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Neuroscience

The neural and physiological substrates of real-world attention change across development.

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Abstract

The capacity to pay attention underpins all subsequent cognitive development. However, we understand little about how attention control is instantiated in the developing brain in realworld settings. We recorded naturalistic attention patterns, together with autonomic arousal and brain activity, in 5- and 10-month-old infants during free play. We examined whether changes in autonomic arousal and brain activity associate with changes in moment-bymoment attentional engagement, and whether they anticipate attention changes, or follow on from them. Early in infancy, slow-varying fluctuations in autonomic arousal forwardpredicted attentional behaviours. Later in infancy, fluctuations in fronto-central theta power after but not before an attentional shift associated with changes in infants' attentiveness, predicted the length of infants' attention durations and modulated changes in arousal. Together, our results suggest that the modulation of real-world attention involves both arousal-based and cortical processes and what changes with developmental time is how these lower- and higher-order endogenous factors modulate real-world attention. As attentional systems mature, stronger associations emerge between attentional behaviour, cortical activity, and autonomic arousal.

eLife assessment

This **important** study explores infants' attention patterns in real-world settings using advanced protocols and cutting-edge methods. The presented evidence for the role of EEG theta power in infants' attention is currently **incomplete**. The study will be of interest to researchers working on the development and control of attention.

Teaser

Understanding how our brains develop the capacity to pay attention to objects and people around them is central for understanding all aspects of subsequent cognitive development and learning. However, we understand little about the mechanisms through which attention control develops during early life in complex, real-world settings. Here, we examined the associations between



naturalistic attention patterns, arousal and neural activity, in 5- and 10-month-olds during free play with toys. Early in infancy, lower-order arousal-based endogenous factors forward-predicted attention; later in infancy, higher- order neural responses after the onset of a new attention episode forward-predicted attention and modulate changes in arousal. Overall, our results suggest that the neural and physiological substrates of real-world attention change between early and later infancy, resulting in a more inter-linked system where associations between attention behaviour, cortical activity, and autonomic arousal are stronger as infants develop.

1. Introduction

The ability to allocate and maintain visual attention enables the flexible regulation of perception and action that is characteristic of strategic behaviour (Hendry et al., 2019 🖒; Rueda et al., 2021 🖒). The capacity to pay attention develops rapidly over the early years of life (Richards, 2010 °C), and individual differences in early attention predict long-term cognitive and clinical outcomes (Colombo & Mitchell, 2009 °C; Wass, 2015 °C). Recent new methodological advances such as naturalistic neuroimaging are allowing us to build on previous research using lab-based behavioural experiments and animal studies.

The development of attention is traditionally conceptualised as the product of interactions among different systems at different levels of maturity (Colombo, 2001 🖒; Hendry et al., 2019 🖒; Johnson, 2002 °Ć). Traditionally, the earliest subcomponent of attention to develop is thought to be the arousal/ alertness subcomponent, mediated via brainstem reticular activating systems centred on the locus coeruleus (LC) and instantiated primarily via norepinephrine neurotransmitter systems (Colombo, 2001 °Ć). In young infants, alertness is more readily initiated by exogenous events (Wolff, 1965 °C); over time, infants gain the ability to both attain and maintain an alert state even in absence of external stimulation. Areas around the brainstem (including the LC) are thought to be some of the earliest to become functionally mature (Deoni et al., 2011 °C; Johnson & Haan, 2015 °C). Consequently, the relative influence of this subcomponent of attention is thought to be strongest during early development (Colombo, 2001 °C).

Behaviourally, the arousal/ alertness subcomponent of attention is thought to reflect a state of anticipatory readiness, or alertness for stimulus input (Colombo, 2001 C). Arousal is generally measured indirectly, via proxy measures of autonomic nervous system activity such as heart rate (Richards, 1980 C). Heart rate has been extensively studied in the context of infant attention (Richards, 2010 C, 2011 C; Wass, 2021 C). During anticipatory readiness, we know that reorientations of visual attention take place periodically, clustered around a preferred modal reorientation rate (Feldman & Mayes, 1999 C; Nuthmann et al., 2010 C; Robertson, 1993 C; Saez de Urabain et al., 2017 C; Wass & Smith, 2014 C). This may reflect rhythmic activity in the central nervous system (Mcauley et al., 1999 C).

With time, it is thought that looking behaviours become increasingly modulated by higher-level executive processes that reflect the infant's internal states, motivation, comprehension, and goals (Colombo & Cheatham, 2006 🖙; Oakes et al., 2002 🖙; Rueda et al., 2021 🖙). Behaviourally, this increase in endogenous or internally directed attention has been shown as: a developmental increase in the degree to which attentional engagement is accompanied by decreases in distractibility (D. R. Anderson et al., 1987 🖙; Lansink & Richards, 1997 🖙); an increase in selective attention as measured indirectly, using the blink reflex (Richards, 2000 🖙); and differences in the trajectory of how attention durations to simple vs complex stimuli change over developmental time (Courage et al., 2006 °).

Other research that used experimenter-controlled, screen-based tasks to examine neural correlates of attention has examined changes in the power spectral density (PSD) of EEG oscillations, in particular infants' theta (3-6Hz) rhythm, which increases during active,



anticipatory, and exploratory behaviour (Begus & Bonawitz, 2020 , Braithwaite et al., 2020 ; Jones et al., 2020 ; Meyer et al., 2019 ; Orekhova et al., 2006 ; Xie et al., 2018). Together, these studies suggest that the expression of theta during attention-eliciting episodes could signify the engagement of neural networks related to executive attention (Braithwaite et al., 2020 ; Orekhova et al., 2006 ; Xie et al., 2018).

How children allocate their attention in experimenter-controlled, screen-based lab tasks differs, however, from actual real-world attention in several ways (Wass & Jones, 2023 🖒; Wass, 2014 ८); Wass & Goupil, 2022 ८). For example, the real-world is interactive and manipulable, and so how we interact with the world determines what information we, in turn, receive from it: experiences generate behaviours (E. M. Anderson et al., 2022 ८).

The present study aims to examine developmental changes in the relationship between autonomic arousal, cortical activity, and attention in real-world settings. To do this, we first explored how naturalistic attention patterns from a solo play interaction change between 5 and 10 months. Then, we explored temporal relations between changes in infant's arousal and attention episodes in typical 5- and 10-month-olds infants. Finally, we investigated changes in EEG theta power relative to attention episodes, and changes in EEG theta relative to arousal. As attentional systems mature and brain regions become increasingly specialised (Grossmann et al., 2008 C); Jones et al., 2015 C), we expected to see both a developmental increase in visual attentiveness towards play objects and a developmental shift in the way different mechanisms (i.e., arousal/ alertness vs. executive attention subsystems) drive attention.

Our first set of analyses examined attentional inertia (the phenomenon that, as individuals become progressively more engaged with an object, their attention progressively increases) as a measure of internally driven attentional engagement (Richards, 2010¹; Richards & Anderson, 2004 🗠; Wass, Clackson, et al., 2018 🖒). We tested whether attentional inertia influenced attentional behaviours more strongly at 10 months compared to 5 months. To do so, we calculated both the Autocorrelation Function (ACF) and the survival probability of spontaneously occurring attention episodes during play (analysis 1). The ACF allowed us to quantify the rate of change of spontaneous attention durations. A faster rate of change would indicate lower attentional inertia. The survival probability, on the other hand, allowed us to quantify the probability between looking (i.e., paying attention) and looking away. A slower decrease in the probability of an attention episode surviving would indicate increased attention engagement and decreased distractibility by other stimuli. We hypothesised that, as slow-varying fluctuations in endogenous interest or engagement start to influence looking behaviour more strongly over time, 10-monthold infants would show increased endogenous attention control indexed by a slower rate of change of attentiveness and slower decreases in the survival probability. We also predicted that we would be able to identify periodic attentional reorientations during early as well as later development (Robertson, 1993 2, 2013 2); later in development, however, we predicted that infants would be more likely to extend visual fixations beyond their modal periodic reorientation rate, possibly indicating a greater or more efficient integration of attention and gaze shifting (Robertson et al., 2012 ^C), and that attention duration episodes would be longer overall.

Next, in order to assess the link between lower-level mechanisms of autonomic arousal and attention, we calculated cross-correlations between autonomic arousal (indexed via heart rate) and attention episodes across the entire play session for both 5- and 10-months olds. This allowed us to examine whether arousal changes tend to forward- predict changes in attention, or vice versa (analysis 2). Based on previous research (de Barbaro et al., 2017 C²), we hypothesized that periods of elevated autonomic arousal would associate with, and forward-predict, shorter attention episodes. We also predicted that such relationship would weaken with time due to the maturation of cortical attentional systems.



We used a similar approach to examine developmental changes in the relationship between neural markers of executive attention and real-world attention behaviours. We were interested to examine whether neural changes (indexed by theta power) anticipate subsequent attentional behaviour shifts (Robertson et al., 2012 ^{C2}); or, whether neural processes after the attention shift relate to increases in infants' attention engagement. To test this, we conducted three analyses. First, we analysed neural activity across a range of time windows both before and after the onsets of new attention episodes and performed linear mixed effect models to examine how neural activity before and after attention onset associated with the subsequent durations of those episodes (analysis 3). Second, we examined changes in neural activity during individual attention episodes (analysis 4). Finally, we used cross-correlations to examine whether, across the entire dataset, neural markers tend to forward-predict changes in attention, or vice versa (analysis 5). We predicted that the associations between neural markers of executive attention and real- world attention behaviours would become stronger with increasing age (i.e., theta activity would show a stronger predictive relation with infants' attentional behaviours at 10 months, as evidence of increased modulatory power from the executive attention system on infants' attention).

