

Title

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

Authors

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Abstract

The ability to allocate and maintain visual attention enables us to adaptively regulate perception and action, guiding strategic behaviour within complex, dynamic environments. This capacity to regulate attention develops rapidly over the early years of life, and underpins all subsequent cognitive development and learning. From screen-based experiments we know something about how attention control is instantiated in the developing brain, but we currently understand little about the development of the capacity for attention control within complex, dynamic, real-world settings. To address this, we recorded brain activity, autonomic arousal and spontaneous attention patterns in N=58 5- and 10-month-old infants during free play. We used time series analyses to examine whether changes in autonomic arousal and brain activity anticipate attention changes or follow on from them. Early in infancy, slow-varying fluctuations in autonomic arousal forward-predicted attentional behaviours, but cortical activity did not. By later infancy, fluctuations in fronto-central theta power associated with changes in infants' attentiveness and predicted the length of infants' attention durations. But crucially, changes in cortical power followed, rather than preceded, infants' attention shifts, suggesting that processes after an attention shift determine how long that episode will last. We also found that changes in fronto-central theta power modulated changes in arousal at 10 but not 5 months. Collectively, our results suggest that the modulation of real-world attention involves both arousal-based and cortical processes but point to an important developmental transition. As development progresses, attention control systems become dynamically integrated and cortical processes gain greater control over modulating both arousal and attention in naturalistic real-world settings.

36 Teaser

37 Understanding how our brains develop the capacity to pay attention to objects and people around
38 them is central for understanding all aspects of subsequent cognitive development and learning.
39 However, we understand little about the mechanisms through which attention control develops
40 during early life in complex, real-world settings. Here, we examined the associations between
41 naturalistic attention patterns, arousal and neural activity, in 5- and 10-month-olds during free play
42 with toys. Early in infancy, lower-order arousal-based endogenous factors forward-predicted
43 attention; later in infancy, higher-order neural responses after the onset of a new attention episode
44 forward-predicted attention and modulated changes in arousal. Overall, our results suggest that the
45 neural and physiological substrates of real-world attention change between early and later infancy,
46 resulting in a more inter-linked system where associations between attention behaviour, cortical
47 activity, and autonomic arousal are stronger as infants develop.

48 **1. Introduction**

49 The ability to allocate and maintain visual attention enables the flexible regulation of perception and action
50 that is characteristic of strategic behaviour (1,2). The capacity to pay attention develops rapidly over the
51 early years of life (3), and individual differences in early attention predict long-term cognitive and clinical
52 outcomes (4,5). Recent new methodological advances such as naturalistic neuroimaging are allowing us to
53 build on previous research using lab-based behavioural experiments and animal studies.

54 The development of attention is traditionally conceptualised as the product of interactions among different
55 systems at different levels of maturity (1,6,7). Traditionally, the earliest subcomponent of attention to
56 develop is thought to be the arousal/ alertness subcomponent, mediated via brainstem reticular activating
57 systems centred on the locus coeruleus (LC) and instantiated primarily via norepinephrine neurotransmitter
58 systems (6). In young infants, alertness is more readily initiated by exogenous events (8); over time, infants
59 gain the ability to both attain and maintain an alert state even in absence of external stimulation. Areas
60 around the brainstem (including the LC) are thought to be some of the earliest to become functionally
61 mature (9,10). Consequently, the relative influence of this subcomponent of attention is thought to be
62 strongest during early development (6).

63 Behaviourally, the arousal/ alertness subcomponent of attention is thought to reflect a state of anticipatory
64 readiness, or alertness for stimulus input (6). Arousal is generally measured indirectly, via proxy measures
65 of autonomic nervous system activity such as heart rate (11). Heart rate has been extensively studied in the
66 context of infant attention (3,12,13). During anticipatory readiness, we know that reorientations of visual
67 attention take place periodically, clustered around a preferred modal reorientation rate (14–18). This may
68 reflect rhythmic activity in the central nervous system (19).

69 With time, it is thought that looking behaviours become increasingly modulated by higher-level executive
70 processes that reflect the infant's internal states, motivation, comprehension, and goals (2,20,21).
71 Behaviourally, this increase in endogenous or internally directed attention has been shown as: a
72 developmental increase in the degree to which attentional engagement is accompanied by decreases in
73 distractibility (22,23); an increase in selective attention as measured indirectly, using the blink reflex (24);
74 and differences in the trajectory of how attention durations to simple vs complex stimuli change over
75 developmental time (25).

76 Other research that used experimenter-controlled, screen-based tasks to examine neural correlates of
77 attention has examined changes in the power spectral density (PSD) of EEG oscillations, in particular
78 infants' theta (3-6Hz) rhythm, which increases during active, anticipatory, and exploratory behaviour (26–

79 31). Together, these studies suggest that the expression of theta during attention-eliciting episodes could
80 signify the engagement of neural networks related to executive attention (28,29,31). Similarly, other studies
81 have reported decreases in alpha band activity under conditions of increased attention (32,33). Both theta
82 and alpha effects are now widely known in the literature as “theta synchronization” and “alpha
83 desynchronization” (29).

84 How children allocate their attention in experimenter-controlled, screen-based lab tasks differs, however,
85 from actual real-world attention in several ways (34–36). For example, the real-world is interactive and
86 manipulable, and so how we interact with the world determines what information we, in turn, receive from
87 it: experiences generate behaviours (37). While lab-based studies can be made interactive (e.g., 38,39), how
88 infants actively and freely initiate and self-structure their attention remains unexplored (40).

89 The present study aims to examine developmental changes in the relationship between autonomic arousal,
90 cortical activity, and attention in real-world settings. To do this, we first explored how naturalistic attention
91 patterns (measured via looking durations to play objects) from a solo play interaction change between 5
92 and 10 months. Then, we explored temporal relations between changes in infant arousal (measured via heart
93 rate) and attention episodes in typical 5- and 10-month-olds infants. Finally, we investigated changes in
94 EEG theta power relative to attention episodes, and changes in EEG theta relative to arousal (see Figure 1).
95 As attentional systems mature and brain regions become increasingly specialised (41,42), we expected to
96 see both a developmental increase in attention towards play objects and a developmental shift in the way
97 different mechanisms (i.e., arousal/ alertness vs. executive attention subsystems) drive attention. To
98 measure attention we used looking time, an approach that is known to have several limitations (12,43,44).
99 For example, we cannot differentiate based on looking time alone whether overt and covert attention are
100 coupled or decoupled (see 3.1).

101 Our first set of analyses examined attentional inertia (the phenomenon that, as individuals become
102 progressively more engaged with an object, their attention progressively increases) as a measure of
103 internally driven attentional engagement (3,45,46). We tested whether attentional inertia influenced
104 attentional behaviours more strongly at 10 months compared to 5 months. To do so, we calculated both the
105 Autocorrelation Function (ACF) and the survival probability of spontaneously occurring attention episodes
106 during play (analysis 1). The ACF allowed us to quantify the rate of change of spontaneous attention
107 durations. A faster rate of change would indicate lower attentional inertia. The survival probability, on the
108 other hand, allowed us to quantify the probability between looking (i.e., paying attention) and looking away.
109 A slower decrease in the probability of an attention episode surviving would indicate increased attention
110 engagement and decreased distractibility by other stimuli. We hypothesised that, as slow-varying

111 fluctuations in endogenous interest or engagement start to influence looking behaviour more strongly over
112 time, 10-month-old infants would show increased endogenous attention control indexed by a slower rate of
113 change of attentiveness and slower decreases in the survival probability. We also predicted that we would
114 be able to identify periodic attentional reorientations during early as well as later development (17,47); later
115 in development, however, we predicted that infants would be more likely to extend visual fixations beyond
116 their modal periodic reorientation rate, possibly indicating a greater or more efficient integration of attention
117 and gaze shifting (48), and that attention duration episodes would be longer overall.

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

125 We used a similar approach to examine developmental changes in the relationship between neural markers
126 of executive attention and real-world attention behaviours. We were interested to examine whether neural
127 changes (indexed by theta power) anticipate subsequent attentional behaviour shifts (48); or, whether neural
128 processes after the attention shift relate to increases in infants' attention engagement. To test this, we
129 conducted three analyses. First, we analysed neural activity across a range of time windows both before
130 and after the onsets of new attention episodes and performed linear mixed effect models to examine how
131 neural activity before and after attention onset associated with the subsequent durations of those episodes
132 (analysis 3). Second, we examined changes in neural activity during individual attention episodes (analysis
133 4). Finally, we used cross-correlations to examine whether, across the entire dataset, neural markers tend to
134 forward-predict changes in attention, or vice versa (analysis 5). We predicted that the associations between
135 neural markers of executive attention and real-world attention behaviours would become stronger with
136 increasing age (i.e., theta activity would show a stronger predictive relation with infants' attentional
137 behaviours at 10 months, as evidence of increased modulatory power from the executive attention system
138 on infants' attention).

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

141

142 2. Results

143

144 2.1 Analysis 1: Developmental changes in attention

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

152 Initially, we conducted four descriptive analyses to test how attention and inattention durations and
153 reorientations change over both the course of the solo play interactions and developmental time. First, we
154 tested how many times per minute 5- and 10-months-old infants redirected their attention from one object
155 to the other. We found that, on average, 5-month-old infants performed significantly more both attentive
156 ($t(10)= 4.346, p=0.001$) and inattentive ($t(10)= 4.202, p=0.002$) reorientations during the solo play
157 interaction than 10-months-old infants (Figure 2A). When we looked at how attention reorientations
158 changed during the course of the solo play episode, we found that 5-month-old infants performed
159 consistently more looks than 10-month-olds throughout the interaction even though the number of looks
160 per minute decreased over the course of the interaction for both age groups (Figure 2B, and Figure S1A
161 and B).

