro, & Clackson, 2015). This is consistent with the conclusion that arousal shows both a single common factor as well as more fine-grained sub-factors (Graham & Jackson, 1970).

Recent research has also investigated individual differences in different profiles of change across different arousal/regulatory subsystems (Quas et al., 2014; Roubinov, Boyce, Lee, & Bush, 2020). For example, one recent paper examined patterns of change across the parasympathetic and sympathetic nervous systems, and the Hypothalamic-Pituitary-Adrenal axis (Roubinov et al., 2020). Although the researchers argue that they have identified some profiles of change between different children that are stable across measurement time and which associate with socioemotional outcomes (Roubinov et al., 2020), other authors have failed to identify consistent cross-system profiles, and associations with behaviour. These subsystems are intertwined in complex, non-linear ways with interactions across multiple timescales, which presents considerable challenges to researchers attempting to study them.

1.1.4 Interaction with affect

Although the main focus of this review is on examining interactions between arousal/regulatory function and effortful control, it will also be important for the discussions that follow to point out that arousal/regulatory system behaviour does not map directly onto affect/emotional valence (Cacioppo et al., 2000; Walter Bradford Cannon, 1915; Kreibig, 2010; Levenson, 2014; Pérez-Edgar, 2019). Positive, and negative, emotional valence are both associated, at higher levels of intensity, with elevated activity within arousal/regulatory systems (see e.g. Kreibig, 2010; S. V. Wass, Smith, Clackson, et al., 2019).

1.2 Effortful control

1.2.1 Neural correlates

Both structurally and functionally, the higher-order association cortices that primarily mediate effortful control take longer to reach maturity compared with lower-order somatosensory and visual cortices (Fair et al., 2008; Fair et al., 2009; Gogtay et al., 2004; Grayson & Fair, 2017; Johnson, 2015; Shaw et al., 2008). Postnatally, myelination proceeds caudocranially from the splenium of the corpus callosum, to the occipital and parietal lobes, reaching the genu of the corpus callosum and frontal and temporal lobes towards the end of the first year of life (Deoni et al., 2011; Paus et al., 2001). Although the prefrontal cortex is active even during early development (Hodel, 2018), functional connectivity analyses suggest that connectivity between prefrontal circuitry and other brain regions take much longer to develop, showing substantial change through childhood and into adolescence (Darki & Klingberg, 2015; Palva, Monto, Kulashekhar, & Palva, 2010).

1.2.2 Operationalising effortful control during infancy and early childhood

Definitions of effortful control are highly diverse (Aktar & Pérez-Edgar; Berger, Kofman, Livneh, & Henik, 2007; Eisenberg, Smith, & Spinrad, 2011; Hendry, Jones, & Charman, 2016;

Rose, Feldman, & Jankowski, 2005, 2012; Rothbart, 2007; White, Lamm, Helfinstein, & Fox, 2012; Zelazo, 2002) – particularly insofar as they pertain to early development, due to inherent difficulties in working with pre-linguistic individuals (Aslin, 2007). Here, I concentrate on two definitions of effortful control that have been well operationalised within the early developmental literature. These have been chosen as a result of practical as well as theoretical criteria, as I describe in detail below. The first is attentional control, as indexed primarily by measuring sustained attention. Second is affective control, as indexed primarily by measuring emotion regulation. Of note, the inclusion of affect regulation within functional definitions of effortful control is not universally accepted, although it is fairly common (Eisenberg et al., 2011; Rothbart, 2007), and I shall take care to differentiate attentional and affective control in the discussions that follow.

In the two sections that follow I give further details about each of these, in turn.

1.2.3 Attentional control – sustained attention

At birth, infants’ shifts of attention are heavily stochastic (Robertson, 2004; Robertson, Bacher, & Huntington, 2001), and they attend primarily towards salient areas of their environment (Berg & Richards, 1997). Whereas responsiveness to external stimuli (exogenous attention) develops rapidly through the first year, the capacity for endogenous attention control (defined as the individual’s capacity to choose what they pay attention to and what they ignore) is traditionally considered to be largely absent until 12 months (Colombo & Cheatham, 2006; Hendry, Johnson, & Holmboe, 2019). More recent research, using sophisticated assessment techniques, has, however, suggested that infants below this age are capable of some elements of volitional/effortful control, including perseverative/switching behaviours (Kovacs & Mehler, 2009; S. V. Wass, Porayska-Pomsta, & Johnson, 2011), short-term memory (Kaldy &

Blaser, 2013) and precursors of inhibition (Karla Holmboe, Fearon, Csibra, Tucker, & Johnson, 2008), and so on (see Hendry et al., 2019; Rose et al., 2005 Gilmore & Johnson, 1995; Johnson, 1990, 1995; Richards, 2000). Overall, however, the effortful control of attention shows a slower developmental trajectory compared with other cognitive domains (Chatham, Frank, & Munakata, 2009; M. C. Davidson, Amso, Anderson, & Diamond, 2006; Hendry et al., 2019).

Sustained attention, as operationalised in this review, is measured simply by recording infants' looking behaviour toward static or dynamic, previously unseen viewing materials. Although highly practical to record with infants, it presents a number of interpretative challenges (Aslin, 2007; Richards, 2010). Sustained attention is thought to be contributed to by both exogenous ('bottom-up') attention capture and by endogenous ('top-down') attention (Luna, Velanova, & Geier, 2008), to an extent that differ depending on whether the stimuli being viewed are dynamic or static (Courage, Reynolds, & Richards, 2006; Shaddy & Colombo, 2004). Early in the first year (0-8 months), look durations towards static images negatively predict long-term cognitive outcomes (Colombo, 2001; Colombo & Mitchell, 2009), although this relationship changes across development. For example, one study found that, whereas looking behaviour toward static images declined throughout the first year, looking behaviour towards more complex stimuli showed a U-shaped trajectory. The authors attributed this to the emergence of endogenous sustained attention towards the end of the first year of life (Courage et al., 2006).

Cutting edge recent research has suggested that sustained attention is associated with synchronisation of neural oscillatory activity in the theta band (2-6Hz) over frontal pole, temporal and parietal electrodes, along with desynchronization in the alpha (6-9Hz) band over frontal, central and parietal electrodes (Xie, Mallin, & Richards, 2018) (see also Xie, Mallin, & Richards, 2019). (Although the relationship of theta power to sustained attention is complex

– see Begus & Bonawitz, 2020; Jones et al., 2020; Jones, Venema, Lowy, Earl, & Webb, 2015; Orekhova, Stroganova, & Posikera, 1999; S. V. Wass, Smith, Stubbs, Clackson, & Mirza, 2019). Another recent study showed that greater sustained attention associated with more general oscillatory activity across physiological measures (heart rate, movement and electrodermal activity) in the 0.2-2Hz range (S. V. Wass, de Barbaro, Clackson, & Leong, 2018). As I discuss further in section 2.2.2 below, extensive research has also shown that sustained attention is also accompanied by event-related physiological changes, such has look-related heart rate decelerations (Richards, 2010, 2011).

1.2.4 Affective control – emotion regulation

Patterns of emotional fluctuation are inherently more labile in younger children, and become more stable and predictable with increasing age (Kim-Spoon, Cicchetti, & Rogosch, 2013). The capacity for the effortful control of affect is, like attentional control, considered one of the later cognitive faculties to emerge (Cole, Lougheed, Chow, & Ram, 2020; Joel T Nigg, 2017). Most research into the early development of affective control emphasises the importance of co-regulation across parent-child dyads as a precursor to endogenous control (Bridgett, Burt, Edwards, & Deater-Deckard, 2015; Feldman, 2007; Kopp, 1982).