Finally, we examined whether there were any interdependencies between autonomic arousal and theta activity. We had no predictions for how this relationship would change over time.

2. Results

2.1 Analysis 1: Developmental changes in attention

Our first set of analyses examined attentional inertia as a measure of internally driven attentional engagement. Attention inertia is the phenomenon that, as individuals become progressively more engaged with an object, their attention progressively increases. We tested whether attention inertia is stronger at 10 months compared to 5 months. To do so, we calculated the ACF and the survival probability of spontaneously occurring attention episodes during play to quantify the rate of change of spontaneous attention durations and the probability between looking (i.e., paying attention) and looking away, respectively.

Initially, we conducted four descriptive analyses to test how attention and inattention durations and reorientations change over both the course of the solo play interactions and developmental time. First, we tested how many times per minute 5- and 10-months-old infants redirected their attention from one object to the other. We found that, on average, 5-month-old infants performed significantly more both attentive (t(10)= 4.346, p=0.001) and inattentive (t(10)= 4.202, p=0.002) reorientations during the solo play interaction than 10-months-old infants (**Figure 1A** ^{C2}). When we looked at how attention reorientations changed during the course of the solo play episode, we found that 5-month- old infants performed consistently more looks than 10-month-olds throughout the interaction even though the number of looks per minute decreased over the course of the interaction for both age groups (**Figure 1B** ^{C2}, and **Figure S1A** ^{C2} and **B** ^{C2}).

Second, we investigated the average duration that 5- and 10-month-old infants spent in attentive and in inattentive states during the solo play interaction and minute by minute (**Figure 1C** and **D** respectively). In general, infants' attention durations toward play objects at 10 months were longer (t(10)= -2.787, p=0.019). At 5 months, moments of inattention were longer than moments spent looking towards the object (t(10) = -3.749, p=0.003). Overall, at 10 months, but not 5 months, infants spent more time in attentive compared to inattentive states (t(58)= 10, p<0.001) (**Figure 1E**). We then calculated a best fit line, individual by individual, to look at how average attention duration changed within the session (see **Figure S1C** and **D**). We found no significant differences in the way attention duration changed during the interaction between the two age groups (**Figure S1C**).

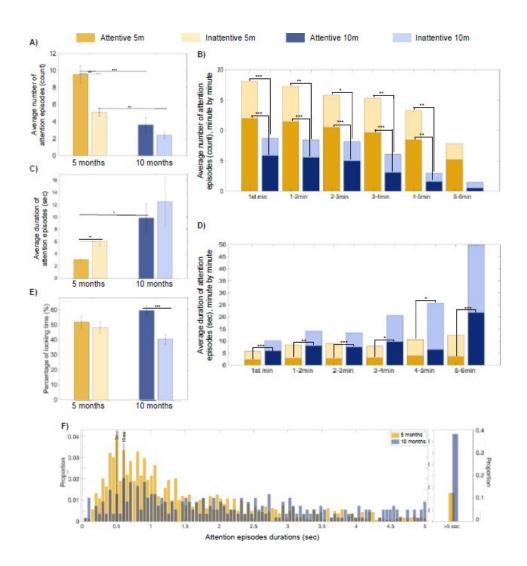


Figure 1.

Descriptive analyses on infant attentional behaviour during the solo play interaction.

(A) Average number of attentive and inattentive looks per minute at 5 months (left) and 10 months (right), (B) Average number of attentive and inattentive looks minute by minute. Asterisks show the significance values of comparisons examining how average number of looks per minute of the interaction differed as a function of age. (C) Average duration spent in one of the two possible attentional states: attentive and inattentive, and (D) minute by minute. Again, asterisks show the significance values of comparisons examining differences as a function of age. (E) Percentage of time infants spent in attentive vs. inattentive states, during the whole interaction. (F) Histogram showing the distribution of the proportion of all the looks that lasted less than or equal to 5 seconds (right) and more than 5 seconds (left) at 5 months (yellow) and 10 months (blue). Continuous black line indicates the mode of each distribution. Significance is indicated with asterisks where * = p<0.05, ** = p<0.01, and *** = p<0.001. Error bars represent SEMs.



Third, we explored the distribution of looks towards the objects (**Figure 1F** \square). At both ages, attention durations shorter than or equal to 5 seconds follow a positively skewed lognormal distribution, with modal attention durations in the 0.5 – 0.6 second range. Modal attention durations were significantly lower at 5 than at 10 months (t(58)= 2.211, p=0.03). Finally, the right plot of **Figure 1F** \square shows extended attention episodes. There was an increasing amount of such looks with increasing age.

Following the descriptive statistics, we calculated both the ACF and the survival probability of the looking behaviour (**Figure 2** C). First, we used time-series analyses to examine the rate of change of attention durations, relative to itself. We calculated the ACF of the attention durations at both time points (more details in 4.3.5.2). The ACF indexes the cross-correlation of a measure with itself at different lag-intervals in time (Wass, Clackson, et al., 2018 C). ACF values were obtained from 0 to 10 seconds lag, in steps of 500 milliseconds. As shown in **Figure 2A** C, the ACF of the time series looking behaviour fell off more sharply at 5 months than at 10 months. The ACF values were compared across ages using independent sample t-tests. From lag +500 milliseconds to 10 seconds, 10-months-old infants showed significantly higher correlation values than 5-months-old infants.

Second, we performed a survival analysis by calculating the survival probability function of the looking behaviour towards the objects at both time points. The survival probability function is the probability that an attention episode survives longer than a certain time. As shown in **Figure 2B** \mathbb{C}^3 , the survival probability of a look decreased abruptly at the beginning, for the very short looks, and flattened as looks got longer. The differences in the speed at which the survival probability decreased can be seen more clearly by calculating the derivative of the survival probability (**Figure 2C** \mathbb{C}^3). To compare survival among the two groups, we performed the log rank test using the Matlab function 'Logrank' (<u>Cardillo, G, 2008</u>). The results for the log-rank test rejected the null hypothesis (p<0.001) indicating that the survival curves for looking behaviour at 5 months and 10 months were significantly different. Notably, the likelihood of a look ending is more tightly clustered around the modal value of 0.5 seconds at 5 months.

Overall, our results showed that older infants demonstrated to have a slower- changing profile of attention with longer attention episodes overall (**Figure 1A** 🖄 and **B** 🖄, **Figure 2A** 🖄). At both ages, there was evidence for a preferred modal reorientation rate in the 0.5-0.6 second range, which was slightly faster at 5 months than 10 months (**Figure 1F** 🖄). Attention durations were more tightly clustered around the modal value at 5 months. At 10 months, attention episodes were more likely to be extended beyond the preferred modal reorientation rate than at 5 months (**Figure 2B** \checkmark and **C** \checkmark).

2.2 Analysis 2. Auto- and cross-correlation analyses between infant autonomic arousal and attention

In this section we investigated the relationship between changes in infant autonomic arousal indexed by heart rate activity and their associations with moment-to- moment changes in attention.

Figure 3 (A and C) shows the results of the autocorrelation analyses for autonomic arousal at 5 and 10 months of age respectively. Significant autocorrelations were observed at relatively short lags around t=0 (from -4 to +4s) at both ages. **Figure 3** (B and D) shows the results of the cross-correlation analysis between autonomic arousal and attention at 5 and 10 months of age respectively. The negative values indicate that, at 5 months, lower heart rate forward-predicted increased likelihood of attention from lags between -9 to -2 seconds (i.e., lower heart rate at time t significantly associated with increased attention at time t+9 seconds). The same pattern was present but not significant at 10 months. The asymmetry of this cluster around the lag t=0 indicates that changes in heart rate tended to forward-predict changes in attention more than vice versa.

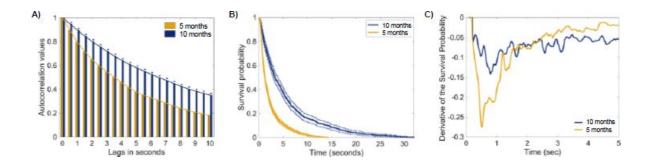


Figure 2.

ACF and survival probability analyses of the looking behaviour.

(A) Autocorrelation of the time series looking behaviour at 5 months (in yellow) and 10 months (in blue). (B) Survival analysis. Survival probability function for looking behaviour toward object toys. The survival function is the probability that a look will survive a given time. Yellow line shows data from 5-months-old infants with confidence bounds (dotted yellow line) and blue line shows data form 10-months- old infants with confidence bounds (dotted blue line). (C) Derivative of the Survival Probability at 5 months (blue).

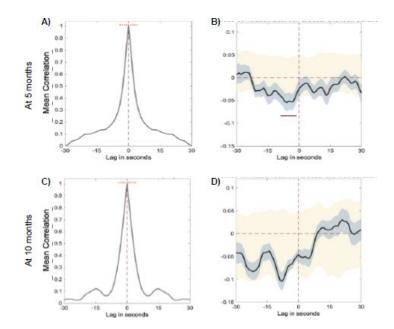


Figure 3.

Relationship between infant autonomic arousal and attention.

Autocorrelation results for infant autonomic arousal at 5 months (**A**) and 10 months (**C**). Significant clusters are indicated by red dots. Cross correlation between infant autonomic arousal and attention at 5 months (**B**) and at 10 months (**D**). Black lines show the cross-correlation values, shaded grey areas indicate the SEM. Shaded yellow areas show confidence intervals from the permuted data. Significant time lags identified by the cluster-based permutation analyses are shown by a thick red line.