162 Second, we investigated the average duration that 5- and 10-month-old infants spent in attentive and in
163 inattentive states during the solo play interaction and minute by minute (Figure 2C and D respectively). In
164 general, infants' attention durations toward play objects at 10 months were longer ($t(10)= -2.787, p=0.019$).
165 At 5 months, moments of inattention were longer than moments spent looking towards the object ($t(10) =$
166 $-3.749, p=0.003$). Overall, at 10 months, but not 5 months, infants spent more time in attentive compared
167 to inattentive states ($t(58)= 10, p<0.001$) (Figure 2E). We then calculated a best fit line, individual by
168 individual, to look at how average attention duration changed within the session (see Figure S1C and D).
169 We found no significant differences in the way attention duration changed during the interaction between
170 the two age groups (Figure S1C and D).

171 Third, we explored the distribution of looks towards the objects (Figure 2F). At both ages, attention
172 durations shorter than or equal to 5 seconds follow a positively skewed lognormal distribution, with modal

173 attention durations in the 0.5 – 0.6 second range. Modal attention durations were significantly lower at 5
174 than at 10 months ($t(58)= 2.211, p=0.03$). Finally, the right plot of Figure 2F shows extended attention
175 episodes. There was an increasing amount of such looks with increasing age.

176 Following the descriptive statistics, we calculated both the ACF and the survival probability of the looking
177 behaviour (Figure 3). First, we used time-series analyses to examine the rate of change of attention
178 durations, relative to itself. We calculated the ACF of the attention durations at both time points (more
179 details in 4.3.5.2). The ACF indexes the cross-correlation of a measure with itself at different lag-intervals
180 in time (46). ACF values were obtained from 0 to 10 seconds lag, in steps of 500 milliseconds. As shown
181 in Figure 3A, the ACF of the time series looking behaviour fell off more sharply at 5 months than at 10
182 months. The ACF values were compared across ages using independent sample t-tests. From lag +500
183 milliseconds to 10 seconds, 10-months-old infants showed significantly higher correlation values than 5-
184 months-old infants.

185 Second, we performed a survival analysis by calculating the survival probability function of the looking
186 behaviour towards the objects at both time points. The survival probability function is the probability that
187 an attention episode survives longer than a certain time. As shown in Figure 3B, the survival probability of
188 a look decreased abruptly at the beginning, for the very short looks, and flattened as looks got longer. The
189 differences in the speed at which the survival probability decreased can be seen more clearly by calculating
190 the derivative of the survival probability (Figure 3C). To compare survival among the two groups, we
191 performed the log rank test using the Matlab function ‘Logrank’ (50). The results for the log-rank test
192 rejected the null hypothesis ($p<0.001$) indicating that the survival curves for looking behaviour at 5 months
193 and 10 months were significantly different. Notably, the likelihood of a look ending is more tightly clustered
194 around the modal value of 0.5 seconds at 5 months.

195 Overall, our results showed that older infants demonstrated to have a slower-changing profile of attention
196 with longer attention episodes overall (Figure 2A and B, Figure 3A). At both ages, there was evidence for
197 a preferred modal reorientation rate in the 0.5-0.6 second range, which was slightly faster at 5 months than
198 10 months (Figure 2F). Attention durations were more tightly clustered around the modal value at 5 months.
199 At 10 months, attention episodes were more likely to be extended beyond the preferred modal reorientation
200 rate than at 5 months (Figure 3B and C).

201

202 **2.2 Analysis 2. Auto- and cross-correlation analyses between infant autonomic arousal and**
203 **attention**

204 In this section we investigated the relationship between changes in infant autonomic arousal (indexed by
205 heart rate activity) and their associations with moment-to-moment changes in attention (indexed as a
206 continuum of looking durations to play objects vs. elsewhere).

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

216

217 **2.3 Analysis 3. Calculation of neural power changes around an attention episode**

218 We used linear mixed effects models to examine the associations between the length of each attention
219 episode (i.e., looking duration to any of the play objects) and relative theta power at different time windows
220 relative to the onset of that attention episode (see Figure 5). At 10 months, relative theta power in the time
221 window of 0 to +1000msec and +1000 to +2000msec after onset of a new attention episode predicted the
222 subsequent duration of that attention episode. At 5 months, the same relationships were not significant. We
223 found no evidence of neural activity before the start of an attention episode forward-predicting the length
224 of that attention episode at any time point (Figure 5).

225 The final number of accepted trials (i.e., attention episodes) in the analyses varied across the three time-
226 windows immediately after the onset of each look. More trials were obtained for the first window (total
227 number of looks at 5 months was 790, and 411 at 10 months) than the second (total number of looks at 5
228 months was 473, and 336 at 10 months) and the third (total number of looks at 5 months was 301, and 277
229 at 10 months). All three conditions ended up with enough number of clean trials that was greater than the
230 recommended number of trials in the infant EEG literature (51–53). Thus, the differences between the
231 number of trials for each time window are not expected to contribute to the results described above.
232 However, we repeated this analysis by matching the number of attention episodes at 5 months to the ones
233 analysed at 12 months. We found no differences in the results (see Figure S2).

234

235 **2.4 Analysis 4. Calculation of neural power changes within an attention episode**

236 In addition to the previous analyses, which examined the associations between the length of each attention
237 episode and relative theta power at different time windows relative to the onset of that attention episode,
238 we also wished to examine whether power at the theta and alpha band changed significantly during an
239 attentional look (i.e., any look at a play object) (Figure 6). Relative theta was analysed as a function of these
240 three factors: time within an attentional episode, brain areas and age with a 3-way ANOVA (Figure 6).
241 There was no statistically significant interaction between the three factors. However, the analysis revealed
242 two simple two-way interactions: one between time within an attention episode and age, $F(2) = 5.58$, $p <$
243 $.005$ and the other between channel cluster and age $F(2) = 11.98$, $p < .001$. Next, we performed a multiple
244 comparison test to find out which groups of factors were significantly different. Results are shown in table
245 S1-S3. A follow up analysis showed a significant effect of “time within an attentional episode”: 10-months-
246 old infants had greater theta during the third-to-fourth second into the look (middle) than the first second
247 (start) in both the central and the frontal poles. These effects were not present in 5-months-old infants.
248 Similarly, relative alpha was also analysed as a function of these three factors: time within and attentional,
249 brain areas and age with a 3-way ANOVA. We found no statistically significant interactions. Results are
250 shown in Figure S3.

251 Again, the final number of accepted trials (i.e., attention episodes) in the analyses varied across the three
252 time-windows into each look. More trials were obtained for the first-second window (total number of looks
253 at 5 months was 791, and 415 at 10 months) than the third-to-fourth second (total number of looks was 172
254 at 5 months, and 194 at 10 months) and the last second before look termination (total number of looks was
255 476 at 5 months, and 337 at 10 months).

256

257 **2.5 Analysis 5. Auto- and cross-correlation analyses between infant theta activity and attention**

258 In this section we investigated the relationship between dynamic changes in infant endogenous brain
259 activity and their associations with moment-to-moment changes in attention (measured as a continuum of
260 looking time durations to play objects vs. elsewhere). Figure 7A and D shows the results of the
261 autocorrelation analyses for infant theta activity. Figure 7B and E shows the results for the cross-correlation
262 analyses between infant theta activity and infant attention. Cluster-based permutation analysis revealed a
263 significant positive association between the two variables (marked with a red line) at 10 months around

264 time lag=0. More specifically, increases in infant theta activity at 10 months were significantly correlated
265 with fluctuations in infant attention (Figure 7E). No associations were found between theta activity and
266 infant attention at 5 months of age. Interpreting the exact time intervals over which a cross-correlation is
267 significant is challenging due to the autocorrelation in the data (54,55), but the fact that the significance
268 window is asymmetric around time 0 indicates a temporally specific relationship between infant attention
269 and theta power, such that attention forward-predicts theta power more than vice versa.

270 Finally, to test whether there were any interdependencies between autonomic arousal and brain activity, we
271 performed a cross-correlation analysis between these two variables. We found a significant cluster at 10
272 months (Figure 7F) but not at 5 months (Figure 7C). The asymmetry of this cluster around $t=0$ indicated
273 that changes in brain activity tended to precede changes in autonomic arousal more than vice versa.

274

275

276 **3. Discussion**

277 We examined developmental changes in the physiological and neural correlates of real-world attention
278 patterns during early development. To do so, we measured attention durations (to an accuracy of 50Hz),
279 along with cortical neural activity (EEG) and autonomic arousal (via ECG) from typical 5- and 10-month-
280 old infants playing alone while seated at a tabletop with 3 toys. This age range is a key period for early
281 cognitive development, as differential patterns of brain development (10) drive a transition from primarily
282 subcortical to cortical control (56), and early-emerging atypicalities can have life-long consequences
283 (57,58). However, many of the mechanisms that drive early development remain unclear.

284 From Analysis 1 we found that infants at both ages showed a preferred rate of reorientation (i.e. their visual
285 attention took place periodically). The modal durations of attention episodes towards different play objects
286 were in the 0.5-0.6 second range at both ages but were lower at 5 months (Figure 2F, 2C). This contrasts
287 with analyses of micro-level fixation durations (time intervals between individual refoveating eye
288 movements), which decreases from early infancy (~0.5 secs) through to later infancy (~0.4 secs) through
289 to adulthood (~0.3 secs) (15,18). Research with adults suggests that the minimum time necessary to plan
290 and execute a saccade is ~80msecs in adults (16). Although the equivalent figure is not known in infancy,
291 the fact that modal attention durations towards objects were shorter at 5 months than 10 months, whereas
292 fixation durations decrease with age, makes it likely that the figures we observed do not simply indicate
293 that infants were reorienting at the fastest speed possible, but rather were reorienting according to a
294 preferred modal reorientation rate (15).