Many researchers assess affective control in lab settings by recording a baseline (free interaction period), and then administering a mild known stressor to the child. Commonly used stressors include a ‘still face’ procedure (in which the parent is asked to freeze and to become non-responsive to the child for 2 minutes) (Tronick, 1982, 2007), or variants of a toy removal task (in which the child is allowed to play with a toy before it is removed from reach but retained in sight by the experimenter (Gagne, Van Hulle, Aksan, Essex, & Goldsmith, 2011)). Dependent variables measured typically include facial affect and physiological responses.

Importantly, there is evidence that reactions observed using different types of stressor do not necessarily generalise between stressors (Obradović, Bush, & Boyce, 2011), questioning the generalisability of emotion regulation as a parameter of individual differences - although this question is under-researched.

There is some evidence that behaviours traditionally associated with effortful affective control can be seen during the first year. For example, even at 5 months, infants were more likely to show gaze aversion (a behaviour known to downregulate arousal (T. M. Field, 1981)) in response to toy removal (Buss & Goldsmith, 1998; Stifter & Braungart, 1995) (see also Morasch & Bell, 2012).

Less is known about the neural correlates of affective control during early life (M. I. Posner, Rothbart, Sheese, & Voelker, 2012). A number of researchers have studied non-event-locked asymmetries in power (often in the alpha (6-9Hz) band) between left and right frontal hemispheres, and linked them to a range of different aspects of affective behaviour (Bell & Fox, 1994; R. J. Davidson & Fox, 1989; N. Fox, Calkins, & Bell, 1994; N. Fox & Davidson, 1987; N. A. Fox, 1989; Perry, Swingler, Calkins, & Bell, 2016; Stifter & Fox, 1990), although recently other researchers have struggled to replicate these findings (see e.g. Kolodziej, Magnuski, Ruban, & Brzezicka, 2020).

2 Short-term interactions between arousal/regulatory systems and effortful control – part 1 – the Aston-Jones framework

In the following three sections (sections 2-4) I examine the short-term associations between arousal/regulatory systems and effortful control. In this section, I consider the Aston-Jones framework, which acts as the first integrative framework for this review.

2.1 The Aston-Jones framework

2.1.1 Precursors to the framework

Russian electrophysiologists such as Sechenov and Pavlov first differentiated between two types of reflexive change shown by the ANS: the orienting response, which is elicited by stimuli that are novel, surprising, complex and incongruous, and the defensive response, which is elicited by stimuli that are unexpected and more aversive (Pavlov, 1927; Sechenov, 1965; Sokolov, 1963). Different reactions can be elicited by the same stimulus, depending on the context in which it is presented (Graham & Clifton, 1966; Graham & Jackson, 1970). This first led to the idea that the ANS may be involved in a range of contexts, including both emotional responding to adverse, unexpected or threatening events and 'higher-order' cognitive functions such as attention, and learning.

More recently, adult research has also started to examine how other peripheral indicators of arousal/regulatory systems such as pupil size (Loewenfeld, 1993) relate to brain activity and behaviour (Breeden, Siegle, Norr, Gordon, & Vaidya, 2016; Murphy, Robertson, Balsters, & O'Connell, 2011; Reimer et al., 2016 Chatham et al., 2009; Smallwood et al., 2011; Wainstein et al., 2017). And animal researchers have recorded directly from the brainstem (most often the Locus Coeruleus) to examine associations between arousal/regulatory systems and behaviour (Aston-Jones & Cohen, 2005; Aston-Jones et al., 1999; McCall et al., 2015; Usher, Cohen, Servan-Schreiber, Rajkowski, & Aston-Jones, 1999; Vazey, Moorman, & Aston-Jones, 2018; Waterhouse & Navarra, 2019). This research has given rise to the Aston-Jones framework.

2.1.2 The framework

The Aston-Jones framework was developed (Aston-Jones & Cohen, 2005; Aston-Jones et al., 1999; Usher et al., 1999), building on earlier research from Yerkes and Dodson (Yerkes & Dodson, 1908) (see Figure 1). They examined how slow-varying fluctuations in pre-stimulus (also known as tonic, or baseline) activity within arousal/regulatory systems associated with phasic (or directly stimulus-evoked) changes, and how both relate to fluctuations in cognitive performance. They found that the relationship between tonic (prestimulus) activity and phasic (event-related) responses to sought-for stimuli was U-shaped: extreme high and low levels of tonic activity associated with fewer phasic arousal responses, but mid-level tonic activity associated with more phasic responses (Aston-Jones & Cohen, 2005; Usher et al., 1999), together with superior working memory and selective attention with task irrelevant cues.

INSERT FIGURE 1 HERE

2.2 Testing the framework – infant and child research

Research with human infants and children has tested the predictions of the Aston-Jones framework (see S. V. Wass, 2018 for an in-depth review on this topic). This research has either examined how tonic/baseline arousal relates to attentional control (discussed in section 2.2.1). Or, they have examined how phasic, event-locked changes in arousal relate to attentional control (discussed in section 2.2.2).

2.2.1 Sustained attention - Tonic/baseline arousal

Some researchers have examined the relationship between tonic (or baseline, or resting state) arousal and attentional control, by measuring, for example, RSA to index parasympathetic nervous system activity (S. W. Porges, 2007, 2017)). Findings with infants and children suggest that more resting RSA correlates with better quality attention and learning (Stephen W Porges, Arnold, & Forbes, 1973) – as measured using recognition memory (Frick & Richards, 2001) or sustained attention (Richards, 1985) in 6-12-month-old infants, or a battery of executive function tasks in 3.5-year-old children (Marcovitch et al., 2010). Studies examining resting state arousal in older children and adolescents with ADHD have reported more inconsistent results, with reports of both hypo- and hyper- resting arousal and the majority reporting no difference (Bellato, Arora, Hollis, & Groom, 2020). These inconsistent findings are likely due to heterogeneity in ADHD (J. T. Nigg, Willcutt, Doyle, & Sonuga-Barke, 2005).

Other researchers have recently taken different approaches to demonstrate the associations between slow-varying fluctuations in arousal and sustained attention. For example, de Barbaro and colleagues presented mixed static and dynamic viewing data to typical 12-month-old infants while continuously measuring attention by recording the duration of infants' individual looks to the screen, and autonomic arousal by recording a composite of heart rate, electrodermal activity and movement (de Barbaro, Clackson, & Wass, 2016a). They found that spontaneous fluctuations in ANS activity over the scale of seconds/minutes related to fluctuations in attention, such that increased ANS activity was associated with shorter look durations. They also found that changes in autonomic arousal tend to precede subsequent changes in look duration (de Barbaro et al., 2016a; S. V. Wass, Clackson, & de Barbaro, 2016) (see also Bacher & Robertson, 2001; de Barbaro, Chiba, & Deak, 2011).

Overall, these findings point to associations between tonic/baseline arousal and early sustained attention. Importantly, however, the relationships documented thus far with younger children are all linear relationships – showing that higher arousal associates with decreased attention.

They are not the quadratic relationship predicted by the Aston-Jones framework, such that both extreme low and extreme high arousal are associated with reduced attention. One reason for this, however, may be methodological, insofar as it is hard to examine spontaneously occurring low arousal states in humans during lab visits during the day (for further discussion see section 7, below).

2.2.2 Sustained attention - phasic, event-locked arousal changes

A larger body of research has examined the relationship between phasic reactivity and early attention and learning. This research has either examined event-locked changes relative to external events (such as the appearance of a novel stimulus, following the approach pioneered by Sechenov and Pavlov (see section 2.1.1)). Or, they have examined arousal changes relative to internally determined events – such as individual looks towards attention-eliciting stimuli.