2.3 Analysis 3. Calculation of neural power changes around an attention episode

We used linear mixed effects models to examine the associations between the length of each attention episode and relative theta power at different time windows relative to the onset of that attention episode (see **Figure 4** [□]). At 10 months, relative theta power in the time window of 0 to +1000msec and +1000 to +2000msec after onset of a new attention episode predicted the subsequent duration of that attention episode. At 5 months, the same relationships were not significant. We found no evidence of neural activity before the start of an attention episode forward-predicting the length of that attention episode at any time point (**Figure 4** [□]).

The final number of accepted trials (i.e., attention episodes) in the analyses varied across the three time-windows immediately after the onset of each look. More trials were obtained for the first window (total number of looks at 5 months was 790, and 411 at 10 months) than the second (total number of looks at 5 months was 473, and 336 at 10 months) and the third (total number of looks at 5 months was 473, and 336 at 10 months) and the third (total number of looks at 5 months was 473, and 336 at 10 months) and the third (total number of looks at 5 months was 301, and 277 at 10 months). All three conditions ended up with enough number of clean trials that was greater than the recommended number of trials in the infant EEG literature (De Haan, 2002 C); Monroy et al., 2021 C); Phillips et al., 2023 C). Thus, the differences between the number of trials for each time window are not expected to contribute to the results described above. However, we repeated this analysis by matching the number of attention episodes at 5 months to the ones analysed at 12 months. We found no differences in the results (see **Figure S2** C).

2.4 Analysis 4. Calculation of neural power changes within an attention episode

In addition to the previous analyses, which examined the associations between the length of each attention episode and relative theta power at different time windows relative to the onset of that attention episode, we also wished to examine whether power at the theta and alpha band changed significantly during a look (Figure 5 ^{C2}). Relative theta was analysed as a function of these three factors: time within an attentional episode, brain areas and age with a 3-way ANOVA (Figure 5 ^{C2}). There was no statistically significant interaction between the three factors. However, the analysis revealed two simple two-way interactions: one between time within an attention episode and age, F(2) = 5.58, p < .005 and the other between channel cluster and age F(2) = 11.98, p < .001. Next, we performed a multiple comparison test to find out which groups of factors were significantly different. Results are shown in **table S1 🗹 -S3 🗠**. A follow up analysis showed a significant effect of "time within an attentional episode": 10-months-old infants had greater theta during the thirdto-fourth second into the look (middle) than the first second (start) in both the central and the frontal poles. These effects were not present in 5-months-old infants. Similarly, relative alpha was also analysed as a function of these three factors: time within and attentional, brain areas and age with a 3-way ANOVA. We found no statistically significant interactions. Results are shown in Figure S3 🔼

Again, the final number of accepted trials (i.e., attention episodes) in the analyses varied across the three time-windows into each look. More trials were obtained for the first-second window (total number of looks at 5 months was 791, and 415 at 10 months) than the third-to-fourth second (total number of looks was 172 at 5 months, and 194 at 10 months) and the last second before look termination (total number of looks was 476 at 5 months, and 337 at 10 months).

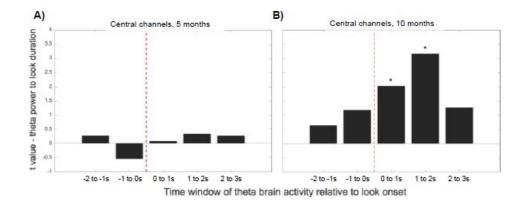


Figure 4.

Calculation of theta power changes around an attention episode.

Results of the linear mixed effects models conducted to examine whether individual looks accompanied by higher theta power are longer lasting. For each look, we calculated the association between the total duration of the look and relative theta power during five time-windows (-2000msec to -1000msec and -1000msec to 0 prior to the look, and 0 to 1000msec, 1000 to 2000msec and 2000 to 3000msec before the look), using a series of separate linear mixed effects models. (**A**) Shows results at 5 months where the y-axis is the t value, and (**B**) shows the results at 10 months. Asterisks (*) indicate p values < .05. Central channels include: 'FC1', 'FC2', 'C3', 'C2', 'C4', 'CP1' and 'CP2'.

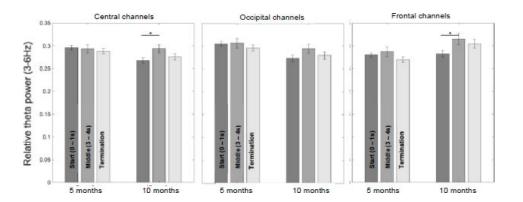


Figure 5.

Calculation of theta power changes within an attention episode.

Bar plots for the average relative theta power throughout a look, at both time points (5 and 10 months) and at different brain networks (central, occipital, and frontal). Asterisks (*) indicate p<0.05. Error bars represent SEMs.

2.5 Analysis 5. Auto- and cross-correlation analyses between infant theta activity and attention

In this section we investigated the relationship between dynamic changes in infant endogenous brain activity and their associations with moment-to-moment changes in attention. Figure 6A ⁽²⁾ and D ⁽²⁾ shows the results of the autocorrelation analyses for infant theta activity. Figure 6B ⁽²⁾ and E ⁽²⁾ shows the results for the cross-correlation analyses between infant theta activity and infant attention. Cluster-based permutation analysis revealed a significant positive association between the two variables (marked with a red line) at 10 months around time lag=0. More specifically, increases in infant theta activity at 10 months were significantly correlated with fluctuations in infant attention (Figure 6E ⁽²⁾). No associations were found between theta activity and infant attention at 5 months of age. Interpreting the exact time intervals over which a cross-correlation is significant is challenging due to the autocorrelation in the data (P. Clifford et al., 1989 ⁽²⁾; Pickup, 2014 ⁽²⁾), but the fact that the significance window is asymmetric around time 0 indicates a temporally specific relationship between infant attention and theta power, such that attention forward-predicts theta power more than vice versa.

Finally, to test whether there were any interdependencies between autonomic arousal and brain activity, we performed a cross-correlation analysis between these two variables. We found a significant cluster at 10 months (**Figure 6F** ⁽²⁾) but not at 5 months (**Figure 6D** ⁽²⁾). The asymmetry of this cluster around t=0 indicated that changes in brain activity tended to precede changes in autonomic arousal more than vice versa.

3. Discussion

We examined developmental changes in the physiological and neural correlates of real-world attention patterns during early development. To do so, we measured attention durations (to an accuracy of 50Hz), along with cortical neural activity (EEG) and autonomic arousal (via ECG) from typical 5- and 10-month-old infants playing alone while seated at a tabletop with 3 toys. This age range is a key period for early cognitive development, as differential patterns of brain development (Johnson & Haan, 2015 (2)) drive a transition from primarily subcortical to cortical control (Johnson, 2005 (2)), and early-emerging atypicalities can have life-long consequences (Johnson et al., 2021 (2); Shephard et al., 2021 (2)). However, many of the mechanisms that drive early development remain unclear.

From Analysis 1 we found that infants at both ages showed a preferred modal reorientation rate. The modal durations of attention episodes towards different play objects were in the 0.5-0.6 second range at both ages but were lower at 5 months (**Figure 1F, 2C** ^C). This contrasts with analyses of micro-level fixation durations (time intervals between individual refoveating eye movements), which decreases from early infancy (~0.5 secs) through to later infancy (~0.4 secs) through to adulthood (~0.3 secs) (Saez de Urabain et al., 2017 ^C; Wass & Smith, 2014 ^C). Research with adults suggests that the minimum time necessary to plan and executive a saccade is ~80msecs in adults (Nuthmann et al., 2010 ^C). Although the equivalent figure is not known in infancy, the fact that modal attention durations towards objects were shorter at 5 months than 10 months, whereas fixation durations decrease with age, makes it likely that the figures we observed do not simply indicate that infants were reorienting at the fastest speed possible, but rather were reorienting according to a preferred modal reorientation rate (Saez de Urabain et al., 2017 ^C).

The survival analysis showed that, at both ages, looks were fragile early in their existence and most likely to terminate in the <1 second range (Richards & Anderson, 2004) but the speed at which the survival probability curve decreased was faster at 5 months, meaning that the probability of a look lasting longer than time t was lower at 5 months. Richards and colleagues have found similar relationships in infants in both lab-based and naturalistic settings (Richards &

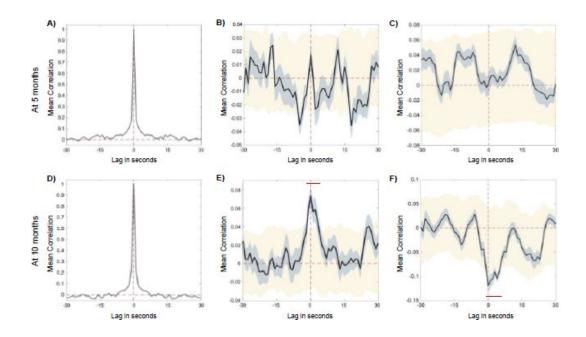


Figure 6.

Relationship between infant relative theta activity, infant attention, and infant autonomic activity.

Autocorrelation for infant theta activity at 5 months (**A**) and at 10 months (**D**). Significant clusters are indicated by red dots. Cross-correlation results between infant theta activity and infant attention at 5 months (**B**) and at 10 months (**E**). Crosscorrelation results between infant autonomic activity (indexed by heart rate activity) and relative theta power at 5 months (**C**) and at 10 months (**F**). Black lines show the Spearman correlation at each time lag, shaded grey areas indicate the SEM. Shaded yellow areas show confidence intervals from the permuted data. Significant time lags identified by the cluster-based permutation analyses are shown by a thick red line.