295 The survival analysis showed that, at both ages, looks were fragile early in their existence and most likely
296 to terminate in the <1 second range (45) but the speed at which the survival probability curve decreased
297 was faster at 5 months, meaning that the probability of a look lasting longer than time t was lower at 5
298 months. Richards and colleagues have found similar relationships in infants in both lab-based and
299 naturalistic settings (45). Overall, attention durations were shorter at 5 months; this faster-changing pattern
300 of attention to the object was also reflected in the ACF of their looking behaviour, which decreased
301 significantly faster, showing lower overall self-similarity. Collectively, these data fit well with what we
302 know about the development of attention. With time, we seem to observe a higher-level control of attention
303 that allowed older infants to prioritize the task at hand – learning about/ exploring the toys – as well as to
304 inhibit the tendency to shift attention away from an interesting task (6,20,25). Alternatively, longer attention
305 episodes might arise because children physically manipulate objects, bringing objects closer to themselves
306 which makes them more exogenously salient (37,59). In this case, then the infant's increased looking
307 behaviour would be the result of increased exogenous attentional capture rather than an increase in
308 endogenous attention control (46).

309 Analysis 2 examined how dynamic fluctuations in autonomic arousal relate to moment-to-moment changes
310 in attention. Consistent with previous work (13,49,60), the average concurrent correlation between
311 autonomic arousal and attention was negative at both age points, indicating that lower arousal was
312 associated with increased likelihood of attention. Such links have been considered within the developmental
313 attention regulation literature, where increases in arousal are thought to lead to distraction or difficulties
314 focusing attention, and vice versa (61). We also found that arousal levels were significantly forward
315 predictive of attention at 5 months but not at 10 months (Figure 4B and D). Theoretically, if attentional
316 episodes drive decelerations in the heart rate (12), and older infants show longer attentional episodes on
317 average, then one could hypothesise that older infants ought also to show a more stable pattern (i.e., higher
318 autocorrelations) in their heart rate fluctuations than younger infants. However, this was not what we
319 observed (Figure 4A and C). Overall, the much shorter attention durations observed in this setting,
320 compared with screen-based TV viewing (12), means that heart rate decelerations relative to individual
321 attention episodes were observed infrequently in our data. However, our data did suggest, consistent with
322 previous research, that at 5 months, changes in autonomic arousal forward-predict subsequent changes in
323 attention.

324 In Analysis 3 we examined the associations between attention episode durations and theta power either
325 before, or after, onset of that attention episode. At 10 but not 5 months, increased theta during the period
326 immediately after the onset of a new attention episode (0-2000msec) forward-predicted the subsequent

327 length of that attention episode (Figure 5). At neither age, however, did cortical neural activity before the
328 onset of an attention episode forward-predicted attention durations.

329 In Analysis 4 we examined whether cortical neural activity changed significantly during an attention
330 episode. Consistent with previous research (29), theta power in central and frontal electrodes increased
331 significantly during an attention episode at 10 months, but not at 5 months (Figure 6). Contrary to our
332 expectations, we did not find a link between attenuated alpha during an attention episode at any age (see
333 Figure S3).

334 In Analysis 5 we investigated the relationship between dynamic changes in infants' theta activity and
335 moment-to-moment changes in attention. We identified a significant positive association between infant
336 theta activity and infant attention at 10 months but not at 5 months (Figure 7B and E). Interpreting the exact
337 time intervals over which a cross-correlation is significant is challenging (54,55), but the asymmetry of the
338 cluster around time 0 indicates that attention forward-predicted theta power more than vice versa, consistent
339 with the findings from Analysis 3.

340 These findings are consistent with previous research suggesting that, by 10 months, but not during early
341 infancy, theta oscillations increase during sustained attention and encoding (29,41,62) and associate with
342 longer attentional periods (63). Importantly, though, we found no evidence that endogenous neural markers
343 before the onset of an attention episode forward-predict the length of an attentional episode at either age.
344 Instead, what we found suggests that neural activity shortly after the onset of an attention episode forward-
345 predicts the length of that episode. One possible interpretation of this is that neural activity associates with
346 the maintenance more than the initiation of attentional behaviours (64).

347 Finally, we examined the relationship between theta power and autonomic arousal (Figure 7C and F). A
348 cross-correlation analysis found a negative forward-predictive relationship between the two, such that
349 increases in theta forward-predicted decreases in autonomic arousal at 10 months, but not at 5 months. This
350 suggests that changes in the brain activity could be modulating subcortical changes (i.e., changes in the
351 heart rate) and may thus be able to initiate or maintain states of arousal that are common to vigilant or
352 sustained attentional states (6,12). Overall, it appears that, by 10 months, the different substrates of attention
353 are more inter-linked, and stronger associations are emerging between behaviour, cortical activity, and
354 autonomic arousal (65).

355 In summary, our results suggest that, earlier in development, attentional episodes are more influenced by
356 lower-order endogenous factors such as a general arousal system (3,12) - that might reflect a stronger
357 influence of subcortical structures over the modulation of attention - and show a preferred modal

358 reorientation timer - which characterises infants' attention shifting more strongly. Such factors would also
359 be present at older ages; however, their association with attention would weaken over developmental time
360 due to the maturation in cortical attentional areas thought to take place throughout the first year of life.
361 Later in infancy, cortical neural activity reliably changes during attention episodes, but does not forward-
362 predict attention at either age; rather, it seems that neural changes associate with the maintenance more than
363 the initiation of attentional behaviours. Overall, the modulation of attention seems to involve both arousal-
364 based and cortical processes. With developmental time, however, the latter increases its control over the
365 modulation of both (i.e., overt attentional behaviours and arousal), resulting in a more inter-linked system
366 where associations between attentional systems are stronger. Theoretically, this is consistent with what we
367 know about the development of executive attention from experimental and neuroanatomical studies.

368

369 **3.1 Limitations and strengths**

370 Our findings should be interpreted with consideration to a number of limitations of the study. First, our
371 events of interest are intrinsically linked with one of the biggest EEG artefacts (i.e., eye movements), and
372 so it is possible that residual artifact in the EEG signal may have contaminated our data. However, our data
373 were processed using algorithms specially designed to clean naturalistic EEG data (66,67), and previous
374 analyses suggest that the electrode locations and frequency bands that we examined should be least affected
375 by artifact, compared with more anterior locations and higher and lower frequencies (68). Additionally, our
376 analyses were carefully designed to preclude this potential confound. First, our analyses compare events
377 that we know share the same level of artefact/ noise (i.e., saccades at 5 months old contribute to comparable
378 noise levels than at 12 months old (69); second, analysis 3 and 4 are time-locked to a saccade to eliminate
379 the possibility that saccadic frequency may have influenced our results; and third, other research (70)
380 suggest that artifact associated with saccades disappears within ~300msecs, whereas the associations
381 between theta and look duration lasts much longer than this, up to ~6 seconds. For all this, we consider that
382 the possibility that our results may have been caused by infants' saccades is unlikely.

383 Second, while the study of theta and alpha activity can offer insights into infants' intrinsically guided
384 attention beyond its behavioural manifestations (26), attributing functional significances to particular
385 frequency bands can be risky, especially when the ways in which they are controlled and the extent to which
386 they interact across attention-related brain networks, still remain largely unknown (71). Similarly, the fact
387 that certain frequency bands seem to covary with attention does not exclude the possibility of their
388 correlation with other processes as well.

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

392 Fourth, we used a different set of toys at the two ages (see Figure S5). Consequently, this introduced a new
393 source of variation (i.e., toy characteristics) that might have contributed to any of the observed differences
394 (20). However, we chose to present developmentally appropriate stimuli at the two ages to ensure that the
395 cognitive demands were similar at the two ages. Thus, while still possible, it is unlikely that the
396 developmental differences observed in the current study might be due to differences in the amount of
397 information processing on the part of the infant and/ or the “interestingness” of the toys.

398 Fifth, it is worth mentioning that, while infants gather information about their world through aggressive
399 visual foraging, looking and attending are not synonymous. Previous research has shown that covert shifts
400 of attention can occur without overt shifts of gaze by 4-6 months of age (72,73). However, the current study
401 has focused exclusively on overt attention.

402 Finally, our laboratory setting was a novel environment for our participants and might have elicited
403 behaviours that are different from the ones that develop at home. However, it still represents a significant
404 advancement relative to other screen-based or highly controlled experimental tasks.

405

406

407 **4. Materials and Methods**

408 **4.1 Experimental Design**

409 Looking behaviour, EEG and ECG data were collected from mothers and their infants at two age points: 5
410 and 10 months while playing alone. At 5 months, infants were seated either in a highchair or on a
411 researcher’s lap and a table was positioned in front so that toys on the table were within easy reach (see
412 Figure 1). To reduce infant’s stress, mothers were present in the room but moved to another smaller table
413 on the right side of the original table and given an identical set of toys which they played with in parallel.
414 A wooden divider was positioned between the two tables to prevent infants from seeing the objects with
415 which their mothers were playing. At 10 months, the same procedure was used but the divider was
416 positioned across the midline of the table and the adult participants were seated directly opposite the infants.
417 In both situations, mothers and infants had direct line of sight to one another but neither could see the
418 others’ toys on the table.

419 The same three age-appropriate toys were always used for each age group. These were small and relatively
420 engaging (see Figure S5). During the solo play interaction, one of the researchers sat behind the infant to
421 collect the toys that fell on the floor (either because the infants threw them or because they fell from their
422 hands) and brought them back on the table. Mothers were allowed to speak during the interaction but were
423 instructed not to name the toys they were playing with to prevent infants from the influence of any
424 exogenous parental' influence. In the Supplementary Materials, we present a set of analyses that preclude
425 the possibility of maternal influence on infants' behaviour and demonstrate that the impact of the mothers
426 on the infants' behaviour did not differ between age groups (SI 3). The average duration of the interactions
427 with usable EEG/ ECG data did not differ significantly between 5 and 10 months (interactions with EEG
428 (average duration at 5m = 292.4s, and 10m = 250.1s, $t(46) = -1.85$, $p = 0.07$); interactions with ECG data
429 (average duration at 5m = 351.2s, and 10m = 317.9s, $t(40) = -1.1$, $p = 0.27$)).

430 The interactions were filmed using three Canon LEGRIA HF R806 camcorders recording at 50 fps. At 5
431 months, one camera was placed in front of the infant and another one was placed in front of the mother. At
432 10 months, two cameras faced the infant: one placed on the left of the divider, and one on the right. The
433 other camera faced the mother and was positioned just behind the right side of the divider. All cameras
434 were placed so that the infant's and the mother's gaze, as well as the three toys placed on the table, were
435 always visible.