Consistent with the Aston-Jones framework, this research suggests that infants and young children who show greater (larger amplitude) heart rate decelerations during attention show better quality attention and learning (reviewed Richards, 2010, 2011). For example, infants are better able to recognise material that was presented during phases of heart rate decelerations (Frick & Richards, 2001; Richards & Gibson, 1997), and infants are less distractible during heart rate decelerations (Casey & Richards, 1988; Lansink & Richards, 1997) (see Figure 2). In older children, evidence for reduced task-related changes in heart rate has also been shown in children with ADHD (Bellato et al., 2020).

INSERT FIGURE 2 HERE

Other research has examined phasic, event-locked changes in RSA (Beauchaine, 2001). These results are, however less consistent: for example, they are inconsistent as to whether greater phasic decreases (Becker et al., 2012; Blair & Peters, 2003) or increases (Utendale et al., 2014) associate with better attention. And some research has suggested that, whereas phasic changes in RSA are adaptive up to a point, *excessive* phasic (reactive) changes are a marker of psychopathology (Beauchaine, 2001; Beauchaine, Gatzke-Kopp, & Mead, 2007; Beauchaine & Thayer, 2015; Mezzacappa et al., 1997) and impaired executive functions (Marcovitch et al., 2010). Obradovic & Finch suggested than one reason for these inconsistent results may be that RSA studies tend to study change over relatively long time-scales (minutes) (Obradović & Finch, 2016). This may mean that a number of different subcomponent processes (initial withdrawal, maintenance of change, recovery) are all included in the measure of RSA withdrawal (S. W. Porges, 2007).

A third strand of research has examined pupil dilation amplitude. For example, one study induced phasic increases in arousal with brief sounds and measured with pupil dilation, and examined the relationship between pupil dilation amplitude and orienting on a visual search task in 6.5-month-old infants (Kleberg, del Bianco, & Falck-Ytter, 2019). They observed the U-shaped relationship predicted by the Aston-Jones framework. Finally, one study (following Murphy et al., 2011) examined the relationship between ANS arousal and neural Evoked Response Potentials to auditory stimuli, using an oddball paradigm. Children with higher mean heart rate (HR) and decreased RSA showed smaller amplitude N250 responses to frequently presented standard tones (S. V. Wass, Daubney, Golan, Logan, & Kushnerenko, 2019). Follow-up analyses showed that the modal evoked response was in fact similar, but accompanied by more inconsistent responding in the high arousal group.

In summary, these findings are largely consistent with the Aston-Jones framework, insofar as they suggest that larger phasic/event-locked changes in arousal associate with better quality early attention and learning. Again, the limitation is that the relationships documented with arousal are generally linear: hyper-arousal is associated with reduced phasic responsiveness, but hypo-arousal as well is not. The reasons for this may, again, be methodological, and attributable to difficulties in measuring low arousal states in children in lab settings.

2.2.3 Emotion regulation

Despite evidence suggesting that the same arousal/regulatory systems implicated in attentional control are also involved in affective control (McCall et al., 2015) (see also section 2.2.1), relatively little research has, to our knowledge, tested how the Aston-Jones framework applies to affective control. Evidence consistent with this framework has, however, been obtained by Porges and colleagues, who find that infants and children who consistently show phasic decreases in Respiratory Sinus Arrhythmia following a social challenge tend to show better recovery (see Beauchaine & Thayer, 2015; S. W. Porges, 2007; S. W. Porges & Furman, 2011 for reviews). Temporal withdrawal of vagal (parasympathetic) control of the heart (known as removal of the ‘vagal brake’) is thought to increase metabolic activity, to allow for recovery following challenge (S. W. Porges & Furman, 2011). Attenuated RSA reactivity is associated with less effective regulation (Beauchaine & Thayer, 2015; Busuito & Moore, 2017). Unlike in the field of attentional control, however, *excessive* vagal withdrawal following a challenge has also been characterised as a marker of psychopathology (Beauchaine & Thayer, 2015), suggesting that, for RSA, phasic changes may only be optimal up to a point.

An extensive body of research has also linked lower tonic parasympathetic activity to decreased affective control (see Beauchaine & Thayer, 2015; S. W. Porges, 2007 for reviews).

Again, though, the observed relationships are linear (decreased parasympathetic activity associated with reduced affective control) and not the quadratic relationship predicted by the Aston-Jones framework (such that both extremes of arousal are associated with reduced affective control). It is unclear whether Respiratory Sinus Arrhythmia is sensitive to hypo- and as well as hyper-arousal. To our knowledge, no research has examined this using arousal measures other than Respiratory Sinus Arrhythmia.

In summary, these findings are consistent with the Aston-Jones frames, insofar as they suggest that larger phasic/event-locked changes in Respiratory Sinus Arrhythmia associate with superior affective control, and that elevated baseline arousal is associated with reduced affective control. Again, the limitation is that the relationships documented with arousal are linear: hyper-arousal is associated with reduced phasic responsiveness and reduced affective control, but hypo-arousal as well is not.

3 Short-term interactions between arousal/regulatory systems and effortful control – part 2 – the Arnsten framework

3.1 Adult and animal research

The Aston-Jones framework, discussed above, suggests only that superior effortful control is observed at intermediate levels of arousal, with hyper- and hypo-arousal associated with reduced effortful control. In this section, I discuss research that builds on this finding, by examining the hyper-aroused phenotype in more detail. The picture that emerges is that hyper-arousal actually associates with superior performance at some types of tasks associated with effortful control, as well as worse performance at other types of task.

Neuroimaging with adults suggests that experimental manipulations that cause increases in short-term stress (which cause increased overall activity within arousal/regulatory systems McCall et al., 2015)) are associated with the immediate down-regulation of areas such as the dorsolateral pre-frontal cortex, together with up-regulation of areas including the hypothalamus, striatum, amygdala and occipital cortices (Arnsten, 2009; Liston, McEwen, & Casey, 2009) (see also Zerbi et al., 2019). Behaviourally, whereas increased short-term stress is associated with decreased voluntary control of attention, it simultaneously enhances processes dependent on subcortical structures, such as basic memory consolidation, habit formation and fear conditioning (Cahill & McGaugh, 1996; Luethi, Meier, & Sandi, 2009). 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; Dayan & Angela, 2003; Zerbi et al., 2019).

3.1.1 The framework

Based on this adult research, the Arnsten framework (Arnsten, 2009) suggests that elevated arousal is associated with a profile of cognitive weaknesses, and strengths (see Figure 3). Weakness include reduced top-down control of cognition and affect; strengths include more bottom-up, or stimulus-driven responding, including faster learning in some contexts.

INSERT FIGURE 3 HERE

3.2 Testing the framework – infant and child research

Although it is well validated within adult and animal research, only relatively little research with infants and children has explicitly tested the applicability of this framework to understanding early learning. One study with 12-month-old infants examined the relationship between ANS reactivity (heart rate response to watching videos of another child crying) and performance on measures of sustained attention and visual recognition memory for briefly presented targets (de Barbaro, Clackson, & Wass, 2016b). Results suggested that infants with elevated stress showed shorter look durations, but better recognition memory for briefly presented stimuli – consistent with the predictions of the Arnsten framework.

Also consistent with this, another recent paper examined attention in a cohort of 12-month-olds from high-density urban environments, who showed higher physiological stress (S. V. Wass, Smith, Stubbs, et al., 2019). Behaviourally, high-density urban infants showed lower sustained attention in the lab, and decreased emotion regulation. However, consistent with the previous study, they showed better recognition memory for briefly presented stimuli, along with more neural engagement with novel stimuli (as indexed by measuring Theta power). This was assessed by measuring the associations between cortical theta power (Begus & Bonawitz, 2020; Jones et al., 2020) and looking behaviour during attention phases (S. V. Wass, Smith, Stubbs, et al., 2019). Again, this finding is consistent with the predictions of the Arnsten framework.