Anderson, 2004 ^{C2}). Overall, attention durations were shorter at 5 months; this faster-changing pattern of attention to the object was also reflected in the ACF of their looking behaviour, which decreased significantly faster, showing lower overall self-similarity. Collectively, these data fit well with what we know about the development of attention. With time, we seem to observe a higher-level control of attention that allowed older infants to prioritize the task at hand – learning about/ exploring the toys – as well as to inhibit the tendency to shift attention away from an interesting task (Colombo, 2001 ^{C2}; Courage et al., 2006 ^{C2}; Oakes et al., 2002 ^{C2}). Alternatively, longer attention episodes might arise because children physically manipulate objects, bringing objects closer to themselves which makes them more exogenously salient (E. M. Anderson et al., 2022 ^{C2}; Méndez et al., 2021 ^{C2}). In this case, then the infant's increased looking behaviour would be the result of increased exogenous attentional capture rather than an increase in endogenous attention control (Wass, Clackson, et al., 2018 ^{C2}).

Analysis 2 examined how dynamic fluctuations in autonomic arousal relate to moment-to-moment changes in attention. Consistent with previous work (de Barbaro et al., 2017 2; Pfeffer et al., 2022 C; Wass, 2021 C), the average concurrent correlation between autonomic arousal and attention was negative at both age points, indicating that lower arousal was associated with increased likelihood of attention. Such links have been considered within the developmental attention regulation literature, where increases in arousal are thought to lead to distraction or difficulties focusing attention, and vice versa (Gardner & Karmel, 1995 🗹). We also found that arousal levels were significantly forward predictive of attention at 5 months but not at 10 months (Figure 3B C and D C). Theoretically, if attentional episodes drive decelerations in the heart rate (Richards, 2011), and older infants show longer attentional episodes on average, then one could hypothesise that older infants ought also to show a more stable pattern (i.e., higher autocorrelations) in their heart rate fluctuations than younger infants. However, this was not what we observed (Figure 3A 🖾 and C 🖾). Overall, the much shorter attention durations observed in this setting, compared with screen-based TV viewing (Richards, 2011 C), means that heart rate decelerations relative to individual attention episodes were observed infrequently in our data. However, our data did suggest, consistent with previous research, that at 5 months, changes in autonomic arousal forward-predict subsequent changes in attention.

In Analysis 3 we examined the associations between attention episode durations and theta power either before, or after, onset of that attention episode. At 10 but not 5 months, increased theta during the period immediately after the onset of a new attention episode (0-2000msec) forward-predicted the subsequent length of that attention episode (**Figure 4** ^C). At neither age, however, did cortical neural activity before the onset of an attention episode forward-predicted attention durations.

In Analysis 4 we examined whether cortical neural activity changed significantly during an attention episode. Consistent with previous research (Xie et al., 2018 ^{C2}), theta power in central and frontal electrodes increased significantly during an attention episode at 10 months, but not at 5 months (**Figure 5** ^{C2}). Contrary to our expectations, we did not find a link between attenuated alpha during an attention episode at any age (see **Figure S3** ^{C2}).

In Analysis 5 we investigated the relationship between dynamic changes in infants' theta activity and moment-to-moment changes in attention. We identified a significant positive association between infant theta activity and infant attention at 10 months but not at 5 months (**Figure 6B** [□] and **E** [□]). Interpreting the exact time intervals over which a cross correlation is significant is challenging (P. Clifford et al., 1989 [□]; Pickup, 2014 [□]), but the asymmetry of the cluster around time 0 indicates that attention forward-predicted theta power more than vice versa, consistent with the findings from Analysis 3.



These findings are consistent with previous research suggesting that, by 10 months, but not during early infancy, theta oscillations increase during sustained attention and encoding (Begus et al., 2016 ; Jones et al., 2015 ; Xie et al., 2018) and associate with longer attentional periods (Wass, Noreika, et al., 2018). Importantly, though, we found no evidence that endogenous neural markers before the onset of an attention episode forward- predict the length of an attentional episode at either age. Instead, what we found suggests that neural activity shortly after the onset of an attention episode forward-predicts the length of that episode. One possible interpretation of this is that neural activity associates with the maintenance more than the initiation of attentional behaviours (Cohen, 1972).

Finally, we examined the relationship between theta power and autonomic arousal (**Figure 6C** and **F** (2). A cross-correlation analysis found a negative forward-predictive relationship between the two, such that increases in theta forward-predicted decreases in autonomic arousal at 10 months, but not at 5 months. This suggests that changes in the brain activity could be modulating subcortical changes (i.e., changes in the heart rate) and may thus be able to initiate or maintain states of arousal that are common to vigilant or sustained attentional states (Colombo, 2001 (2); Richards, 2011 (2)). Overall, it appears that, by 10 months, the different substrates of attention are more inter-linked, and stronger associations are emerging between behaviour, cortical activity, and autonomic arousal (Tardiff et al., 2021 (2)).

In summary, our results suggest that, earlier in development, attentional episodes are more influenced by lower-order endogenous factors such as a preferred modal reorientation timer – which characterises infants' attention shifting more strongly -, and a general arousal system (Richards, 2010 , 2011) – that might reflect a stronger influence of subcortical structures over the modulation of attention. Such factors would also be present at older ages; however, their association with attention would weaken over developmental time due to the maturation in cortical attentional areas thought to take place throughout the first year of life. Later in infancy, cortical neural activity reliably changes during attention episodes, but does not forward-predict attention at either age; rather, it seems that neural changes associate with the maintenance more than the initiation of attentional behaviours. Overall, the modulation of attention seems to involve both arousal-based and cortical processes. With developmental time, however, the latter increases its control over the modulation of both (i.e., overt attentional behaviours and arousal), resulting in a more inter-linked system where associations between attentional systems are stronger. Theoretically, this is consistent with what we know about the development of executive attention from experimental and neuroanatomical studies.

3.1 Limitations and strengths

Our findings should be interpreted with consideration to a number of limitations of the study. First, our events of interest are intrinsically linked with one of the biggest EEG artefacts (i.e., eye movements), and so it is possible that residual artifact in the EEG signal may have contaminated our data. However, our data were processed using algorithms specially designed to clean naturalistic EEG data (Haresign et al., 2021 ; Kayhan et al., 2022), and previous analyses suggest that the electrode locations and frequency bands that we examined should be least affected by artifact, compared with more anterior locations and higher and lower frequencies (Georgieva et al., 2020). Additionally, our analyses were carefully designed to preclude this potential confound. First, our analyses compare events

that we know share the same level of artefact/ noise (i.e., saccades at 5 months old contribute to comparable noise levels than at 12 months old (Noreika et al., 2020); second, analysis 3 and 4 are time-locked to a saccade to eliminate the possibility that saccadic frequency may have influenced our results; and third, other research (Marriott Haresign et al., 2023) suggest that artifact associated with saccades disappears within ~300msecs, whereas the associations between theta and look duration lasts much longer than this, up to ~6 seconds. For all this, we consider that the possibility that our results may have been caused by infants' saccades is unlikely.



Second, the use of different EEG systems (32- vs. 64-channel BioSemi gel-based ActiveTwo) and age groups might have contributed to the differences we observed over time. However, we compared the EEG signal quality between groups and found no significant differences (**Table S5** 🖄-6 🖄, **Figure S4** 🖄).

Third, we used a different set of toys at the two ages (see **Figure S5**^C). Consequently, this introduced a new source of variation (i.e., toy characteristics) that might have contributed to any of the observed differences (Oakes et al., 2002^C). However, we chose to present developmentally appropriate stimuli at the two ages to ensure that the cognitive demands were similar at the two ages. Thus, while still possible, it is unlikely that the developmental differences observed in the current study might be due to differences in the amount of information processing on the part of the infant and/ or the "interestingness" of the toys.

Finally, it is worth mentioning that, while infants gather information about their world through aggressive visual foraging, looking and attending are not synonymous. Previous research has shown that shifts of attention can occur without shifts of gaze by 4-6 months of age (Hood, 1993 2; Johnson et al., 1994). However, the current study has treated them interchangeably, focusing on the study of overt attention exclusively.

4. Materials and Methods

4.1 Experimental Design

Looking behaviour, EEG and ECG data were collected from mothers and their infants at two age points: 5 and 10 months while playing alone. At 5 months, infants were seated either in a highchair or on a researcher's lap and a table was positioned in front so that toys on the table were within easy reach (see **Figure 7**). To reduce infant's stress, mothers were present in the room but moved to another smaller table on the right side of the original table and given an identical set of toys which they played with in parallel. A wooden divider was positioned between the two tables to prevent infants from seeing the objects with which their mothers were playing. At 10 months, the same procedure was used but the divider was positioned across the midline of the table and the adult participants were seated directly opposite the infants. In both situations, mothers and infants had direct line of sight to one another but neither could see the others' toys on the table.

The same three age-appropriate toys were always used for each age group. These were small and relatively engaging (see **Figure S5** \cong). During the solo play interaction, one of the researchers sat behind the infant to collect the toys that fell on the floor (either because the infants threw them or because they fell from their hands) and brought them back on the table. Mothers were allowed to speak during the interaction but were instructed not to name the toys they were playing with to prevent infants from the influence of any exogenous parental' influence. The average duration of the interactions with usable EEG/ ECG data did not differ significantly between 5 and 10 months (interactions with EEG (average duration at 5m = 292.4s, and 10m = 250.1s, t(46)= -1.85, p= 0.07); interactions with ECG data (average duration at 5m = 351.2s, and 10m = 317.9s, t(40)= -1.1, p= 0.27)).