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

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

440

441 **4.2 Participants**

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

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

456 Since the analyses are performed conducted relative to specific events (such as the frequency and duration
457 of looks to objects), and each participant averaged around 10 looks per minute at 5 months and
458 approximately 4 looks at 10 months (see Figure 1A and B), we believe that the relatively low N for this
459 study is balanced by the considerable amount of data points accessible.

460

461 **4.3 Data processing and Statistical Analysis**

462 **4.3.1 Synchronisation between behavioural and EEG/ ECG data**

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

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

471

472 **4.3.2 Video coding**

473 The looking behaviour of the infants was manually coded offline on a frame-by-frame basis, at 50fps. The
474 start of a look was considered to be the first frame in which the gaze was static after moving to a new
475 location. The following categories of gaze were coded: looks to objects (where the infant was focussing on
476 one of the three objects), looks to partner (where the infant was looking at their partner), inattentive (where

477 the infant was not looking to any of the objects nor the partner) and uncodable. Uncodable moments
478 included periods where: 1) the infant's gaze was blocked or obscured by an object and/or their own hands,
479 2) their eyes were outside the camera frame, and/ or 3) a researcher was within the camera frame and the
480 infant turned to them and/or realised a researcher was around. Video coding was completed by three coders,
481 who were trained by the first author. To assess inter-rater reliability, ~15% of our data (10 datasets) were
482 double-coded by a second coder and Cohen's kappa was calculated. There was moderate agreement ($\kappa =$
483 0.581, $\text{std} = 0.183$) (74). Due to the unusual nature of our behavioural coding (with gaze coded across many
484 20ms bins) the interrater reliability is heavily contingent on how we calculate it. We chose to report the
485 most stringent calculator of inter-rater reliability.

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

489

490 **4.3.3 EEG artefact rejection and pre-processing**

491 EEG data was pre-processed and cleaned from oculomotor and other contaminatory artefacts using a fully
492 automatic artefact rejection procedure specially designed for naturalistic infant EEG data by Mariott
493 Haresign (66), building on previous related work (59, 60). Briefly, this involved the following steps: 1) data
494 were high-pass filtered at 1Hz, 2) line noise at 50Hz was eliminated using the EEGLAB function
495 `clean_line.m`, 3) data were low-pass filtered at 20Hz, 4) the data were referenced to a robust average
496 reference 5) noisy channels were rejected using the EEGLAB function `pop_rejchan.m`, 6) the channels
497 identified in the previous stage were then interpolated back, using the EEGLAB function `eeg_interp.m`, 7)
498 continuous data were automatically rejected (NaN-ed) in a sliding 1s epoch based on a percentage of bad
499 channels (set here at 70% of channels) that exceed 5 standard deviations of the mean channel EEG power,
500 and 8) Independent Component Analyses (ICA) were computed on the continuous data using the EEGLAB
501 function `runica.m`. Only participants with fewer than 30% of channels interpolated at 5 months and 25% at
502 10 months (step 6) made it to the final step (step 8, ICA) and final analyses. To compare the quality of the
503 EEG data at 5 and 10 months we performed a series of analyses on percentage of channels interpolated,
504 total segments removed (i.e., zeroed out) and total ICA components rejected (see Table S5-6 and Figure
505 S4).

506 The higher density array was down sampled so that all the EEG analyses described below used only shared
507 channels between the 32- and the 64- channel EEG systems. We selected three main clusters of electrodes

508 for our analyses: Frontal channels ('Fp1', 'Fp2', 'AF3', 'AF4', 'Fz'), Central channels ('FC1', 'FC2', 'C3', 'Cz',
509 'C4', 'CP1', 'CP2'), and Occipital channels ('PO3', 'PO4', 'O1', 'Oz', 'O1') (see Figure S6).

510

511 **4.3.4 Heart Rate – Beats per minute**

512 R-peak identification was performed using the in-built Matlab function 'findpeaks'. The minimum peak
513 height was manually defined as a simple amplitude threshold after visualising the raw data, minimum peak
514 distance, instead, was set at 230msec. Following this, automatic artefact rejection was performed by
515 excluding those beats showing an inter-beat interval (IBI) <330 or >750msec (i.e., allowing a minimum of
516 ~80BPM and maximum of ~180BPM), and by excluding those samples showing a rate of change of IBI
517 greater than 90msec between samples. Next, we converted IBI values into beats-per-minute (BPM) values
518 and removed outliers in the BPM time series. These were defined as values falling 2.5 interquartile ranges
519 above the upper quartile and below the lower quartile. Outliers were then interpolated using the Matlab in-
520 built function 'fillmissing' with the 'spline' method. Finally, we epoched the data into one-second epochs
521 by averaging all the BPM values comprised in each one-second epoch.

522

523 **4.3.5 Analysis 1. Developmental changes in attention**

524 4.3.5.1 Overt attention and inattention extraction

525 The aim of our analysis was to identify moments where the infants paid attention to (i.e. looked at) any of
526 the play objects as opposed to inattentive moments. Accordingly, all looks to object and inattentive looks
527 were selected and categorised as attentional and inattentive episodes, respectively. Looks to partner were
528 excluded from all analyses.

529 Following this, we extracted the first and last frame of all looks of interest (i.e., looks to objects and
530 inattentive looks). To calculate attention and inattention durations, we subtracted the last frame from the
531 first frame of each look of interest and divided it by the sampling rate (i.e., 50) to convert “duration in
532 frames” to “duration in seconds”. Attentive and inattentive reorientations (count) were calculated by
533 counting the occurrence of each of these two attentional states and dividing it by the length of the session.

534 4.3.5.2 ACF of the attention duration

535 Here, we extracted the duration (in seconds) of all the attentional episodes that happened within the play
536 session and zero-ed out all the non-attentional episodes. This allowed us to create a time series string with
537 the durations of each consecutive attention episode. We then calculate the autocorrelation of that signal and
538 repeated these steps for each behavioural dataset. Finally, we averaged the ACF values within each age
539 group to obtain the ACF values reported in Figure 3A.

540

541 **4.3.6 Analysis 2. Auto- and cross-correlation analyses between infant autonomic arousal and** 542 **attention**

543 4.3.6.1 Attention, one-second epochs

544 To calculate the “attention” variable, we epoched the gaze data into one-second epochs and calculated the
545 duration (in msec) of each attention episode relative to the one-second epochs. Most epochs were coded as
546 either 1000 (epochs where the child was attending throughout) or 0 (epochs where the child was inattentive
547 throughout). If an attention episode started halfway through a one-second epoch, then it was coded as 500.
548 The other non-attention episodes (i.e., inattentive looks, looks to partner) were zeroed. See Figure 1 for a
549 schematic view of the procedure we followed to parse the looking behaviour into one-second epochs.

550 4.3.6.2 Cross-correlation analyses

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

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

563 To assess significance of the cross-correlations, we first used bootstrapping to generate confidence
564 intervals, using an approach that controls for the level of autocorrelation in the data. To do this, the time
565 series data of one participant (e.g., attention of participant 1) was randomly paired with the time series data
566 of another participant (e.g., autonomic arousal of participant 13). If the time series datasets had different
567 lengths (due to different participants having different session lengths), we appended zeros to the end of the
568 shorter vector to match the length of the longest vector. We then computed the cross-correlation between
569 all the unique combinations that could be found within each sample (e.g., in a sample $N=23$, the maximum
570 of unique combinations is 529). Next, the cross-correlation results in the permuted data were randomly
571 grouped in samples that were the same size as the original data (e.g., $N= 23$) and averaged together. This
572 procedure was repeated 1000 times and used to generate the 95% confidence intervals. In this way, we
573 identified whether the observed cross-correlation values at each time interval differed significantly from
574 chance.

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

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

587

588 **4.3.7 Analysis 3. Calculation of neural power changes around an attention episode**

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

592 To conduct these analyses, each infant attention episode onset (i.e., gaze shift to a different toy) was
593 identified in the EEG signal by calculating the time from the start of the interaction (first LED) to the onset
594 of the look (in the behavioural data) and adding it to the first EEG trigger. For each look, we extracted theta
595 (3-6Hz) power for two time-windows immediately prior to the onset of each look (-2000 to -1000msec and
596 -1000 to 0 msec pre-look onset) and three time-windows immediately after the onset of each look (0 to
597 1000ms, 1000ms to 2000msec and 2000 to 3000msec post look onset) (see Figure 1). To calculate the EEG
598 power spectra, we use the ‘mtmfft’ method from the ft_freqanalysis function in FieldTrip, an open-source
599 Matlab toolbox (75); <http://fieldtriptoolbox.org>). Extreme power values that were 4 times greater than the
600 interquartile range were treated as outliers and excluded from further analyses (similar to 29). More detail
601 on the amount of data available (i.e., average duration of the session per participant and number and duration
602 of attentional episodes per minute) can be accessed in Table S1.

603 For each epoch, we only selected power within our cluster of central channels (similar to 60). Power at each
604 bin was expressed as relative power, defined as the total power at a specific frequency band (e.g. 3 to 6Hz
605 for theta) divided by the total power across all frequency bands (1 to 20Hz) during that epoch. After
606 extracting the relative power in the theta band, we calculated separate linear mixed effects models for each
607 of the five windows to examine the relationship between EEG power within that time window and attention
608 duration.

609

610 **4.3.8 Analysis 4. Calculation of neural power changes within an attention episode**

611 In addition, we also wanted to look at power changes within attention episodes. Infant attention episodes
612 and attention duration were calculated as explained above (section 4.3.5.1) and each infant look onset
613 towards an object was identified in the EEG signal as described in analysis 3 (section 4.3.7). For each look,
614 we extracted the first (0 to +1000msec, “start”) and third-to-fourth (3000 to 4000msec, “middle”) second
615 into the look, and the last second (-1000msec prior to look offset to look offset, “termination”) before look
616 termination (see Figure 1). Looks that did not make it to the full second segment were excluded from further
617 analysis. Similarly, only looks that were longer than 5 seconds were included to the “middle” group. This
618 was done to avoid an overlap between the activity from the “middle” and the “termination” groups.