Overall, adult and animal research suggests that elevated activity within arousal/regulatory systems is associated with a profile of cognitive strengths (such as more vigilance and better memory formation in some contexts) as well as weaknesses. Only a small number of studies have tested this in infants, but the available evidence is consistent with this model.

4 Short-term interactions between arousal/regulatory systems and effortful control – part 3 – interaction dynamics

4.1 The importance of studying short-term dynamical interactions with the environment

Both the Aston-Jones and Arnsten frameworks I have discussed so far look at reactivity to individual stimulus events. Although this trial-based approach is near universal in lab-based studies, it is important to remember that it lacks ecological validity. In most real-world contexts in which effortful control has to be exerted, the control is not relative to discrete stimuli. Our experience of the world is not discrete, but continuous and overlapping (Edelman, 2016; Spivey & Dale, 2006).

Take, for example, the toy removal task, which is a common test of affective control (see section 1.2.4) (S. V. Wass, pre-print). In the lab-based version of this paradigm (Gagne et al., 2011), a child plays with a toy for a period of time (a baseline period) before an experimenter takes it and places it out of reach (the test period), before returning it after a time interval (the recovery period). The removal of the toy, and its return, are controlled by the experimenter. The child's capacity for self-regulation is measured by averaging the child's behavioural and physiological responses during the test period, and subtracting the baseline period from the test period.

Compare this with an ecologically valid equivalent of the same scenario – say, a child tantrumming at not being allowed to buy a toy while out shopping. A child might pick up a toy, and announce that they want it; their parent, tired and in a hurry, might abruptly say ‘no’, and attempt to take the toy off them, leading to a physical tug of war. The child might lose this, sit down with a bump, and burst out crying. Or, they might start bashing the toy on the floor and break it; others in the shop might turn around to look at the noise.

The real-world scenario I have described differs from the lab version in two related, but important, ways. First, the real-world version has a dynamical aspect – one thing causes another, which causes another, in a chain reaction – which the lab-based version fails to capture, due to its reliance on experimenter-controlled events. Second, the real-world version there are a series of different (but causally related) events – being abruptly told ‘no’, a tug of war, sitting down with a bump, making a loud noise, being stared at by strangers – which are independent, and which act both as consequences, *and causes*, of increased arousal. These operate through interactions between the child and their social environment. The lab-based version does not capture these (Chow, 2019; Cole, Bendezú, Ram, & Chow, 2017; Morales et al., 2018; Ram & Diehl, 2015).

Similar considerations also apply when I examine sustained attention. Thus, a child’s arousal state can influence how they react when a complex or slow-paced new stimulus is presented (Richards, 1987; Van der Meere & Sergeant, 1988) – either engaging with it, or not. At the same time, comprehensible stimuli elicit greater decreases in arousal during presentation compared with incomprehensible ones (e.g. TV programs with the shots correctly ordered vs randomly re-shuffled - Pempek et al., 2010; Richards, 2010). Thus, a child’s attentional engagement when a complex or slow-paced new stimulus is presented may be both a *consequence* of their arousal state at the time it is presented, and a *cause* of it (because comprehension causes decreases in arousal).

As a result of these limitations, an increasing number of studies with humans are starting to move beyond an exclusive reliance on analysing change relative to experimenter-controlled events. Instead they are using different, dynamical methods to measure the relationships between arousal/regulatory system activity and effortful control within more ecologically valid settings (Chow, 2019; Cole et al., 2017; Cole et al., 2020; Morales et al., 2018).

4.2 During infancy, hyper- and hypo-aroused states are more long-lasting than intermediate states

Seminal research using a dynamical approach to study arousal/regulatory system activity and sustained attention was conducted by Anderson and Richards. They identified a pattern which they named 'attentional inertia': that the longer a look lasts, the more its likelihood of ending during the next successive time interval diminishes (Anderson, Choi, & Lorch, 1987; Lorch et al., 2004; Richards & Anderson, 2004).

More recent work has studied naturalistic home recordings to examine how both high, and low, arousal states fluctuate in 12-month-old infants (S. V. Wass, Clackson, & Leong, 2018; S. V. Wass, Smith, Clackson, & Mirza, 2020). Specifically, they examined how the stability of arousal (the likelihood of being in the same arousal state at time t+1) varied contingent on arousal levels at time t. They found that both high and low arousal states were more long-lasting than intermediate arousal states. This finding may be seen as surprising given traditional approaches to self-regulation that suggest that increases and decreases in arousal are corrected for via affect regulation (Walter B Cannon, 1929; Fiske & Maddi, 1961; M. Gunnar & Quevedo, 2007; McEwen & Seeman, 1999; McEwen & Wingfield, 2003; S. W. Porges, 1995; Selye, 1951; Ulrich-Lai & Herman, 2009) – albeit that this capacity is considered trace during infancy (see section 1.2.4). However, they build on the findings from Anderson and Richards that low arousal states take on a self-sustaining character, suggesting that similar principles apply to both low and high arousal states in naturalistic settings.

One explanation for this finding is that different arousal states have different intrinsic levels of hysteresis. For example, sleep is an intrinsically more stable arousal state (Saper, Fuller, Pedersen, Lu, & Scammell, 2010) and, although sleeping sections were excluded from that study, it is possible that other arousal states (including both extreme high and low states) may also show differing intrinsic hysteresis in the same way. An alternative possibility is that both extreme low and high arousal states may lead to changes in how I interact with the external environment and with people (Cole et al., 2017) - changes that may in turn lead to extreme arousal states becoming progressively amplified over time, through a dynamical process termed ‘metastasis’.

4.3 Allostasis and metastasis

Allostasis describes the dynamical process through which internal equilibrium (homeostasis) is achieved and maintained (Walter B Cannon, 1929; McEwen & Wingfield, 2003; Ramsay & Woods, 2014; Sterling, 2012 Selye, 1951). When there is a discrepancy between the current level of activation and the optimal level or range for the given situation, the organism will typically engage in behaviour designed to shift activation to reduce the discrepancy (Fiske & Maddi, 1961). When used by psychologists and cognitive neuroscientists, allostasis typically refers to the active behavioural processes through which an intermediate level of arousal is established and maintained (S. V. Wass, pre-print).

If allostasis is the dynamical principle underlying arousal regulation, through which small initial increases and decreases in arousal are corrected for over time, then metastasis is the opposite. It is the dynamical principle underlying arousal *dys*regulation, through which small initial increases and decreases in arousal become progressively amplified over time (S. V. Wass, pre-print). Both dynamical principles can be applied to describe both our interactions with the environment (actor-environment interactions) and our interactions with other people (actor-actor interactions).

Evidence for basic actor-environment allostatic mechanisms, such as closing eyes while overstimulated, can be readily observed in neonates (Brazelton, 1983). Other experimenters have shown that even 5-month-old infants were more likely to spontaneously show behaviours such as gaze aversion (which down-regulates arousal) following toy removal (which up-regulates arousal) (Buss & Goldsmith, 1998; Stifter & Braungart, 1995; see also Doherty-Sneddon, Riby, & Whittle, 2012). Similarly, Gardner, Karmel and colleagues showed that, whereas highly aroused individuals prefer to look to less arousing, low-frequency stimuli, less aroused infants prefer more arousing, high-frequency stimuli (Gardner & Karmel, 1984, 1995; Gardner, Karmel, & Flory, 2003; Gardner, Karmel, & Magnano, 1992; Geva, Gardner, & Karmel, 1999) - suggesting that infants effortfully alter their attentional behaviours to downregulate their own arousal when it is high, and to upregulate it when it is low.