The interactions were filmed using three Canon LEGRIA HF R806 camcorders recording at 50 fps. At 5 months, one camera was placed in front of the infant and another one was placed in front of the mother. At 10 months, two cameras faced the infant: one placed on the left of the divider, and one on the right. The other camera faced the mother and was positioned just behind the right side of the divider. All cameras were placed so that the infant's and the mother's gaze, as well as the three toys placed on the table, were always visible.

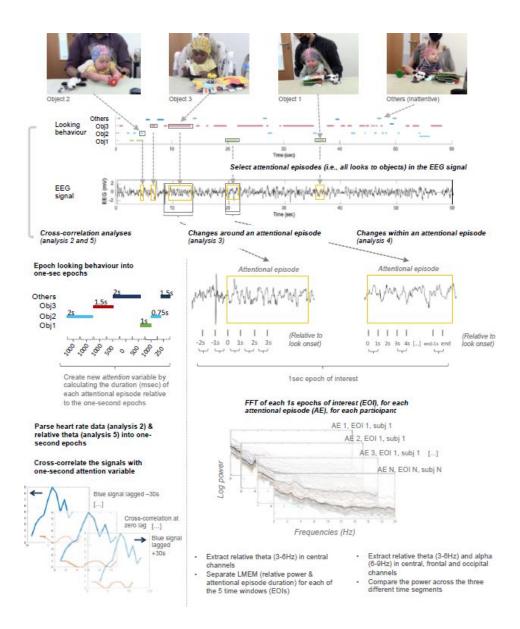


Figure 7.

Schematic illustration of the procedure followed for analysis 2 to 5.

On the left, procedure followed to parse the looking behaviour and create the variable "attention", and further crosscorrelation analyses (analysis 2 and 5). On the right, steps followed to identify attentional episodes in the EEG signal and further EEG analyses (analysis 3 and 4).



Brain activity was recorded using a 64-channel at 5 months and a 32-channel at 10 months, BioSemi gel-based ActiveTwo system with a sampling rate of 512Hz with no online filtering using Actiview Software.

Heart rate activity was recorded using a BioPac[™] (Santa Barbara, CA) system recording at 2000Hz. ECG was recorded using disposable Ag-Cl electrodes placed in a lead II position.

4.2 Participants

Participants were typically developing infants and their mothers. The catchment area for this study was East London, including boroughs such as Tower Hamlets, Hackney and Newham. Participants were recruited postnatally through advertisements at local baby groups and local preschools/ nurseries. We also operated a word-of-mouth approach, asking parents who got involved to ask if their local networks would be interested in participating. Ethical approval was obtained from the University of East London ethics committee (application ID: ETH2021-0076).

Initial exclusion criteria included complex medical conditions (e.g., heart rate condition, neurological/ genetic abnormality), known developmental delays, prematurity, uncorrected vision difficulties, and parents below 18 years of age. Further exclusion criteria as well as final numbers of data included in each of the analyses for both samples are summarised in **Table S7** . The final sample included 12 infant females and 19 infant males at 5 months and 14 infant females and 15 infant males at 10 months. Average age was 5.32 months (std = 0.58) and 10.49 months (std = 0.87). This is the first time that any of this data has been analysed and reported.

4.3 Data processing and Statistical Analysis

4.3.1 Synchronisation between behavioural and EEG/ ECG data

The cameras were synchronised to the EEG and ECG via radio frequency (RF) receiver LED boxes attached to each camera. The RF boxes received trigger signals from a single source (computer running Matlab) at the beginning and end of the play session, and concurrently emitted light impulses, visible from each camera. At the same time, triggers were sent and stored in the Actiview Software and recorded to the EEG data as well as to the Acknowledge Software and recorded to the ECG data.

The video coding and EEG/ ECG data synchronisation was done by aligning the times of the LED lights and the EEG/ ECG triggers. We also checked for dropped/missing frames by checking that the time between the LED lights matched the times between the EEG/ ECG triggers.

4.3.2 Video coding

The looking behaviour of the infants was manually coded offline on a frame-by frame basis, at 50fps. The start of a look was considered to be the first frame in which the gaze was static after moving to a new location. The following categories of gaze were coded: looks to objects (where the infant was focussing on one of the three objects), looks to partner (where the infant was looking at their partner), inattentive (where the infant was not looking to any of the objects nor the partner) and uncodable. Uncodable moments included periods where: 1) the infant's gaze was blocked or obscured by an object and/or their own hands, 2) their eyes were outside the camera frame, and/ or 3) a researcher was within the camera frame and the infant turned to them and/or realised a researcher was around. To assess inter-rater reliability, ~15% of our data (10 datasets) were double-coded by a second coder and Cohen's kappa was calculated. There was moderate agreement (k = 0.581, std= 0.183) (Landis & Koch, 1977 🖸). Due to the unusual nature of our



behavioural coding (with gaze coded across many 20ms bins) the interrater reliability is heavily contingent on how we calculate it. We chose to report the most stringent calculator of inter-rater reliability.

Looking behaviour data was then processed such that any look preceding and following an "uncodable" period was NaN-ed and excluded from further analyses. Similarly, both the first and the last look of every interaction were also NaN-ed and excluded from further analyses.

4.3.3 EEG artefact rejection and pre-processing

EEG data was pre-processed and cleaned from oculomotor and other contaminatory artefacts using a fully automatic artefact rejection procedure specially designed for naturalistic infant EEG data by Mariott Haresign (Haresign et al., 2021 🖄), building on previous related work (59, 60). Briefly, this involved the following steps: 1) data were high-pass filtered at 1Hz, 2) line noise at 50Hz was eliminated using the EEGLAB function clean line.m, 3) data were low-pass filtered at 20Hz, 4) the data were referenced to a robust average reference 5) noisy channels were rejected using the EEGLAB function pop_rejchan.m, 6) the channels identified in the previous stage were then interpolated back, using the EEGLAB function eeg interp.m, 7) continuous data were automatically rejected (NaN-ed) in a sliding 1s epoch based on a percentage of bad channels (set here at 70% of channels) that exceed 5 standard deviations of the mean channel EEG power, and 8) ICAs were computed on the continuous data using the EEGLAB function runica.m. Only participants with fewer than 30% channels interpolated at 5 months and 25% at 10 months made it to the final step (ICA) and final analyses. To compare the quality of the EEG data at 5 and 10 months we performed a series of analyses on percentage of channels interpolated, total segments removed (i.e., zeroed out) and total ICA components rejected (see Table S5 C -6 C and Figure S4 🔼).

The higher density array was down sampled so that all the EEG analyses described below used only shared channels between the 32- and the 64- channel EEG systems. We selected three main clusters of electrodes for our analyses: Frontal channels ('Fp1', 'Fp2', 'AF3', 'AF4', 'Fz'), Central channels ('FC1', 'FC2', 'C3', 'Cz', 'C4', 'CP1', 'CP2'), and Occipital channels ('PO3', PO4', O1', 'Oz', 'O1') (see **Figure S6** \square).

4.3.4 Heart Rate – Beats per minute

R-peak identification was performed using the in-built Matlab function 'findpeaks'. The minimum peak height was manually defined as a simple amplitude threshold after visualising the raw data, minimum peak distance, instead, was set at 230msec. Following this, automatic artefact rejection was performed by excluding those beats showing an inter-beat interval (IBI) <330 or >750msec (i.e., allowing a minimum of ~80BPM and maximum of ~180BPM), and by excluding those samples showing a rate of change of IBI greater than 90msec between samples. Next, we converted IBI values into beats-per-minute (BPM) values and removed outliers in the BPM time series. These were defined as values falling 2.5 interquartile ranges above the upper quartile and below the lower quartile. Outliers were then interpolated using the Matlab in-built function 'fillmissing' with the 'spline' method. Finally, we epoched the data into one-second epochs by averaging all the BPM values comprised in each one-second epoch.

4.3.5 Analysis 1. Developmental changes in attention

4.3.5.1 Overt attention and inattention extraction

The aim of our analysis was to identify moments where the infants paid attention to any of the play objects as opposed to inattentive moments. Accordingly, all looks to object and inattentive looks were selected and categorised as attentional and inattentive episodes, respectively. Looks to partner were excluded from all analyses.



Following this, we extracted the first and last frame of all looks of interest (i.e., looks to objects and inattentive looks). To calculate attention and inattention durations, we subtracted the last frame from the first frame of each look of interest and divided it by the sampling rate (i.e., 50) to convert "duration in frames" to "duration in seconds". Attentive and inattentive reorientations were calculated by counting the occurrence of each of these two attentional states, irrespective of their durations.

4.3.5.2 ACF of the attention duration

Here, we extracted the duration (in seconds) of all the attentional episodes that happened within the play session and zero-ed out all the non-attentional episodes. This allowed us to create a time series string with the durations of each consecutive attention episode. We then calculate the autocorrelation of that signal and repeated these steps for each behavioural dataset. Finally, we averaged the ACF values within each age group to obtain the ACF values reported in **Figure 2A** $\tilde{2}$.