619 Frequency analysis was conducted to assess the power spectral density for both theta (3-6Hz) and alpha (6-
620 9Hz) frequency rhythms for each of the three time-segments. These analyses were calculated for the three
621 prespecified clusters of channels: Frontal, Central and Occipital (see Figure S6). Again, power at each time
622 segment was expressed as relative power.

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

625

626 **4.3.9 Analysis 5. Auto- and cross-correlations analyses between infant theta activity and attention**

627 4.3.9.1 EEG relative power, one-second epochs

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

630 4.3.9.2 Cross-correlation analysis

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

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

639

640

641

642 **References**

- 643 1. Hendry A, Johnson MH, Holmboe K. Early Development of Visual Attention: Change, Stability, and
644 Longitudinal Associations. *Annu Rev Dev Psychol* 2019 [Internet]. 2019;1:251–75. Available from:
645 <https://doi.org/10.1146/annurev-devpsych-121318->
- 646 2. Rueda MR, Moyano S, Rico-Picó J. Attention: The grounds of self-regulated cognition. *Wiley Interdiscip*
647 *Rev Cogn Sci*. 2021 Jan 1;
- 648 3. Richards JE. The development of attention to simple and complex visual stimuli in infants: Behavioral and
649 psychophysiological measures. Vol. 30, *Developmental Review*. 2010. p. 203–19.
- 650 4. Colombo J, Mitchell DW. Infant visual habituation. *Neurobiol Learn Mem*. 2009 Sep;92(2):225–34.
- 651 5. Wass S V. Applying cognitive training to target executive functions during early development. *Child*
652 *Neuropsychology*. 2015 Mar 4;21(2):150–66.
- 653 6. Colombo J. The development of visual attention in infancy. *Annu Rev Psychol* [Internet]. 2001;52(1):337–
654 67. Available from: www.annualreviews.org
- 655 7. Johnson MH. The development of visual attention: A cognitive neuroscience perspective. *Brain*
656 *Development and Cognition*. 2002;134–50.
- 657 8. Wolff PH. The development of attention in young infants. 1965;
- 658 9. Deoni SCL, Mercure E, Blasi A, Gasston D, Thomson A, Johnson M, et al. Mapping infant brain
659 myelination with magnetic resonance imaging. *Journal of Neuroscience*. 2011 Jan 12;31(2):784–91.
- 660 10. Johnson MH, Haan M. *Developmental Cognitive Neuroscience*. 2015.
- 661 11. Richards JE. The statistical analysis of heart rate: a review emphasizing infancy data. *Psychophysiology*.
662 1980;17(2):153–66.
- 663 12. Richards JE. *Infant Attention, Arousal and the Brain*. Oxford University Press; 2011.
- 664 13. Wass S V. The origins of effortful control: How early development within arousal/regulatory systems
665 influences attentional and affective control. *Developmental Review*. 2021 Sep 1;61.
- 666 14. Feldman R, Mayes LC. The cyclic organization of attention during habituation is related to infants'
667 information processing. *Infant Behav Dev*. 1999;37–49.
- 668 15. Saez de Urabain IR, Nuthmann A, Johnson MH, Smith TJ. Disentangling the mechanisms underlying
669 infant fixation durations in scene perception: A computational account. *Vision Res*. 2017 May 1;134:43–
670 59.
- 671 16. Nuthmann A, Smith TJ, Engbert R, Henderson JM. CRISP: A Computational Model of Fixation Durations
672 in Scene Viewing. *Psychol Rev*. 2010 Apr;117(2):382–405.
- 673 17. Robertson SS. Oscillation and Complexity in Early Infant Behavior. Vol. 64. 1993.
- 674 18. Wass S V., Smith TJ. Individual differences in infant oculomotor behavior during the viewing of complex
675 naturalistic scenes. *Infancy*. 2014;19(4):352–84.
- 676 19. Mcauley JH, Rothwell JC, Marsden CD. Human anticipatory eye movements may reflect rhythmic central
677 nervous activity. *Neuroscience*. 1999;94(2):339–50.
- 678 20. Oakes LM, Kannass KN, Shaddy DJ. Developmental Changes in Endogenous Control of Attention: The
679 Role of Target Familiarity on Infants' Distraction Latency. Vol. 73, *Child Development*. 2002.
- 680 21. Colombo J, Cheatham CL. The emergence and basis of endogenous attention in infancy and early
681 childhood. 2006.
- 682 22. Anderson DR, Choi HP, Puzles E. Attentional Inertia Reduces Distractibility during Young Children's TV
683 Viewing. Vol. 58, *Lorch Source: Child Development*. 1987.
- 684 23. Lansink JM, Richards JE. Heart rate and behavioral measures of attention in six-, nine-, and twelve-month-
685 old infants during object exploration. *Child Dev*. 1997;68(4):610–20.
- 686 24. Richards JE. Development of multimodal attention in young infants: Modification of the startle reflex by
687 attention. *Psychophysiology*. 2000 Jan;37(1):65–75.
- 688 25. Courage ML, Reynolds GD, Richards JE. Infants' attention to patterned stimuli: Developmental change
689 from 3 to 12 months of age. *Child Dev*. 2006 May;77(3):680–95.
- 690 26. Begus K, Bonawitz E. The rhythm of learning: Theta oscillations as an index of active learning in infancy.
691 Vol. 45, *Developmental Cognitive Neuroscience*. Elsevier Ltd; 2020.
- 692 27. Jones EJM, Goodwin A, Orekhova E, Charman T, Dawson G, Webb SJ, et al. Infant EEG theta modulation
693 predicts childhood intelligence. *Sci Rep*. 2020 Dec 1;10(1).
- 694 28. Orekhova E V., Stroganova TA, Posikera IN, Elam M. EEG theta rhythm in infants and preschool children.
695 *Clinical Neurophysiology*. 2006 May;117(5):1047–62.

- 696 29. Xie W, Mallin BM, Richards JE. Development of infant sustained attention and its relation to EEG
697 oscillations: an EEG and cortical source analysis study. *Dev Sci*. 2018 May 1;21(3).
- 698 30. Meyer M, Endedijk HM, van Ede F, Hunnius S. Theta oscillations in 4-year-olds are sensitive to task
699 engagement and task demands. *Sci Rep*. 2019 Dec 1;9(1).
- 700 31. Braithwaite EK, Jones EJH, Johnson MH, Holmboe K. Dynamic modulation of frontal theta power predicts
701 cognitive ability in infancy. *Dev Cogn Neurosci*. 2020 Oct 1;45.
- 702 32. Libertus ME, Pruitt LB, Woldorff MG, Brannon EM. Induced alpha-band oscillations reflect ratio-
703 dependent number discrimination in the infant brain. *J Cogn Neurosci*. 2009 Dec;21(12):2398–406.
- 704 33. Xie W, Mallin BM, Richards JE. Development of brain functional connectivity and its relation to infant
705 sustained attention in the first year of life. *Dev Sci*. 2019 Jan 1;22(1).
- 706 34. Wass S V., Goupil L. Studying the Developing Brain in Real-World Contexts: Moving From Castles in the
707 Air to Castles on the Ground. Vol. 16, *Frontiers in Integrative Neuroscience*. Frontiers Media S.A.; 2022.
- 708 35. Wass S, Jones EJH. Editorial perspective: Leaving the baby in the bathwater in neurodevelopmental
709 research. *Journal of Child Psychology and Psychiatry and Allied Disciplines*. John Wiley and Sons Inc;
710 2023.
- 711 36. Wass S V. Comparing methods for measuring peak look duration: Are individual differences observed on
712 screen-based tasks also found in more ecologically valid contexts? *Infant Behav Dev*. 2014;37(3):315–25.
- 713 37. Anderson EM, Seemiller ES, Smith LB. Scene saliencies in egocentric vision and their creation by parents
714 and infants. *Cognition*. 2022 Dec 1;229.
- 715 38. Meyer M, van Schaik JE, Poli F, Hunnius S. How infant-directed actions enhance infants' attention,
716 learning, and exploration: Evidence from EEG and computational modeling. *Dev Sci*. 2023 Jan 1;26(1).
- 717 39. Stets M, Stahl D, Reid VM. A meta-analysis investigating factors underlying attrition rates in infant ERP
718 studies. *Dev Neuropsychol*. 2012 Apr 1;37(3):226–52.
- 719 40. Mendez AH, Yu C, Smith LB. Controlling the input: How one-year-old infants sustain visual attention.
720 *Dev Sci*. 2023 Mar 1;
- 721 41. Jones EJH, Venema K, Lowy R, Earl RK, Webb SJ. Developmental changes in infant brain activity during
722 naturalistic social experiences. *Dev Psychobiol*. 2015 Nov 1;57(7):842–53.
- 723 42. Grossmann T, Johnson MH, Lloyd-Fox S, Blasi A, Deligianni F, Elwell C, et al. Early cortical
724 specialization for face-to-face communication in human infants. *Proceedings of the Royal Society B:*
725 *Biological Sciences*. 2008 Dec 22;275(1653):2803–11.
- 726 43. Aslin RN. What's in a look? *Dev Sci*. 2007;48–53.
- 727 44. Csibra G, Henrik M, Mascaro O, Tatone D, Lengyel M. Statistical Treatment of Looking-Time Data. *Dev*
728 *Psychol*. 2016;
- 729 45. Richards JE, Anderson DR. *Attentional Inertia in Children's Extended Looking at Television*. Elsevier.
730 2004;163–213.
- 731 46. Wass S V., Clackson K, Georgieva SD, Brightman L, Nutbrown R, Leong V. Infants' visual sustained
732 attention is higher during joint play than solo play: is this due to increased endogenous attention control or
733 exogenous stimulus capture? *Dev Sci*. 2018 Nov 1;21(6).
- 734 47. Robertson SS. Empty-headed dynamical model of infant visual foraging. *Dev Psychobiol*. 2013;
- 735 48. Robertson SS, Wamura SE, Wilbourn MP. Attentional dynamics of infant visual foraging. *Proc Natl*
736 *Acad Sci U S A*. 2012 Jul 10;109(28):11460–4.
- 737 49. de Barbaro K, Clackson K, Wass S V. Infant attention is dynamically modulated with changing arousal
738 levels. *Child Dev*. 2017 Mar 1;88(2):629–39.
- 739 50. Wass S, Phillips E, Smith C, Fatimehin EOOB, Goupil L. Vocal communication is tied to interpersonal
740 arousal coupling in caregiver-infant dyads. *Elife*. 2022 Dec 1;11.
- 741 51. Monroy C, Domínguez-Martínez E, Taylor B, Marin OP, Parise E, Reid VM. Understanding the causes and
742 consequences of variability in infant ERP editing practices. *Dev Psychobiol*. 2021 Dec 1;63(8).
- 743 52. De Haan M. Introduction to infant EEG and event-related potentials. 2002.
- 744 53. Phillips E, Goupil L, Marriot Haresign I, Whitehorn M, Leong V, Wass S V. Proactive or reactive? Neural
745 oscillatory insight into the leader-follower dynamics of early infant-caregiver interaction. *Proceedings of*
746 *the National Academy of Sciences*. 2023;120(15).
- 747 54. Clifford P, Richardson S, Hemon D. Assessing the Significance of the Correlation between Two Spatial
748 Processes [Internet]. Vol. 45. 1989. Available from: <https://www.jstor.org/stable/2532039>
- 749 55. Clifford SM, Hudry K, Elsabbagh M, Charman T, Johnson MH. Temperament in the first 2 years of life in
750 infants at high-risk for autism spectrum disorders. *J Autism Dev Disord*. 2013 Mar;43(3):673–86.