Evidence for actor-actor allostatic mechanisms is also comparatively well documented: caregivers dynamically, and effortfully, alter their own behaviours to compensate for changes in their infant, which has the effect of helping the child maintain stable arousal (Kopp, 1982; Tronick, 2007; S. V. Wass, Smith, Clackson, et al., 2019). Previous research has also investigated how these actor-actor allostatic compensatory mechanisms relate to the development of child effortful control over time (Feldman, 2007; Feldman, Greenbaum, & Yirmiya, 1999).

Research into metastatic actor-environment interactions processes during development is less well advanced. Although it seems intuitively likely that, for example, a child banging a spoon on a table can act both as a consequence, and a cause, of elevated arousal, relatively little work has tested this possibility. Within Attention Deficit Hyperactivity Disorder (ADHD) research, for example, some researchers have suggested that a preference for fast-paced visual stimuli (Beyens, Valkenburg, & Piotrowski, 2018; Van der Meere & Sergeant, 1988), delay aversion (Sonuga-Barke, Wiersema, van der Meere, & Roeyers, 2010) and hyperkineticism (Sonuga-Barke & Taylor, 2015) can all act both as causes, and consequences, of hyper-arousal, and similar discussions have been mooted within the context of children with emotion dysregulation (Wolke, Bilgin, & Samara, 2017). However, little research has evaluated this systematically.

Similarly, some research into atypical development has investigated metastatic actor-actor interactions – such as the relationship between parental expressed emotions (i.e., hostility, criticism, low warmth) and oppositional child behaviour in ADHD (Harold et al., 2013; Taylor, 1999) (see also Baker, Fenning, Howland, & Huynh, 2019). Other research has examined parent-child interactions in cases where the parent has anxiety (Feldman et al., 2009; T.M. Field, Healy, Goldstein, & Guthertz, 1990; Granat, Gadassi, Gilboa-Schechtman, & Feldman, 2017; Smith et al., in press) or depression (T.M. Field et al., 1990). Again, though, research in this area is not currently well advanced.

In summary, this section has described how lab-based studies, which study reactivity to individual stimulus events, fail to capture the dynamical aspect of the real world – how one thing causes another, which causes another (Cole et al., 2017). They also fail to capture the interactive element: how changes in arousal can be both consequences, and causes, of our behaviors. I have contrasted two principles: allostasis, in which increases and decreases in arousal are corrected for; and metastasis, in which increases and decreases in arousal become amplified. Overall, in infants, both hypo- and hyper-aroused states appear to take on dynamically self-sustaining characters, suggesting that both may be influenced by metastatic processes.

5 Long-term interactions between arousal/regulatory systems and effortful control – part 1

Sections 2-4 examined dynamical interactions between arousal/regulatory systems and effortful control over timescales of seconds or minutes. In sections 5 and 6 I examine associations over much longer time-scales, of months and years. Generally, these long-term interactions were examined by recording static snapshots at different ages, and thus offer only a limited perspective on large-scale dynamics (Pérez-Edgar, 2019). Interactive dynamics will doubtless exist at time-scales between seconds/minutes and years, but these are largely undocumented.

In section 5.1 I examine correlational evidence examining how early arousal/regulatory system development can predict later effortful control. In section 5.2 I examine evidence for how early attentional control can predict later affective control. In section 6 I build on this by considering how the environment may moderate the relationships observed between early arousal/regulatory system development and effortful control.

5.1 Early arousal/regulatory system development predicts effortful control

A series of studies by Geva and colleagues have examined how mild atypicalities within arousal/regulatory systems shortly after birth predict long-term effortful control. They examined the Auditory Brainstem Response, which is often administered in hospital settings shortly after birth. Infants who show mild atypicalities on this measure, indicating minor disruptions to early brainstem development, were tracked and followed up longitudinally. (Severe atypicalities tend, sadly, to lead to death.) Mild brainstem disruption at birth is associated with less motor initiation of responses at 4 months, which influenced affective control such that infants with neonatal brainstem disruption were more likely to remain inactive during separation from their mothers (Geva, Schreiber, Segal-Caspi, & Markys-Shiffman, 2013). By 12 months, the same infants show a reduced ability to initiate self-regulatory activities in response to a socioemotional challenge, which again compromised affective control (Geva, Sopher, et al., 2013). The same cohort were also followed up at 8 years where some mild evidence for atypicalities was still present, such as atypical performance on the alerting (but not other) components of the Attention Network Test (Geva et al., 2017). In a separate study, the degree of Central Nervous System injury at birth (measured via the Auditory Brainstem Response, along with cranial ultrasound) was found to predict performance on an intradimensional shift card sort task at 34-60 months, which is well established in research with older children as a measure of attentional control (Kittler et al., 2013; see also Cohen et al., 2013). Although the possibility cannot be excluded that children showing early atypical brainstem development also show other, more generalised patterns of early impairment, every effort was made to match the groups on other risk factors as far as possible.

Other research has used a combination of the Auditory Brainstem Response, cranial ultrasound and neonatal behavioural assessment (Gardner et al., 2006) to identify early atypicalities within arousal/regulatory systems. As an outcome measure, they examined infants' capacity to endogenously regulate their gaze behaviours to maintain stable levels of arousal – a process known as allostasis (see Atzil, Gao, Fradkin, & Barrett, 2018; McEwen & Wingfield, 2003) (see also section 4.3). As described above (section 4.3), typical infants preferentially look to less arousing, low frequency visual stimuli at times when their own arousal levels are high, and at more arousing, high frequency visual stimuli at times when their own arousal levels are low (Gardner & Karmel, 1984, 1995; Gardner et al., 2003; Gardner et al., 1992; Geva et al., 1999). In infants with brainstem dysfunction, however, this pattern was less pronounced. Neonates with brainstem dysfunctions showed poorer attention regulation as a function of arousal states at one month of age (Gardner et al., 2003); poorer attentional responses that were hyper-responsive to elevated endogenous arousal at four months (Karmel, Gardner, & Freeland, 1996); and less regulated inhibitory control on rapid automatized naming tasks at three years of age (Geva, Schreiber, et al., 2013).

Other studies have examined how early regulatory functions (crying, feeding, sleeping) at 5 months relate to attention regulation at 6 and 8 years (Baumann et al., 2019). Results suggested that regulatory problems in infant were associated with later attention regulation abilities even after controlling for socio-demographic factors. Inhibitory control at 20 months weakly mediated the relationship between early regulatory functions and later attention regulation; however, this relationship disappeared when other cognitive outcomes were also included, suggesting that the effects may be accounted for by children's general cognitive abilities.

Overall, these findings suggest that atypicalities at birth in arousal/regulatory systems correlate with long-term atypical effortful control, implicating both attentional and affective control. They also suggest a potential mechanism, which is that infants with compromised brainstem function are less capable of initiations, which compromises affective control via allostasis.

5.2 Early attentional control predicts affective control

Ideas consistent with those reviewed above have come from research suggesting that a child's capacity for endogenous attention control can positively predict their long-term capacity for affective control (M.I. Posner & Rothbart, 2007, 2009 Bush, Luu, & Posner, 2000; Kelly et al., 2009; Pessoa, 2008). Consistent with this, one study found that anticipatory looking in 24- and 30-month-old children correlated with parent-related affective control (Rothbart, Ellis, Rueda, & Posner, 2003 see also Rothbart, 2007). Longer latencies to disengage visual attention at 6 months have also been associated with greater negative affect (McConnell & Bryson, 2005 Nakagawa & Sukigara, 2019), although several results in this area have not replicated (Hendry et al., 2019). And sustained attention at 7 and 15 months predicts teacher-reported emotion regulation in children of pre-kindergarten age after controlling for demographic covariates (Brandes-Aitken, Braren, Swingler, Voegtline, & Blair, 2019) (see also Kochanska, Murray, & Harlan, 2000; Reck & Hund, 2011). However, other results may be inconsistent with this model, in predicting that better early attention control correlates with *more* negative affect (Sheese, Rothbart, Posner, White, & Fraundorf, 2008 Aksan & Kochanska, 2004 K. Holmboe, 2008).