4.3.6 Analysis 2. Auto- and cross-correlation analyses between infant autonomic arousal and attention

4.3.6.1 Attention, one-second epochs

To calculate the "attention" variable, we epoched the gaze data into one-second epochs and calculated the duration (in msec) of each attention episode relative to the one- second epochs. Most epochs were coded as either 1000 (epochs where the child was attending throughout) or 0 (epochs where the child was inattentive throughout). If an attention episode started halfway through a one-second epoch, then it was coded as 500. The other non-attention episodes (i.e., inattentive looks, looks to partner) were zeroed. See **Figure 7** C for a schematic view of the procedure we followed to parse the looking behaviour into one-second epochs.

4.3.6.2 Cross-correlation analyses

To investigate the relationship between autonomic arousal and fluctuations in attention we performed a cross-correlation analysis between the two variables. Importantly, these analyses are not time locked to specific moments (i.e., start of an attentional event) and are conducted on two time series (i.e., attention and heart rate fluctuations) as a whole. Because of this, the strength of the overall correlation is weakened by the fact that periods of expected stronger correlation are balanced by weaker correlations where we would not necessarily expect any correlation at all.

Additionally, we also computed the autocorrelation for autonomic arousal to assess how well it predicts itself over time and evaluate its stability. All analyses were computed at lags from -30 to +30s in 1s intervals. The cross-correlations values at each time-lag were computed individually and then averaged across all participants. The procedure was identical for the autocorrelation, except that instead of examining the relationship of two different time series at variable time intervals, we assessed the relationship of one time series to itself at variable time intervals.

To assess significance of the cross-correlations, we first used bootstrapping to generate confidence intervals, using an approach that controls for the level of autocorrelation in the data. To do this, the time series data of one participant (e.g., attention of participant 1) was randomly paired with the time series data of another participant (e.g., autonomic arousal of participant 13). If the time series datasets had different lengths (due to different participants having different session lengths), we appended zeros to the end of the shorter vector to match the length of the longest vector. We then computed the cross-correlation between all the unique combinations that could be found within each sample (e.g., in a sample N=23, the maximum of unique combinations is 529). Next, the cross-correlation results in the permuted data were randomly grouped in samples that were the same size as the original data (e.g., N= 23) and averaged together. This procedure



was repeated 1000 times and used to generate the 95% confidence intervals. In this way, we identified whether the observed cross-correlation values at each time interval differed significantly from chance.

Next, to control for multiple comparisons across time intervals, we used a cluster-based permutation approach. On each iteration, one permutation was compared with the 999 other permutations, and significant time-points were identified as values falling above the 97.5th centile and below the 2.5th centile (corresponding to a significance level of 0.05). We then identified the two largest clusters of significance that occurred by chance: one for positive correlation values and the other for negative correlation values. We repeated this 1000 times. Following this, we created a distribution of cluster sizes for positive and negative correlation values and took the size value corresponding to the 95th percentile in each distribution to define our cluster-size threshold. Finally, we compared the cluster sizes obtained in the observed data against the cluster-size threshold and only considered significant the ones that exceeded such threshold.

Calculating the significance levels of the autocorrelation was more straightforward. This was done by first calculating the autocorrelations based on individual datasets, and then averaging the significance values of the Spearman's correlations at each time interval.

4.3.7 Analysis 3. Calculation of neural power changes around an attention episode

We examined the associations between the duration of infant attention episodes and infant theta changes around these looks using linear-mixed effects models. Infant attention episodes and attention duration were calculated as explained above in section 4.3.5.1.

To conduct these analyses, each infant attention episode onset (i.e., gaze shift to a different toy) was identified in the EEG signal by calculating the time from the start of the interaction (first LED) to the onset of the look (in the behavioural data) and adding it to the first EEG trigger. For each look, we extracted theta (3-6Hz) power for two time-windows immediately prior to the onset of each look (-2000 to -1000msec and -1000 to 0 msec pre-look onset) and three time-windows immediately after the onset of each look (0 to 1000ms, 1000ms to 2000msecand 2000 to 3000msec post look onset) (see **Figure 7** ^{C2}). To calculate the EEG power spectra, we use the 'mtmfft' method from the ft_freqanalysis function in FieldTrip, an open-source Matlab toolbox (Maris & Oostenveld, 2007 ^{C2}); *http://fieldtriptoolbox.org* ^{C2}). Extreme power values that were 4 times greater than the interquartile range were treated as outliers and excluded from further analyses (similar to Xie et al., 2018 ^{C2}). More detail on the amount of data available (i.e., average duration of the session per participant and number and duration of attentional episodes per minute) can be accessed in **Table S1** ^{C2}.

For each epoch, we only selected power within our cluster of central channels (similar to Wass, Noreika, et al., 2018). Power at each bin was expressed as relative power, defined as the total power at a specific frequency band divided by the total power across all frequency bands during that epoch. After extracting the relative power in the theta band, we calculated separate linear mixed effects models for each of the five windows to examine the relationship between EEG power within that time window and attention duration.

4.3.8 Analysis 4. Calculation of neural power changes within an attention episode

In addition, we also wanted to look at power changes within attention episodes. Infant attention episodes and attention duration were calculated as explained above (section 4.3.5.1) and each infant look onset towards an object was identified in the EEG signal as described in analysis 3 (section 4.3.7). For each look, we extracted the first (0 to +1000msec, "start") and third-to-fourth (3000 to 4000msec, "middle") second into the look, and the last second (-1000msec prior to look



offset to look offset, "termination") before look termination (see **Figure 7** ²²). Looks that did not make it to the full second segment were excluded from further analysis. Similarly, only looks that were longer than 5 seconds were included to the "middle" group. This was done to avoid an overlap between the activity from the "middle" and the "termination" groups.

Frequency analysis was conducted to assess the power spectral density for both theta (3-6Hz) and alpha (6-9Hz) frequency rhythms for each of the three time-segments. These analyses were calculated for the three prespecified clusters of channels: Frontal, Central and Occipital (see **Figure S6** ☑). Again, power at each time segment was expressed as relative power.

The selection of both theta (3-6Hz) and alpha (6-9Hz) frequency bands was led by previous work using this same approach (e.g., 28, 29, 30, 37).

4.3.9 Analysis 5. Auto- and cross-correlations analyses between infant theta activity and attention

4.3.9.1 EEG relative power, one-second epochs

For this analysis, we parsed the EEG data into one-second segments and calculated the relative theta power for each one-second segment as described above (see 4.3.7).

4.3.9.2 Cross-correlation analysis

To explore whether modulations in endogenous theta activity related to fluctuations in infants' attention, we conducted a cross-correlation analysis between infants' relative theta and attention. Attention was calculated as described in analysis 2 (4.3.6.1, and **Figure 7** ⁽²⁾). Additionally, we also computed the autocorrelation for relative theta to assess how theta predicts itself over time. Again, all analyses were computed at lags from -30 to +30s in 1s intervals. Significance was assessed following the steps described in analysis 2 (4.3.6.2).

Finally, to explore interdependencies between autonomic arousal and theta activity we conducted a cross-correlation analysis between infants' autonomic activity and relative theta.

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Formal analysis: MPA.

Funding acquisition: SVW.

Investigation: EG, JI, PL, IMH, EAMP, NKV, MW, MPA.

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Project administration: EG, JI, PL, IMH, TJN, EAMP, NKV, MW, SVW, MPA. Supervision: SVW, EJHJ.

Visualisation: MPA.

Writing – original draft: MPA.

Writing – review & editing: EG, JI, PL, IMH, TJN, EAMP, NKV, MW, EJHJ, SVW, MPA.

Data and materials availability

Partial restrictions to the data and/or materials apply. Due to the personally identifiable nature of this data (video recordings from infants) the raw data will not be made publicly accessible. Researchers who wish to access the raw data should email the lead author. Permission to access the raw data will be granted as long as the applicant can guarantee that certain privacy guidelines (e.g. storing the data only on secure, encrypted servers, and a guarantee not to share it with anyone else) can be provided.

Supplementary Materials



SI 1. Changes in the number and duration of attentional episodes throughout the solo play interaction

These analyses are aimed to explore whether the average number of attentional episodes and duration changed throughout the play session and are complementary to analysis 1 (Figure 1B 🗹 and D 🗹). To do this, we calculated the best fit lines for number (Figure S1 🗹 A and B) and duration (Figure S1 C 🖓 and D 🖒) of attentional episodes and compared their gradients between ages (to check for developmental differences) and against zero (to see whether there were increases or decreases in these variables throughout the interaction at both ages). Average number (count) of attentional reorientations per minute (Fig1 A 🗠 and B 🗠)

- 5-months-old infants, mean gradient = -2.33179.
- 10-months-old infants, mean gradient = -1.20763.

We observed a significant decrease in attentional reorientations over the course of the interaction at both time points (at 5 months: t(30)=-3.483, p=0.0015; at 10 months: t(28)=- 3.331, p=0.0024). We found no significant differences between the two groups.

Average duration (sec) of attentional episodes per minute (**Fig1** C¹ and D¹)

- 5-months-old infants, mean gradient = 0.2528.
- 10-months-old infants, mean gradient = 0.689.

No significant differences were found in the way attentional episodes durations changed throughout the interaction, neither within nor between groups.

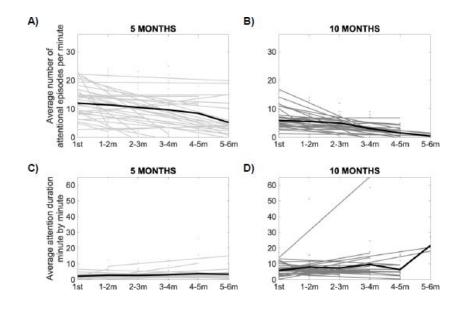


Figure S1.