- 751 56. Johnson MH. Subcortical face processing. *Nat Rev Neurosci* [Internet]. 2005;6(10):766–74. Available
752 from: <https://doi.org/10.1038/nrn1766>
- 753 57. Shephard E, Zuccolo PF, Godoy PBG, Salomone E, Ferrante C, Sorgato P, et al. Systematic Review and
754 Meta-analysis: The Science of Early-Life Precursors and Interventions for Attention-Deficit/ Hyperactivity
755 Disorder. *J Am Acad Child Adolesc Psychiatry* [Internet]. 2021; Available from: www.jaacap.org
- 756 58. Johnson MH, Charman T, Pickles A, Jones EJH. Annual Research Review: Anterior Modifiers in the
757 Emergence of Neurodevelopmental Disorders (AMEND)—a systems neuroscience approach to common
758 developmental disorders. Vol. 62, *Journal of Child Psychology and Psychiatry and Allied Disciplines*.
759 Blackwell Publishing Ltd; 2021. p. 610–30.
- 760 59. Méndez AH, Yu C, Smith LB. One-year old infants control bottom-up saliencies to purposely sustain
761 attention. 2021.
- 762 60. Pfeiffer T, Keitel C, Kluger DS, Keitel A, Russmann A, Thut G, et al. Coupling of pupil-and neuronal
763 population dynamics reveals diverse influences of arousal on cortical processing. *Elife*. 2022 Feb 1;11.
- 764 61. Gardner JM, Karmel BZ. Development of Arousal-Modulated Visual Preferences in Early Infancy. Vol. 31,
765 *Developmental Psychology*. 1995.
- 766 62. Begus K, Gliga T, Southgate V. Infants’ preferences for native speakers are associated with an expectation
767 of information. *Proceedings of the National Academy of Sciences*. 2016;113(44):12397–402.
- 768 63. Wass S V., Noreika V, Georgieva S, Clackson K, Brightman L, Nutbrown R, et al. Parental neural
769 responsivity to infants’ visual attention: How mature brains influence immature brains during social
770 interaction. *PLoS Biol*. 2018 Dec 1;16(12).
- 771 64. Cohen LB. Attention-Getting and Attention-Holding Processes of Infant Visual Preferences. Vol. 43. 1972.
- 772 65. Tardiff N, Medaglia JD, Bassett DS, Thompson-Schill SL. The modulation of brain network integration
773 and arousal during exploration. *Neuroimage*. 2021 Oct 15;240.
- 774 66. Haresign M, Phillips E, Whitehorn M, Noreika V, Jones EJH, Leong V, et al. Automatic classification of
775 ICA components from infant EEG using MARA. 2021; Available from:
776 <https://doi.org/10.1101/2021.01.22.427809>
- 777 67. Kayhan E, Matthes D, Marriott Haresign I, Bánki A, Michel C, Langeloh M, et al. DEEP: A dual EEG
778 pipeline for developmental hyperscanning studies. *Dev Cogn Neurosci*. 2022 Apr 1;54.
- 779 68. Georgieva S, Lester S, Noreika V, Yilmaz MN, Wass S, Leong V. Toward the Understanding of
780 Topographical and Spectral Signatures of Infant Movement Artifacts in Naturalistic EEG. *Front Neurosci*.
781 2020 Apr 28;14.
- 782 69. Noreika V, Georgieva S, Wass S, Leong V. 14 challenges and their solutions for conducting social
783 neuroscience and longitudinal EEG research with infants. Vol. 58, *Infant Behavior and Development*.
784 Elsevier Ltd; 2020.
- 785 70. Marriott Haresign I, Phillips EAM, Whitehorn M, Lamagna F, Eliano M, Goupil L, et al. Gaze onsets
786 during naturalistic infant-caregiver interaction associate with ‘sender’ but not ‘receiver’ neural responses,
787 and do not lead to changes in inter-brain synchrony. *Sci Rep*. 2023 Dec 1;13(1).
- 788 71. Clayton MS, Yeung N, Cohen Kadosh R. The roles of cortical oscillations in sustained attention. Vol. 19,
789 *Trends in Cognitive Sciences*. Elsevier Ltd; 2015. p. 188–95.
- 790 72. Hood BM. Inhibition of return produced by covert shifts of visual attention in 6-month-old infants. *Infant*
791 *Behav Dev* [Internet]. 1993;16(2):245–54. Available from:
792 <https://www.sciencedirect.com/science/article/pii/0163638393800209>
- 793 73. Johnson MH, Posner MI, Rothbart MK. Facilitation of Saccades toward a Covertly Attended Location in
794 Early Infancy. Vol. 5, *Science*. 1994.
- 795 74. Landis JR, Koch GG. An Application of Hierarchical Kappa-type Statistics in the Assessment of Majority
796 Agreement among Multiple Observers [Internet]. Vol. 33. 1977. Available from:
797 <https://www.jstor.org/stable/2529786>
- 798 75. Maris E, Oostenveld R. Nonparametric statistical testing of EEG- and MEG-data. *J Neurosci Methods*.
799 2007 Aug 15;164(1):177–90.

800

801

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816 of the infants tested. Specific informed consent was also obtained from the caregivers of the infants featured
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818

819 **Author contributions:**

820 Conceptualization: SVW, EJHJ, MPA.

821 Data curation: IMH, MW, MPA.

822 Formal analysis: MPA.

823 Funding acquisition: SVW.

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

825 Methodology: IMH, EAMP, SVW, EJHJ, MPA.

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

827 Supervision: SVW, EJHJ.

828 Visualisation: MPA.

829 Writing – original draft: MPA.

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

831

832 **Competing interests:**

833 Authors declare that they have no competing interests.

834

835 **Data and materials availability:**

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

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846 **Figures and Tables**

847
 848 **Figure 1. Experimental set up and schematic illustration of the procedure followed for analysis 2 to**
 849 **5.** Top figure shows the experimental set up for solo play. Below, on the left, is shown the procedure
 850 followed to parse the looking behaviour and create the variable “attention”, and further cross-correlation
 851 analyses (analysis 2 and 5). On the right, instead, is shown the steps followed to identify attentional episodes
 852 in the EEG signal and further EEG analyses (analysis 3 and 4).

853
 854 **Figure 2. Descriptive analyses on infant attentional behaviour during the solo play interaction. (A)**
 855 **Average number of attentive and inattentive looks per minute at 5 months (left) and 10 months (right), (B)**
 856 **Average number of attentive and inattentive looks minute by minute. Asterisks show the significance values**
 857 **of comparisons examining how average number of looks per minute of the interaction differed as a function**
 858 **of age. (C) Average duration spent in one of the two possible attentional states: attentive and inattentive,**
 859 **and (D) minute by minute. Again, asterisks show the significance values of comparisons examining**
 860 **differences as a function of age. (E) Percentage of time infants spent in attentive vs. inattentive states,**
 861 **during the whole interaction. (F) Histogram showing the distribution of the proportion of all the looks that**
 862 **lasted less than or equal to 5 seconds (right) and more than 5 seconds (left) at 5 months (yellow) and 10**
 863 **months (blue). Continuous black line indicates the mode of each distribution. Significance is indicated with**
 864 **asterisks where * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$. Error bars represent SEMs.**

865
 866 **Figure 3. ACF and survival probability analyses of the looking behaviour. (A) Autocorrelation of the**
 867 **time series looking behaviour at 5 months (in yellow) and 10 months (in blue). (B) Survival analysis.**
 868 **Survival probability function for looking behaviour toward object toys. The survival function is the**
 869 **probability that a look will survive a given time. Yellow line shows data from 5-months-old infants with**
 870 **confidence bounds (dotted yellow line) and blue line shows data form 10-months-old infants with**
 871 **confidence bounds (dotted blue line). (C) Derivative of the Survival Probability at 5 months (yellow) and**
 872 **10 months (blue).**

873
 874 **Figure 4. Relationship between infant autonomic arousal and attention.** Autocorrelation results for
 875 **infant autonomic arousal at 5 months (A) and 10 months (C). Significant clusters are indicated by red dots.**
 876 **Cross correlation between infant autonomic arousal and attention at 5 months (B) and at 10 months (D).**
 877 **Infant autonomic arousal forward-predicting infant attention on the negative lags, infant attention forward-**
 878 **predicting infant autonomic arousal on the positive lags. Black lines show the cross-correlation values,**
 879 **shaded grey areas indicate the SEM. Shaded yellow areas show confidence intervals from the permuted**

880 data. Significant time lags identified by the cluster-based permutation analyses are shown by a thick red
881 line.