A smaller number of studies have also looked at causal mechanisms by administering training targeted at improving infants' endogenous attention control, to assess the impact on affective control. A number of studies have shown that training leads to short-term changes in infants' sustained attention (Ballieux et al., 2016; Forssman & Wass, 2017; S. V. Wass, Cook, & Clackson, 2017; S. V. Wass et al., 2011). But one study found that these changes were not immediately accompanied by improvements in affective control on an emotion regulation task (S. V. Wass, de Barbaro, et al., 2018).

In summary, then, a number of studies have suggested that attentional control during early development correlates positively with affective control during later development, but evidence from training studies has thus far failed to provide evidence for a causal link between the two domains.

6 Long-term interactions between arousal/regulatory systems and effortful control – part 2 – Differential Susceptibility Theory

6.1 Moderating roles of the environment

The research findings reviewed in section 5.1 above put forward a simple deficit model, such that early atypical development within arousal/regulatory systems associates with impaired long-term effortful control. In this section, I consider research that additionally considers the moderating influence of the environment.

6.1.1 Differential Susceptibility Theory

The traditional diathesis–stress framework suggests that poor environmental experiences (e.g., low-quality parenting) are most likely to negatively impact the development of individuals who carry vulnerability factors (e.g. high sensitivity within arousal/regulatory systems) (Monroe & Simons, 1991). Differential Susceptibility Theory, in contrast, suggests that some individuals may be more susceptible than others to *both* negative (risk-promoting) and positive (development-enhancing) environmental conditions (Belsky, Bakermans-Kranenburg, & van

IJzendoorn, 2007; Boyce & Ellis, 2005; B. J. Ellis, Essex, & Boyce, 2005) (see Figure 4). Individuals with high biological sensitivity to context show superior long-term outcomes in positive environments, but worse long-term outcomes in negative environments; children with lower sensitivity show a lesser influence of environment on long-term outcomes. Although others have defined sensitivity via genetic (e.g. Bakermans-Kranenburg & van Ijzendoorn, 2011; Belsky et al., 2007; Belsky et al., 2009) or temperament-based criteria (Slagt, Dubas, Deković, & van Aken, 2016) others have used arousal/regulatory reactivity to index biological sensitivity to context (Obradovic, 2016; S. V. Wass, 2018).

INSERT FIGURE 4 HERE

For example, one study examined RSA responses to a social challenge task in 3-5-year-old children, half of whom had been exposed to childhood maltreatment. In the same children, they also measured inhibitory control. They found that higher task-based RSA was associated with less optimal performance on the inhibitory control task in children exposed to maltreatment, and with more optimal performance among non-maltreated children (Skowron, Cipriano-Essel, Gatzke-Kopp, Teti, & Ammerman, 2014). A number of other studies have found at least partially comparable results (Conradt, Measelle, & Ablow, 2013; Gueron-Sela, Atzaba-Poria, Meiri, & Marks, 2015; Holochwost, Gariépy, Propper, Mills-Koonce, & Moore, 2014; Obradovic, Bush, Stamperdahl, Adler, & Boyce, 2010; Peltola et al., 2016; Ursache, Blair, Stifter, & Voegtline, 2013). Notably, however, a number of other papers have reported the *opposite* findings – that *low* RSA confers increasing sensitivity to environmental effects on long-term outcomes. For example, one recent study found that that the link between sensitive parenting and EF performance was only evident in children with low RSA (Gueron-Sela et al., 2017); and another that, amongst a cohort of high-risk children, only those with low RSA performed more poorly on tasks of inhibitory control (Holochwost, Volpe, Gueron-Sela, Propper, & Mills-Koonce, 2018) (see also Skibo, Sturge-Apple, & Suor, 2020). Other studies have suggested that RSA does not mediate or moderate the relationship between parenting and later internalising outcomes (Wagner, Propper, Gueron-Sela, & Mills-Koonce, 2016).

6.1.2 Arousal reactivity to positive, attention-eliciting events and negative, aversive events

Another challenge to the suggestion that higher reactivity within arousal/regulatory systems can act both as a risk, and opportunity, factor contingent on context is that it rests on the assumption that reactivity within arousal/regulatory systems is, in fact, a one-dimensional construct. But is it actually the case that the same individuals who show a large autonomic change to a negative stimulus (mild experimental stressors such as arm restraint) also show a large autonomic change to a positive stimulus (such has a new attention/eliciting object)?

Prior research has, certainly, suggested that higher levels of RSA have been associated with elevated reactivity to both positive, and negative stimulus events. For example, infants with higher RSA exhibited larger cortisol responses to a heel-prick procedure (M. R. Gunnar, Porter, Wolf, Rigatuso, & Larson, 1995), elevated reactions to circumcision (Porter, Porges, & Marshall, 1988), and cried more following pacifier withdrawal (Stifter & Fox, 1990) (see also DiPietro, Porges, & Uhly, 1992); and other studies have suggested that infants with higher RSA respond to the onsets and offsets of auditory (Stephen W Porges et al., 1973) and visual (S. W. Porges, Stamps, & Walter, 1974) stimulus with greater heart rate responsivity (see also Richards, 1985; Richards & Casey, 1991). However, relatively few studies have examined reactivity to both types of event (positive and negative) within an individual stimulus cohort.

One recent study that did provided evidence that reactivity to positive and negative stimuli may not, in fact, be related – and may indeed be negatively associated. The study examined arousal reactivity to both negative, mildly aversive stimuli (videos of other children crying) and to positive, attention-eliciting stimuli (videos of interesting, attention-eliciting animations) (S. V. Wass, de Barbaro, et al., 2018). Infants who were generally more attentive showed greater arousal changes to positive, attention-eliciting stimuli; but these infants also showed *less* arousal reactivity to the negative stimuli. Attention training led to greater arousal responses to positive stimuli, but to no changes in reactivity to negative stimuli (S. V. Wass, de Barbaro, et al., 2018). Overall, these results suggest, consistent with other behavioural findings (Slagt et al., 2016; Slagt, Dubas, van Aken, Ellis, & Deković, 2017), that arousal reactivity to positive and negative events may represent differentiable constructs. If true, this evidence would be more consistent with the diathesis-stress framework (see Figure 5).

Overall, then, several studies have suggested that activity within arousal/regulatory systems may interact with environmental influences in determining long-term outcomes, such that individuals with highly sensitive arousal/regulatory systems may be more susceptible to *both* negative (risk-promoting) and positive (development-enhancing) environmental conditions. However, other work has challenged this, by suggesting that some individuals may be highly sensitive to positive (development-enhancing) conditions and others highly sensitive to negative (risk-promoting conditions). Of note, both perspectives may be partially true: it is possible that sensitivity may be a partially unitary construct, as well as one that is partially separable into different sub-factors.

7 Conclusions

In this review I have examined the reciprocal associations between arousal/regulatory system development and attentional and affective effortful control during early development. Our discussion has contrasted short-term interactions between arousal and effortful control (over a time-scale of seconds/minutes) with long-term interactions (over a time-scale of months/years).