Figure showing the best fit lines for individual number of attentional episodes per minute at 5 months (A) and at 10 months (B); and best fit lines for average duration of attentional episodes at 5 months (C) and at 10 months (D).

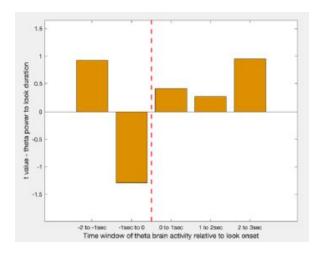


Figure S2.

Calculation of theta power changes around an attention episode at 5 months after matching the final number of accepted trials to those at 12 months.

Results of the linear mixed effects models conducted to examine whether individual looks accompanied by higher theta power are longer lasting. For each look, we calculated the association between the total duration of the look and relative theta power during five time-windows (-2000msec to -1000msec and -1000msec to 0 prior to the look, and 0 to 1000msec, 1000 to 2000msec and 2000 to 3000msec before the look), using a series of separate linear mixed effects models. Y-axis is the t value. Asterisks (*) indicate p values < .05. Central channels include: 'FC1', 'FC2', 'C3', 'C2', 'C4', 'CP1' and 'CP2'.

Analysis of Variance							
Source	Sum Sq.	d.f.	Mean Sq.	F	Prob>F		
attentional phase	0.174	2	0.08719	4.56	0.0105		
channel cluster	0.045	2	0.02255	1.18	0.3077		
age	0.022	1	0.02245	1.17	0.2788		
attentional phase*channel cluster	0.019	4	0.00478	0.25	0.9098		
attentional phase*age	0.213	2	0.10668	5.58	0.0038		
channel cluster∗age	0.458	2	0.22918	11.98	0		
attentional phase*channel cluster*age	0.026	4	0.00644	0.34	0.8535		
Error	136.545	7137	0.01913				
Total	137.741	7154					

Constrained (Type III) sums of squares.

Table S1.

Results from the 3-way ANOVA performed in Analysis 4 for theta PSD. "Attentional phase refers" to time within an attentional episode (i.e., start, middle, termination); "Channel cluster" includes Central, Frontal and Occipital channels; and "age" includes 5- and 10-months-old infants.

time within an attentional episode (AE)	age	Lower Limit	A-B	Upper Limit	P-value
AE=1,age=1	AE=2,age=1	-0.021	-0.002	0.017	1.000
AE=1,age=1	AE=3,age=1	-0.004	0.009	0.022	0.365
AE=1,age=1	AE=1,age=2	0.006	0.019	0.033	0.001
AE=1,age=1	AE=2,age=2	-0.026	-0.007	0.011	0.860
AE=1,age=1	AE=3,age=2	-0.007	0.007	0.022	0.719
AE=2,age=1	AE=3,age=1	-0.009	0.011	0.031	0.643
AE=2,age=1	AE=1,age=2	0.001	0.021	0.042	0.039
AE=2,age=1	AE=2,age=2	-0.029	-0.006	0.018	0.986
AE=2,age=1	AE=3,age=2	-0.012	0.009	0.030	0.826
AE=3,age=1	AE=1,age=2	-0.005	0.010	0.026	0.382
AE=3,age=1	AE=2,age=2	-0.036	-0.016	0.003	0.150
AE=3,age=1	AE=3,age=2	-0.018	-0.002	0.014	1.000
AE=1,age=2	AE=2,age=2	-0.047	-0.027	-0.007	0.002
AE=1,age=2	AE=3,age=2	-0.029	-0.012	0.005	0.305
AE=2,age=2	AE=3,age=2	-0.006	0.015	0.035	0.318

Table S2

Multiple comparison test between time within an attentional episode and age (in theta PSD activity). AE indicates "time within an attentional episode" where AE1= first second into the look (start), AE2 = third to fourth second into the look (middle), and AE3 = last second into the look (termination). Age1 = 5 months, age2 = 10 months.

channel cluster (ch)	age	Lower Limit	A-B	Upper Limit	P-value
Ch=1,age=1	Ch=2,age=1	-0.028	-0.010	0.008	0.571
Ch=1,age=1	Ch=3,age=1	-0.004	0.014	0.031	0.252
Ch=1,age=1	Ch=1,age=2	-0.005	0.014	0.032	0.287
Ch=1,age=1	Ch=2,age=2	-0.009	0.010	0.028	0.651
Ch=1,age=1	Ch=3,age=2	-0.026	-0.008	0.010	0.820
Ch=2,age=1	Ch=3,age=1	0.006	0.024	0.042	0.002
Ch=2,age=1	Ch=1,age=2	0.005	0.024	0.042	0.003
Ch=2,age=1	Ch=2,age=2	0.002	0.020	0.039	0.023
Ch=2,age=1	Ch=3,age=2	-0.016	0.002	0.021	0.999
Ch=3,age=1	Ch=1,age=2	-0.018	0.000	0.018	1.000
Ch=3,age=1	Ch=2,age=2	-0.022	-0.004	0.015	0.993
Ch=3,age=1	Ch=3,age=2	-0.040	-0.022	-0.003	0.011
Ch=1,age=2	Ch=2,age=2	-0.023	-0.004	0.015	0.993
Ch=1,age=2	Ch=3,age=2	-0.041	-0.022	-0.003	0.016
Ch=2,age=2	Ch=3,age=2	-0.037	-0.018	0.001	0.082

Table S3

Multiple comparison test between channel cluster and age (in theta PSD activity). Ch1 = central channels, Ch2 = occipital channels, and Ch3 = frontal channels. Age1 = 5 months and Age2 = 10 months.

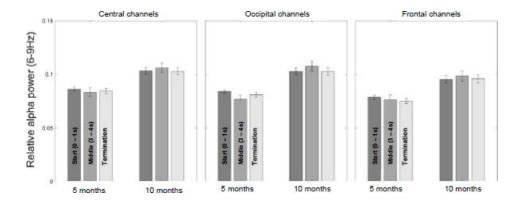


Figure S3.

Calculation of alpha power changes within an attention episode.

Bar plots for the average relative alpha power throughout a look, at both time points (5 and 10 months) and at different groups of electrodes (central, occipital, and frontal). Error bars represent SEMs.

Source	Sum 5q.	d.f.	Mean Sq.	F	Prob>F
attentional phase	0.0027	2	0.00136	0.39	0.6757
channel cluster	0.0597	2	0.02983	8.58	0.0002
age	0.6072	1	0.60725	174.6	0
attentional phase∗channel cluster	0.0002	4	0.00006	0.02	0.9994
attentional phase*age	0.0117	2	0.00585	1.68	0.186
channel cluster∗age	0.0051	2	0.00256	0.74	0.4787
attentional phase*channel cluster*age	0.0025	4	0.00062	0.18	0.949
Error	24.8216	7137	0.00348		
Total	25.5905	7154			

Constrained (Type III) sums of squares.

Table S4

Results from the 3-way ANOVA performed in Analysis 4 for alpha PSD. "Attentional phase refers" to time within an attentional episode (i.e., start, middle, termination); "Channel cluster" includes Central, Frontal and Occipital channels; and "age" includes 5- and 10-months-old infants.



SI 2. Analyses on EEG data quality

To compare the quality of the EEG data at 5 and 10 months we performed a series of analyses on percentage of channels interpolated, percentage of segments removed (i.e., zeroed out) and percentage of ICA components rejected. None of these variables differed significantly between age groups.

We also calculated the percentage of channel interpolation within our clusters of channels of interest (i.e., frontal, central, occipital VS other channels). The percentage of interpolated channels within our cluster of channels of interest did not statistically differ between our two groups. Instead, the percentage of other channels removed (i.e., channels not included in any of our analyses) did differ significantly.

	Channels interpolated (%)		Segments removed (%)		ICA components rejected (%)	
	Mean	Std	Mean	Std	Mean	Std
5 months	14.130	8.782	8.066	9.617	51.630	15.479
10 months	9.783	10.292	8.360	6.216	48.153	16.243
Statistics	t(44)= 1.541, p= 0.1304 *		t(44) = -0.124, p = 0.902 *		t(43) = -0.735, $p = 0.466^{\dagger}$	

Table S5

Table showing the average percentage (and standard deviation) of channel interpolation, segments removed, and ICA components rejected at 5 and 10 months.

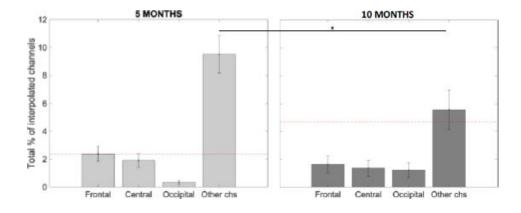


Figure S4.

Bar plots showing the average of interpolated channels per cluster of channels of interest. Red lines indicate the equivalent percentage of 1.5 channel interpolated.

Significance is indicated with asterisks where * = p < 0.05.

	Frontal		Central		Occipital		Others	
	Mean	Std	Mean	Std	Mean	Std	Mean	Std
5 months	2.378	2.575	1.902	2.400	0.340	0.659	9.511	6.458
10 months	1.630	2.960	1.359	2.799	1.223	2.621	5.571	6.792
Stats (t-test)	t(44)= p=0.		100 C 100	0.710, .483	t(44)=- p=0.		t(44)=2.0163 p= 0.050	

Table S6

Table showing the average percentage (and standard deviation) of interpolated channels for each cluster of channels of interest.



Figure S5.