882

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

891

892 **Figure 6. Calculation of theta power changes within an attention episode.** Bar plots for the average
893 relative theta power throughout a look, at both time points (5 and 10 months) and at different brain networks
894 (central, occipital, and frontal). Asterisks (*) indicate $p < 0.05$. Error bars represent SEMs.

895

896 **Figure 7. Relationship between infant relative theta activity, infant attention, and infant autonomic**
897 **activity.** Autocorrelation for infant theta activity at 5 months (A) and at 10 months (D). Significant clusters
898 are indicated by red dots. Cross-correlation results between infant theta activity and infant attention at 5
899 months (B) and at 10 months (E). Infant theta activity forward-predicting infant attention on the negative
900 lags, infant attention forward-predicting infant theta activity on the positive lags. Cross-correlation results
901 between infant autonomic activity (indexed by heart rate activity) and relative theta power at 5 months (C)
902 and at 10 months (F). Infant autonomic activity forward-predicting infant theta activity on the negative
903 lags, infant theta activity forward-predicting infant autonomic activity on the positive lags. Black lines show
904 the Spearman correlation at each time lag, shaded grey areas indicate the SEM. Shaded yellow areas show
905 confidence intervals from the permuted data. Significant time lags identified by the cluster-based
906 permutation analyses are shown by a thick red line.



Object 2



Object 3

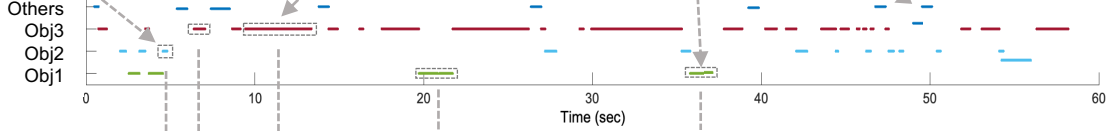


Object 1



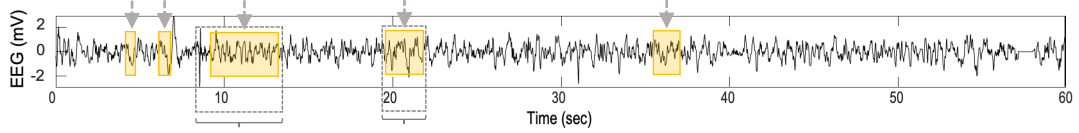
Others (inattentive)

Looking behaviour



Select attentional episodes (i.e., all looks to objects) in the EEG signal

EEG signal

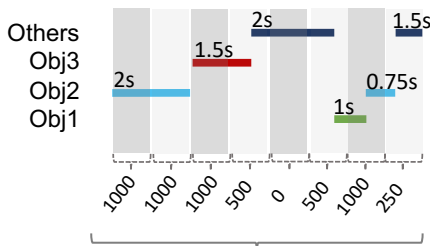


Cross-correlation analyses (analysis 2 and 5)

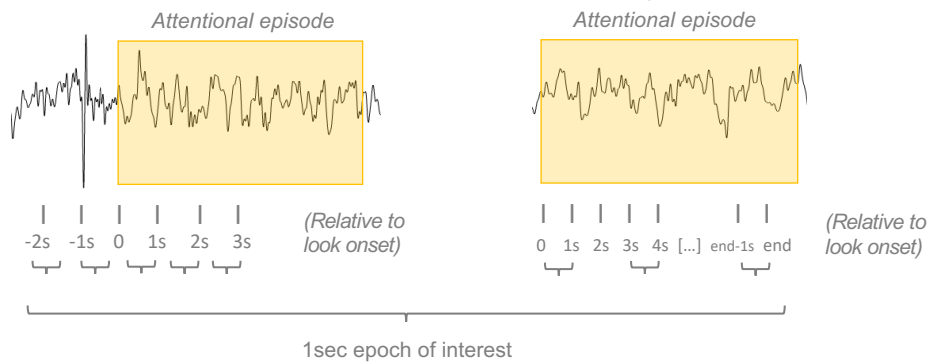
Changes around an attentional episode (analysis 3)

Changes within an attentional episode (analysis 4)

Epoch looking behaviour into one-sec epochs

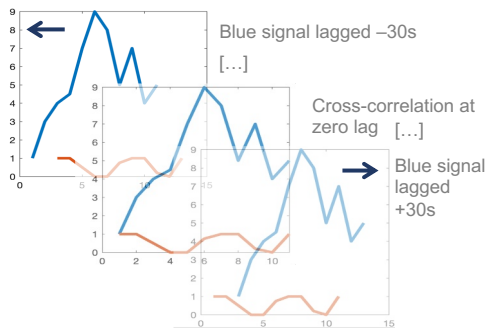


Create new attention variable by calculating the duration (msec) of each attentional episode relative to the one-second epochs

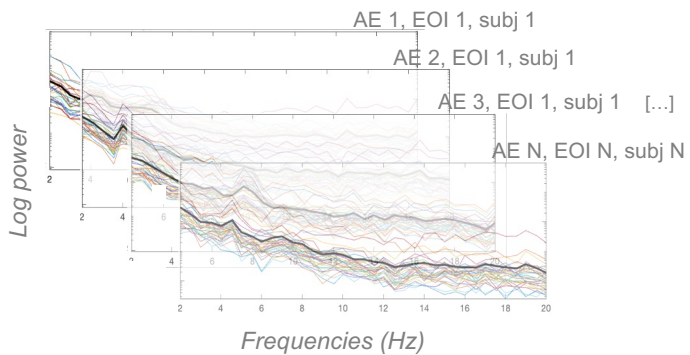


Parse heart rate data (analysis 2) & relative theta (analysis 5) into one-second epochs

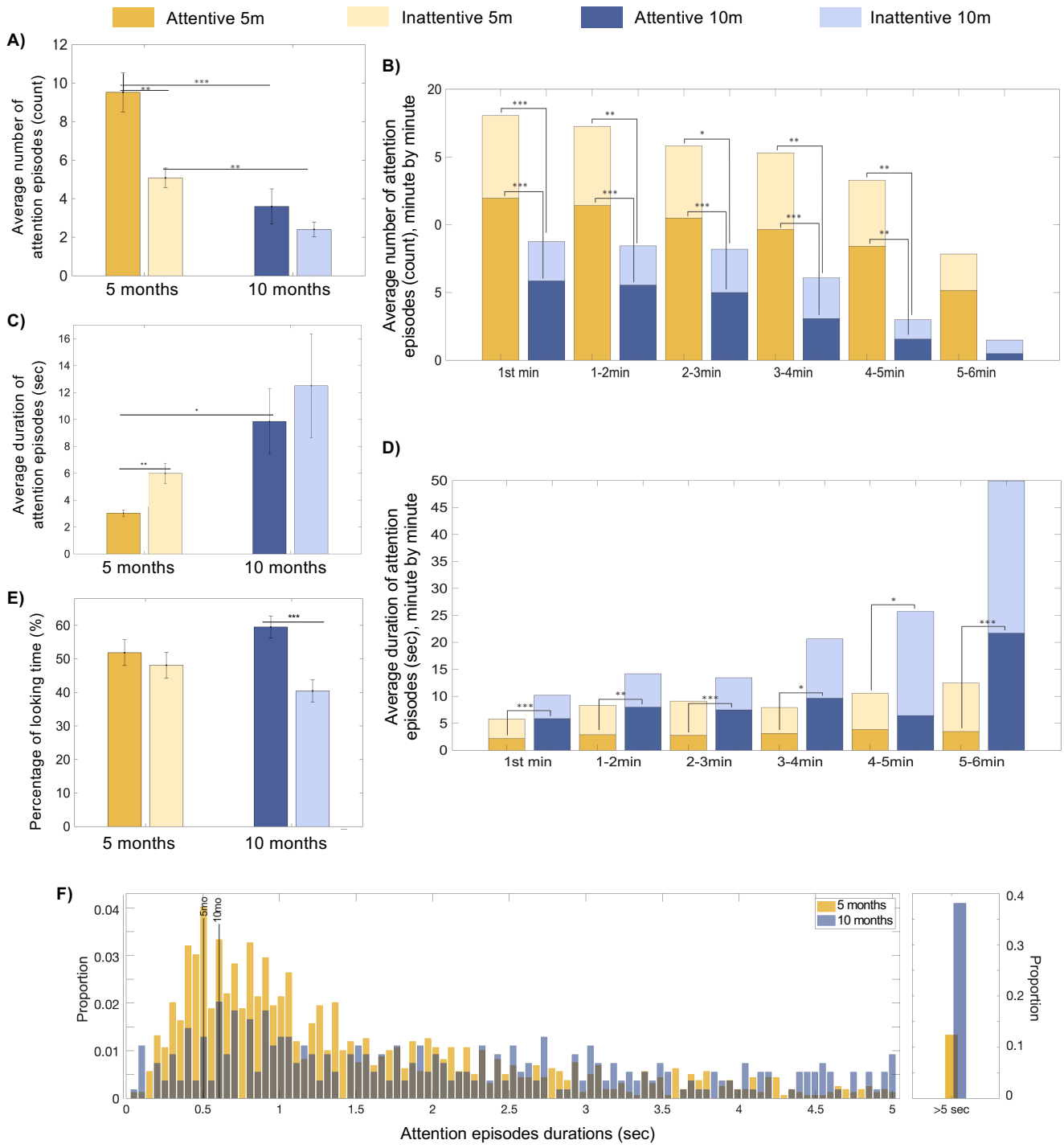
Cross-correlate the signals with one-second attention variable