7.1 Short-term interactions

7.1.1 Fluctuations in arousal associate with fluctuations in effortful control

First, when examining short-term interactions, I suggested that a U-shaped relationship between arousal and effortful control is predicted based on animal research, with both hypo- and hyper-arousal associated with worse effortful control (section 2). However, almost all available evidence points to a linear relationship, with children at higher tonic activity within arousal-regulatory systems showing smaller phasic event-locked arousal changes, and worse attentional and (probably) affective control (section 2). Evidence that hypo-arousal also associates with reduced effortful control during early childhood is lacking. This is striking given that, in older children and adolescents with ADHD, both hypo- and hyper-arousal has been noted (Bellato et al., 2020). It is unclear whether this because: i) the model is incorrect for describing early childhood; ii) hypo-arousal is naturally less prevalent in young children; iii) it is harder to elicit and study hypo-aroused states in lab studies. Future work could examine the hypo-aroused phenotype in more detail, by considering fluctuations both within individuals (e.g. by looking at effortful control in individuals immediately prior to sleep), and between individuals.

I also examined the hyper-aroused phenotype by investigating a prediction from animal and adult research that hyper-aroused children should show cognitive strengths (faster learning speeds) as well as weaknesses (reduced effortful control) (section 3). Here, I found only two studies with children that provided evidence consistent with this prediction. Future research should explore in more detail the types of cognitive task at which hyper-aroused children may show superior performance. Recent papers (Bruce J Ellis et al., 2020; Frankenhuis, Young, & Ellis, 2020) have argued that too much of our educational practice is focused on tasks that hyper-aroused children would find challenging (e.g. sustained attention). Instead, they argue, educationalists working with hyper-aroused children should focus more on discovering learning tasks at which they might excel (e.g. faster learning speeds). Future work should explore in more detail the types of task at which hyper-aroused children show superior performance (Bruce J Ellis et al., 2020; Frankenhuis et al., 2020), for example by building on previous research into the relationship between stress and learning (de Quervain, Schwabe, & Roozendaal, 2017; Schwabe, Joëls, Roozendaal, Wolf, & Oitzl, 2012).

Thus far, however, I have only considered whether *the same* associations between arousal/regulatory system activity and effortful control are observed in children as have previously been observed in adults and animals. A second question is: are the short-term interactions between arousal and effortful control stronger during early development compared with later development? Here, despite plentiful evidence on which to base this prediction (section 1.2.1) - for example, attention behaviours become progressively more cortically mediated over time (Johnson, 2005, 2015), and functional activation patterns associated with effortful control become more localised and specialised with age (Fair et al., 2009; Johnson, 2000) – we have identified no studies that have explicitly tested it. Investigating this should be a target for future work.

7.1.2 Bidirectional relationship between arousal and effortful control

In the previous section, we discussed how short-term fluctuations in arousal associate with altered effortful control. Here, we consider the short-term *bidirectional* relationship between arousal and effortful control – i.e. how effortful control influences arousal and *vice versa*. Here, we expected to find evidence that even young children effortfully modulate their attention to regain equilibrium following increases and decreases in arousal. Actually, though, although behaviours such as gaze aversion in response to emotional challenge have been noted in infants as young as 5 months (Buss & Goldsmith, 1998), we found little evidence to suggest that young children systematically and effortful modulate their attention to correct for increases and decreases in arousal.

In fact, the available evidence points more towards the *opposite* pattern. In 12-month-old infants, both high and low arousal states appear to take on actively self-sustaining characters, becoming *more* long-lasting than expected by chance (section 4). This suggests that young children may not systematically correct for increases and decreases in arousal, as we had expected. It may also point to the existence of the *opposite* type of mechanism: 'metastatic processes' – e.g. oppositional parent-child interactions - through which small initial increases in arousal can become progressively amplified over time (S. V. Wass, pre-print; S. V. Wass et al., 2020).

A number of important questions remain here. First, how do arousal dynamics change? Do they become more self-correcting with increasing age? Second, do different children have different levels of 'optimal' arousal (cf Zuckerman, 1979), such that a given arousal level might elicit down-regulation in one child (because that arousal level is above the 'optimal' arousal level for that child) – but up-regulation in another child (S. V. Wass, pre-print)? If true, such a finding would challenge many theoretical definitions of emotion regulation. Third, is it correct to view autonomic arousal as a one-dimensional construct (see section 1.1.3)? Or would the effortful modulation of attention following changes in arousal vary in response to different types of arousal – e.g. positively vs negatively valenced events? This is particularly true given evidence from section 6.1.1 that reactivity to positive and negative events shows at least a partially separable phenotype.

7.2 Long-term interactions

7.2.1 Early atypical arousal affects the long-term development of effortful control

We also discussed evidence that early atypical development within arousal/regulatory sub-systems correlates with poorer effortful control over longer time-frames (months/years) (section 5.1). Most of this evidence comes from children who show atypical early brainstem maturation as identified using the Auditory Brainstem Response, and one limitation of this research is that these children may show more general developmental delays as well. Only a smaller group of studies have examined how arousal differences in typical children associate with differences in later effortful control; the evidence here is inconsistent (sections 5.1, 5.2). Some studies also point to atypical early arousal/regulatory function in children who go on to develop effortful control impairments during later life (e.g. children with ADHD) (Bedford et al., 2019; Shephard et al., 2019). However, progress here is impaired by the fact that a variety of different types of impairment to early arousal/regulatory function, including both hypo- and hyper-arousal, may all cause atypical effortful control later on (Bellato et al., 2020), but no criteria currently exist for consistently identifying these subgroups (Johnson, Gliga, Jones, & Charman, 2015; Johnson, Jones, & Gliga, 2015; J. T. Nigg et al., 2005).

If true, then the suggestion that early atypical arousal might correlate with poorer long-term effortful control is consistent with what we understand of brain development as an interactive, ongoing process of progressive elaboration, building on foundations laid down during early life (Geva & Feldman, 2008; Johnson, 2015). Seen in this light it is unsurprising that the prefrontal cortex, which shows a slower developmental trajectory (see section 1.2.1), is more sensitive to developmental disruption than other areas of the brain (Hodel, 2018).

But how, though, on a behavioural level, are we to understand the link between *short-term* interactions between arousal and effortful control (such that increases in arousal are associated with immediate decreases in effortful control) and *long-term* interactions (such that atypical early arousal associates with long-term deficits in effortful control)?

One mechanism that might mediate this relationship is a simple one, that is hard to test. As described above (sections 2 and 7.1.1) short-term increases in arousal are associated with short-term reductions in effortful control (more ‘bottom-up’, and less ‘top-down’); it is possible, then, that spending more time at elevated arousal leads children to develop an attentional style that is overall more ‘bottom-up’. In some ways this is analogous to suggestions that spending longer periods in a ‘bottom-up’ attention state during TV viewing can lead to long-term deficits in the capacity for top-down attention control away from screens (Beyens et al., 2018). Both suggestions are, however, hard to verify experimentally, based purely on correlational evidence.

In addition to simple deficit models, other research is also pointing to more subtle ways in which early atypical arousal can affect the long-term development of effortful control. For example, adaptive calibration models (Del Giudice, Ellis, & Shirtcliff, 2011; Bruce J Ellis & Del Giudice, 2019) posit that early stress may prompt the development of adaptive strategies that promote survival and reproduction under adverse conditions. According to this approach, reduced effortful control might be seen more as an adaptation, rather than a deficit.