Photos of the toys employed at 5 months (A to C) and at 10 months (D to F).

	at 5 months	%	at 10 months	%
total SP sessions	60	100	102	100
EEG datasets	23	38.3	25	24.5
bad EEG data *	33	55.0	21	20.6
technical issues with data recording (e.g., video missing)	1	1.7	8	7.8
further rejection - sync problems	-	17.1	19	18.6
further rejection - behaviour not coded	-	-	26	25.5
further rejection - too few looks	3	5.0	3	2.9
ECG [†]	28	90.3	14	<mark>48.3</mark>
noisy/ bad data	2	6.5	2	6.9
sync problems	1	3.2	3	10.3
file corrupted/ recording error/ missing data	-	-	10	34.5
Final datasets (N)				
Looking behaviour coded	31		29	
Behaviour + EEG	23		25	
Behaviour + ECG	28		14	
ECG + EEG	22		10	

* Bad EEG data also includes these datasets where the infant was fussing out, pulling out the EEG wires, falling asleep, etc.

[†]ECG data is explained based on the datasets that have gaze behaviour coded

Table S7

Table summarising the numbers of datasets included in each of the analyses for both samples as well as reason for exclusion.

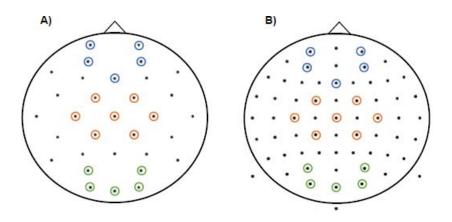


Figure S6.

Topoplot showing our channel clusters in the 32-channel (A, 10 months) and the 64-channel (B, 5 months) BioSemi gel-based ActiveTwo montage.

In blue, Frontal channels ('Fp1', 'Fp2', 'AF3', 'AF4', 'Fz'); in orange, Central channels ('FC1', 'FC2', 'C3', 'C2', 'C4', 'CP1', 'CP2'); and in green, Occipital channels ('PO3', PO4', O1', 'Oz', 'O1). Channel names are organised from top to bottom and from left to right.



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Editors

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Senior Editor

Yanchao Bi Beijing Normal University, Beijing, China

Reviewer #1 (Public Review):

Summary:

The paper investigates the physiological and neural processes that relate to infants' attention allocation in a naturalistic setting. Contrary to experimental paradigms that are usually employed in developmental research, this study investigates attention processes while letting the infants be free to play with three toys in the vicinity of their caregiver, which is closer to a common, everyday life context. The paper focuses on infants at 5 and 10 months of age and finds differences in what predicts attention allocation. At 5 months, attention episodes are shorter and their duration is predicted by autonomic arousal. At 10 months, attention episodes are longer, and their duration can be predicted by theta power. Moreover, theta power predicted the proportion of looking at the toys, as well as a decrease in arousal (heart rate). Overall, the authors conclude that attentional systems change across development, becoming more driven by cortical processes.

Strengths:

I enjoyed reading the paper, I am impressed with the level of detail of the analyses, and I am strongly in favour of the overall approach, which tries to move beyond in-lab settings. The collection of multiple sources of data (EEG, heart rate, looking behaviour) at two different ages (5 and 10 months) is a key strength of this paper. The original analyses, which build onto robust EEG preprocessing, are an additional feat that improves the overall value of the paper. The careful consideration of how theta power might change before, during, and in the



prediction of attention episodes is especially remarkable. However, I have a few major concerns that I would like the authors to address, especially on the methodological side.

Points of improvement

1. Noise

The first concern is the level of noise across age groups, periods of attention allocation, and metrics. Starting with EEG, I appreciate the analysis of noise reported in supplementary materials. The analysis focuses on a broad level (average noise in 5-month-olds vs 10-month-olds) but variations might be more fine-grained (for example, noise in 5mos might be due to fussiness and crying, while at 10 months it might be due to increased movements). More importantly, noise might even be the same across age groups, but correlated to other aspects of their behaviour (head or eye movements) that are directly related to the measures of interest. Is it possible that noise might co-vary with some of the behaviours of interest, thus leading to either spurious effects or false negatives? One way to address this issue would be for example to check if noise in the signal can predict attention episodes. If this is the case, noise should be added as a covariate in many of the analyses of this paper. Moving onto the video coding, I see that inter-rater reliability was not very high. Is this due to the fine-grained nature of the coding (20ms)? Is it driven by differences in expertise among

the two coders? Or because coding this fine-grained behaviour from video data is simply too difficult? The main dependent variable (looking duration) is extracted from the video coding, and I think the authors should be confident they are maximising measurement accuracy.

2. Cross-correlation analyses

I would like to raise two issues here. The first is the potential problem of using autocorrelated variables as input for cross-correlations. I am not sure whether theta power was significantly autocorrelated. If it is, could it explain the cross-correlation result? The fact that the cross-correlation plots in Figure 6 peak at zero, and are significant (but lower) around zero, makes me think that it could be a consequence of periods around zero being autocorrelated. Relatedly: how does the fact that the significant lag includes zero, and a bit before, affect the interpretation of this effect?

A second issue with the cross-correlation analyses is the coding of the looking behaviour. If I understand correctly, if an infant looked for a full second at the same object, they would get a maximum score (e.g., 1) while if they looked at 500ms at the object and 500ms away from the object, they would receive a score of e.g., 0.5. However, if they looked at one object for 500ms and another object for 500ms, they would receive a maximum score (e.g., 1). The reason seems unclear to me because these are different attention episodes, but they would be treated as one. In addition, the authors also show that within an attentional episode theta power changes (for 10mos). What is the reason behind this scoring system? Wouldn't it be better to adjust by the number of attention switches, e.g., with the formula: looking-time/(1+N_switches), so that if infants looked for a full second, but made 1 switch from one object to the other, the score would be .5, thus reflecting that attention was terminated within that episode?

3. Clearer definitions of variables, constructs, and visualisations

The second issue is the overall clarity and systematicity of the paper. The concept of attention appears with many different names. Only in the abstract, it is described as attention control, attentional behaviours, attentiveness, attention durations, attention shifts and attention episode. More names are used elsewhere in the paper. Although some of them are indeed meant to describe different aspects, others are overlapping. As a consequence, the main results also become more difficult to grasp. For example, it is stated that autonomic arousal predicts attention, but it's harder to understand what specific aspect (duration of looking, disengagement, etc.) it is predictive of. Relatedly, the cognitive process under investigation (e.g., attention) and its operationalization (e.g., duration of consecutive looking toward a toy)



are used interchangeably. I would want to see more demarcation between different concepts and between concepts and measurements.

General Remarks

In general, the authors achieved their aim in that they successfully showed the relationship between looking behaviour (as a proxy of attention), autonomic arousal, and electrophysiology. Two aspects are especially interesting. First, the fact that at 5 months, autonomic arousal predicts the duration of subsequent attention episodes, but at 10 months this effect is not present. Conversely, at 10 months, theta power predicts the duration of looking episodes, but this effect is not present in 5-month-old infants. This pattern of results suggests that younger infants have less control over their attention, which mostly depends on their current state of arousal, but older infants have gained cortical control of their attention, which in turn impacts their looking behaviour and arousal.

• https://doi.org/10.7554/eLife.92171.1.sa2

Reviewer #2 (Public Review):

Summary:

This manuscript explores infants' attention patterns in real-world settings and their relationship with autonomic arousal and EEG oscillations in the theta frequency band. The study included 5- and 10-month-old infants during free play. The results showed that the 5-month-old group exhibited a decline in HR forward-predicted attentional behaviors, while the 10-month-old group exhibited increased theta power following shifts in gaze, indicating the start of a new attention episode. Additionally, this increase in theta power predicted the duration of infants' looking behavior.

Strengths:

The study's strengths lie in its utilization of advanced protocols and cutting-edge techniques to assess infants' neural activity and autonomic arousal associated with their attention patterns, as well as the extensive data coding and processing. Overall, the findings have important theoretical implications for the development of infant attention.

Weaknesses:

Certain methodological procedures require further clarification, e.g., details on EEG data processing. Additionally, it would be beneficial to eliminate possible confounding factors and consider alternative interpretations, e.g., whether the differences observed between the two age groups were partly due to varying levels of general arousal and engagement during the free play.

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Reviewer #3 (Public Review):

Summary:

Much of the literature on attention has focused on static, non-contingent stimuli that can be easily controlled and replicated--a mismatch with the actual day-to-day deployment of attention. The same limitation is evident in the developmental literature, which is further hampered by infants' limited behavioral repertoires and the general difficulty in collecting robust and reliable data in the first year of life. The current study engages young infants as they play with age-appropriate toys, capturing visual attention, cardiac measures of arousal, and EEG-based metrics of cognitive processing. The authors find that the temporal relations between measures are different at age 5 months vs. age 10 months. In particular, at 5 months of age, cardiac arousal appears to precede attention, while at 10 months of age attention processes lead to shifts in neural markers of engagement, as captured in theta activity.



Strengths:

The study brings to the forefront sophisticated analytical and methodological techniques to bring greater validity to the work typically done in the research lab. By using measures in the moment, they can more closely link biological measures to actual behaviors and cognitive stages. Often, we are forced to capture these measures in separate contexts and then infer inthe-moment relations. The data and techniques provide insights for future research work.

Weaknesses:

The sample is relatively modest, although this is somewhat balanced by the sheer number of data points generated by the moment-to-moment analyses. In addition, the study is cross-sectional, so the data cannot capture true change over time. Larger samples, followed over time, will provide a stronger test for the robustness and reliability of the preliminary data noted here. Finally, while the method certainly provides for a more active and interactive infant in testing, we are a few steps removed from the complexity of daily life and social interactions.

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