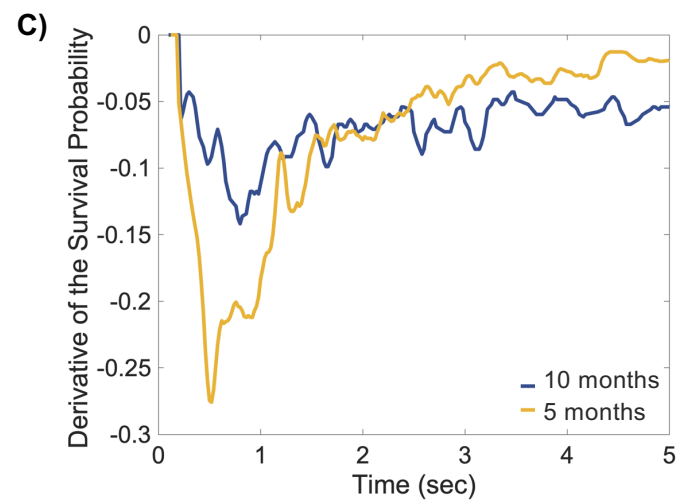
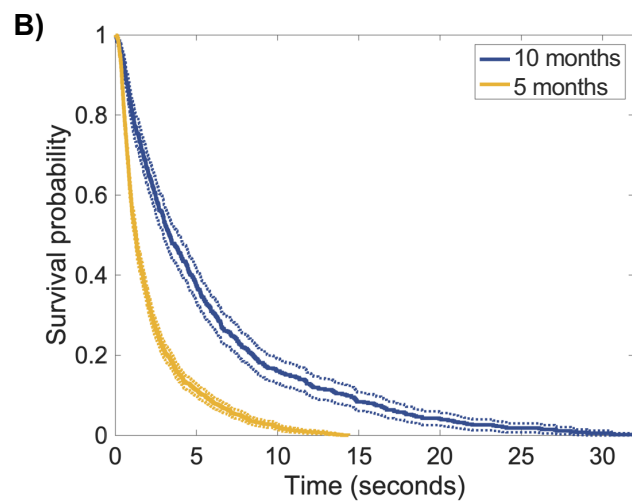
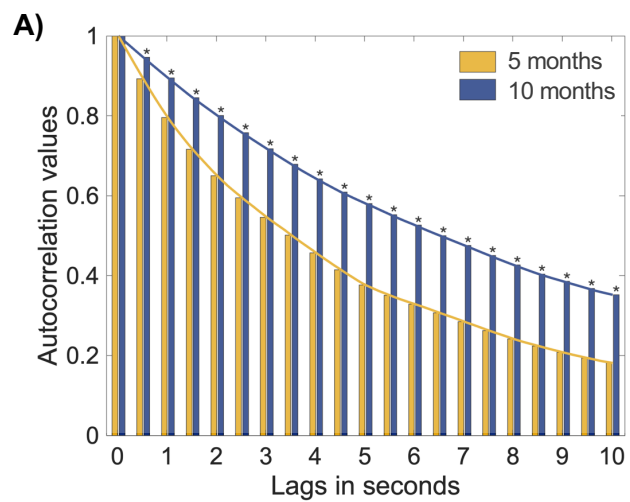


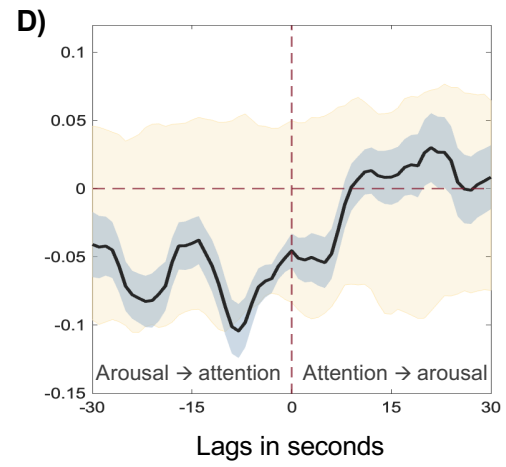
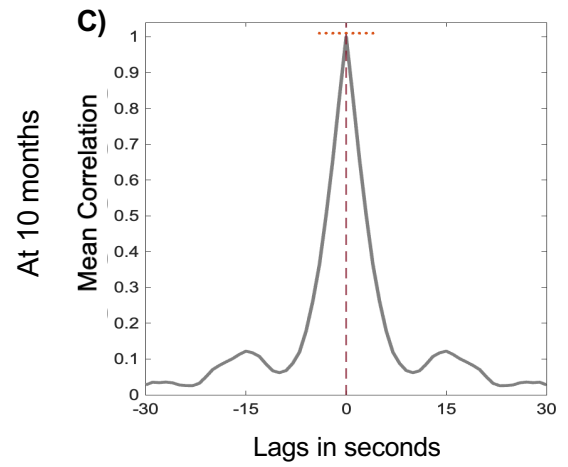
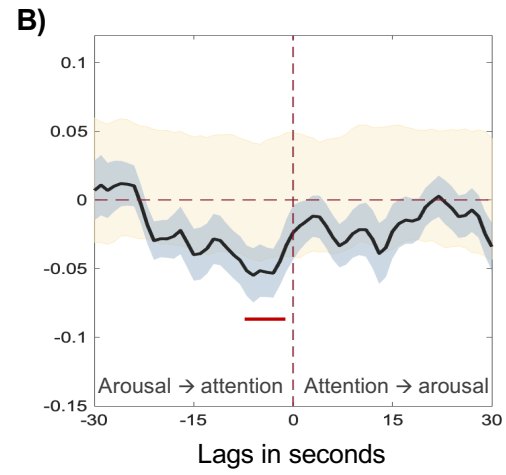
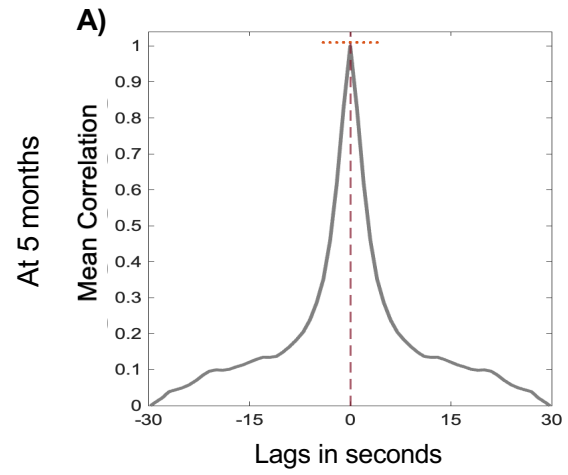
FFT of each 1s epochs of interest (EOI), for each attentional episode (AE), for each participant

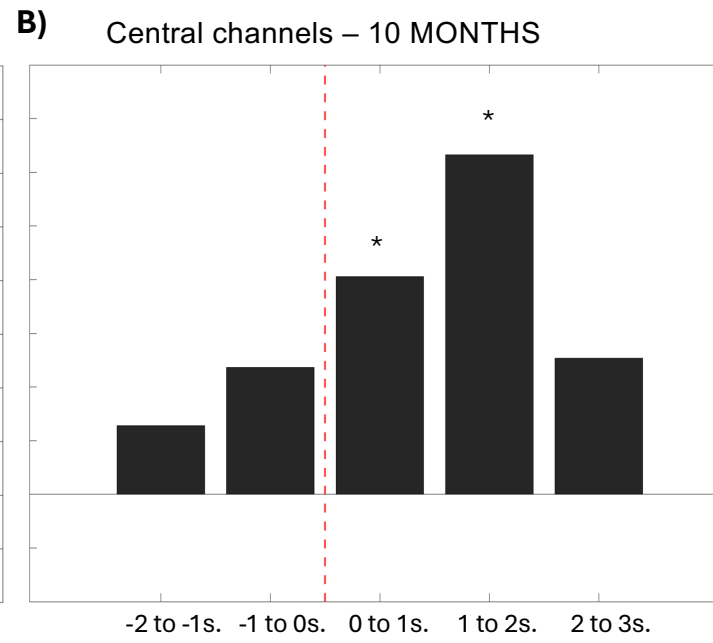
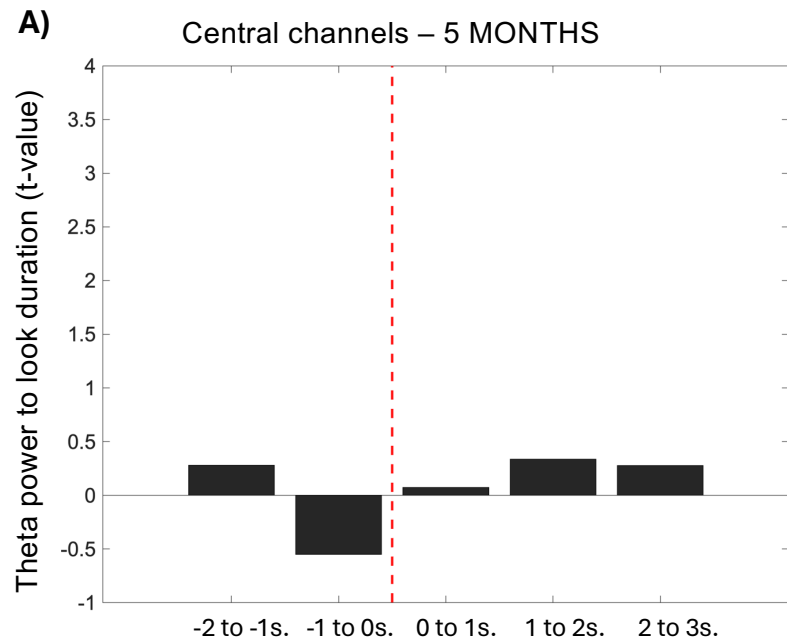


- Extract relative theta (3-6Hz) in central channels
- Separate LMEM (relative power & attentional episode duration) for each of the 5 time windows (EOIs)
- Extract relative theta (3-6Hz) and alpha (6-9Hz) in central, frontal and occipital channels
- Compare the power across the three different time segments









Time window of theta brain activity relative to look onset