Similar principles also apply at the behavioural level, where theoretical work has suggested that atypical early development may give rise to ‘behavioural cascades’, through which early atypicalities can ‘fan out’ over time (Karmiloff-Smith, 1998; S. Wass & Karmiloff-Smith, 2010). For example, atypical early arousal might cause atypical eye gaze behaviours in social settings, which in turn causes impaired learning in domains such as language learning (Cornish, Scerif, & Karmiloff-Smith, 2007). Although these interactive behavioural cascades are hard to show experimentally, the research we reviewed suggested that, for example, infants with early brainstem abnormalities may be less able to initiate behaviours such as self-regulatory activities in response to a socioemotional challenge, which would lead to cascading patterns of subsequent impairment across a variety of domains (section 5.1).

7.2.2 Early effortful control affects the long-term development of arousal

Finally, we considered the possibility that early effortful control might affect the long-term development of arousal (section 5.2). It is possible, for example, that children with superior effortful control might show greater capacity for effortfully redirecting attention to ‘correct for’ changes in arousal (i.e., superior self-regulation), leading to long-term changes in arousal (see section 7.1.2). However, our review provided no evidence to support this possibility. At 12 months, there appears to be little evidence that children effortfully correct for increases in decreases in arousal at all (see section 4.2). Correlations between effortful control and arousal during early childhood are inconsistent, and studies that studied causal mechanisms by training effortful control have largely found that training effects do not transfer to changes in arousal (section 5.2). Future research should investigate how the bidirectional associations between effortful control and arousal change with increasing age.

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Figures

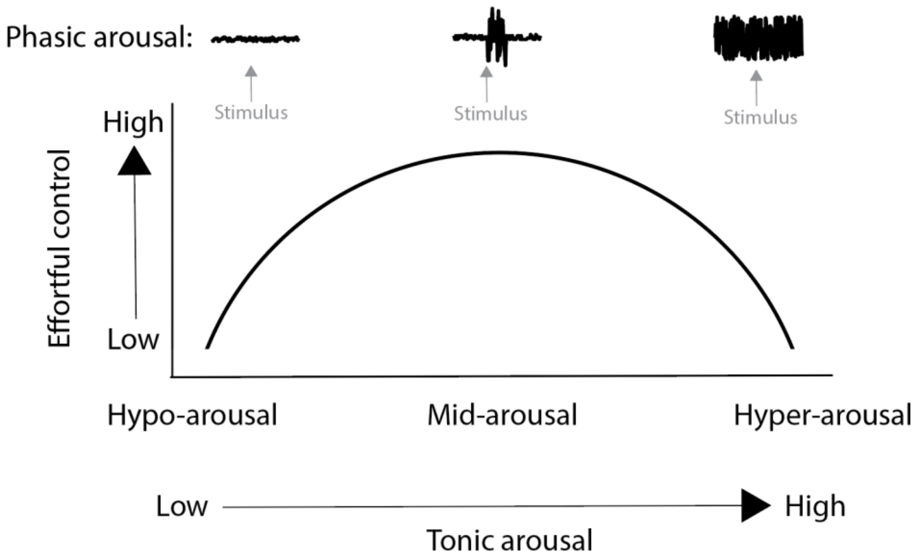

Figure 1: Schematic illustrating the Aston-Jones framework. Extreme low, and high, levels of tonic arousal are both associated with lower effortful control and with lower phasic arousal responses to sought-for stimuli. Figure redrawn from Aston-Jones and Cohen, 2005.

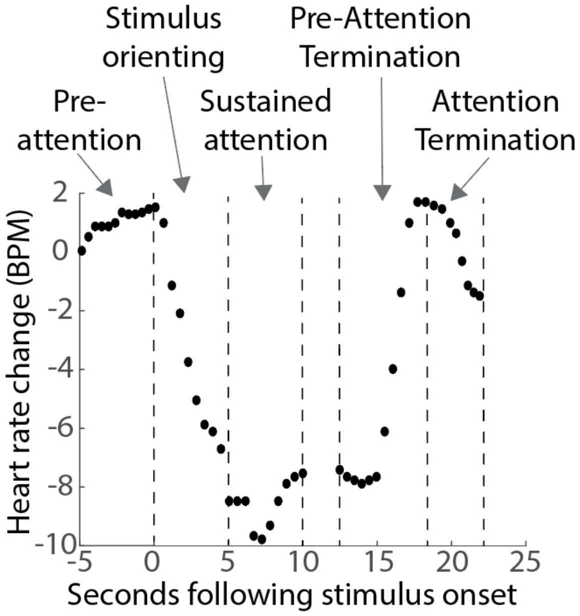

Figure 2: Schematic illustrating attention-related heart rate changes during a typical attention phase in infancy. Figure redrawn from Richards, 2010.

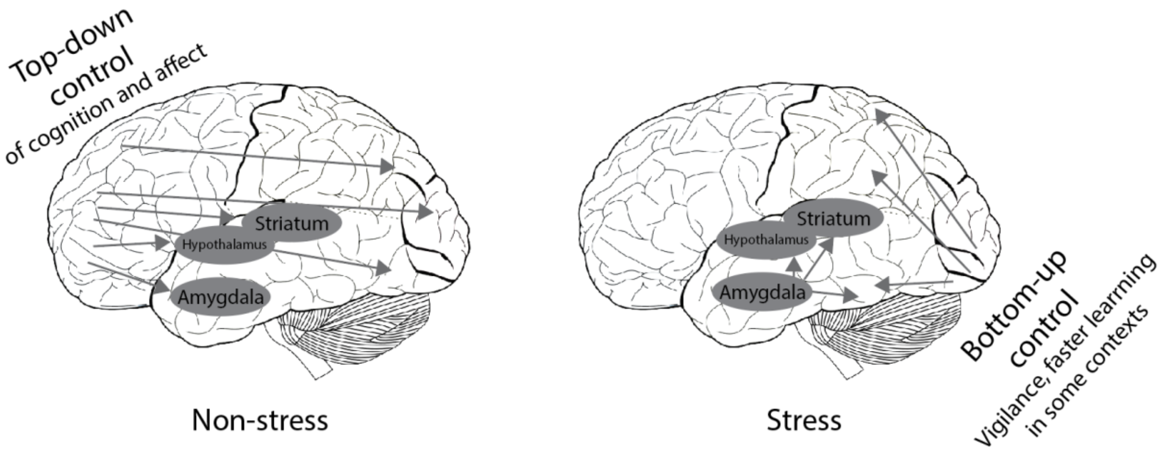

Figure 3: Schematic illustrating the key components of the Arnsten framework. Figure redrawn from Arnsten, 2009.

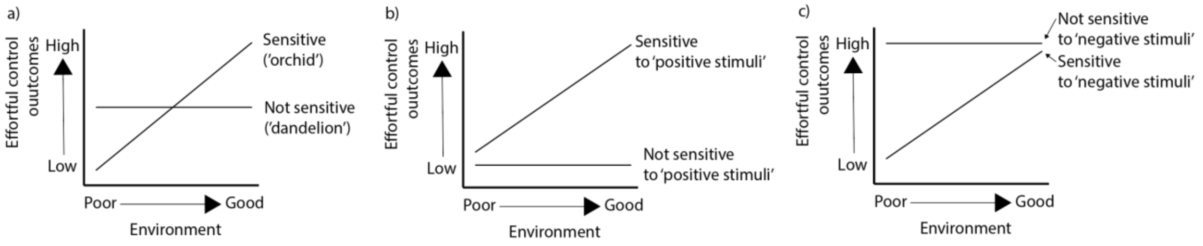

Figure 4: a) Schematic illustrating Differential Susceptibility Theory: some individuals may be more susceptible to both negative (risk-promoting) and positive (development-enhancing) environmental conditions. b) and c) alternatives, based on a diathesis-stress framework, in which sensitivity to positive (attention-eliciting) and negative (aversive) stimuli represent separable parameters of individual differences.