

This is an Open Access document downloaded from ORCA, Cardiff University's institutional repository: <https://orca.cardiff.ac.uk/id/eprint/107496/>

This is the author's version of a work that was submitted to / accepted for publication.

Citation for final published version:

Monroy, Claire, Meyer, Marlene, Schroer, Lisanne, Gerson, Sarah and Hunnius, Sabine 2019. The infant motor system predicts actions based on visual statistical learning. *NeuroImage* 185 , pp. 947-954. 10.1016/j.neuroimage.2017.12.016

Publishers page: <https://doi.org/10.1016/j.neuroimage.2017.12.016>

Please note:

Changes made as a result of publishing processes such as copy-editing, formatting and page numbers may not be reflected in this version. For the definitive version of this publication, please refer to the published source. You are advised to consult the publisher's version if you wish to cite this paper.

This version is being made available in accordance with publisher policies. See <http://orca.cf.ac.uk/policies.html> for usage policies. Copyright and moral rights for publications made available in ORCA are retained by the copyright holders.



1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23

The infant motor system predicts actions based on visual statistical learning

Claire D. Monroy^{a, b}, Marlene Meyer^{a, c}, Lisanne Schröer^a, Sarah A. Gerson^{a, d}, Sabine Hunnius^a

^aDonders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen
Montessorilaan 3, 6500HE Nijmegen, The Netherlands

^bDepartment of Otolaryngology—Head and Neck Surgery, Ohio State University Wexner
Medical Center, Columbus, Ohio, United States (present address)

^cDepartment of Psychology, University of Chicago, Chicago, Illinois, United States

^dSchool of Psychology, Cardiff University, 70 Park Place, Cardiff, CF10 3AT

This work was supported by an Initial Training Network (ITN) of the People Marie Curie
Actions—Seventh Research Programme (FP7) of the European Union (FP7ITN2011-289404).

Correspondence concerning this article should be addressed to Claire Monroy,
Department of Otolaryngology—Head and Neck Surgery, Ohio State University Wexner
Medical Center (present address); email: claire.monroy@osumc.edu

24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46

Abstract

Motor theories of action prediction propose that our motor system combines prior knowledge with incoming sensory input to predict other people’s actions. This prior knowledge can be acquired through observational experience, with statistical learning being one candidate mechanism. But can knowledge learned through observation alone transfer into predictions generated in the motor system? To examine this question, we first trained infants at home with videos of an unfamiliar action sequence featuring statistical regularities. At test, motor activity was measured using EEG and compared during perceptually identical time windows within the sequence that preceded actions which were either predictable (deterministic) or not predictable (random). Findings revealed increased motor activity preceding the deterministic but not the random actions, providing the first evidence that the infant motor system can use knowledge from statistical learning to predict upcoming actions. As such, these results support theories in which the motor system underlies action prediction.

Keywords: mu rhythm, EEG, infants, statistical learning, action prediction

47

48

49 **Visual statistical learning leads to predictive motor activation in the infant brain**

50 **1.0 Introduction**

51 According to motor theories of action observation, we predict the actions of other people
52 by means of our own motor system (Flanagan & Johansson, 2003; Kilner, 2011; Rizzolatti &
53 Craighero, 2004). When we perceive someone reach for a coffee mug at the breakfast table, we
54 already anticipate they will next bring the mug to their mouth. This anticipation takes place in
55 cortical pre-motor regions that are active both when performing and observing actions or their
56 effects (Kilner et al., 2004; Paulus, et al., 2013). Motor predictions of observed actions are
57 thought to underlie adaptive social interaction (Sebanz & Knoblich, 2009) and inferring the goals
58 and mental states of others (Becchio et al., 2012; Gallese & Goldman, 1998; Ondobaka et al.,
59 2015).

60 However, a challenge for the motor system is that perceptually similar actions can result
61 in very different outcomes. As a consequence, predictions cannot always be made on the basis of
62 the current ongoing action alone (Jacob & Jeannerod, 2005). Motor accounts of action prediction
63 have been criticized for failing to explain how action predictions can be generated for cases in
64 which the observed motor act itself does not contain enough information to make an accurate
65 prediction (Kilner et al., 2007). To solve this ambiguity problem, recent probabilistic accounts
66 have emerged that are largely based on principles of predictive coding (Friston, 2003, 2005). The
67 core idea in this approach is that the motor system combines prior knowledge with incoming
68 sensory input to determine the most likely action outcome (Kilner et al., 2007; Ondobaka et al.,
69 2015; Wolpert et al., 2003). If the person reaching for her coffee mug is standing next to the sink

70 with a sponge in hand, this will elicit a different motor prediction based on the observer's world
71 knowledge that her intention is most likely to wash the mug. Crucially, these accounts rest on the
72 assumption that this prior knowledge is 'fed' into the motor system and allows it to generate an
73 accurate prediction based on the current action context.

74 Predictive processing accounts provide a solution for the ambiguity problem, yet raise a
75 new challenge: how does new action knowledge—acquired from perceptual information—
76 become encoded in the motor system? Observational experiences are one important route to prior
77 knowledge, particularly during development (Hunnius & Bekkering, 2014). An infant may, for
78 instance, observe a parent reach for a peanut butter jar, which could be followed by many
79 possible outcomes. However, if the majority of the time their parent then removes the lid, scoops
80 peanut butter from the jar and reaches for a slice of bread, after multiple observations, the infant
81 can predict what is most likely to occur next when their parent first grasps the jar. In this
82 example, the statistical regularities between action steps provide information that the infant can
83 learn through observational experiences.

84 This ability is referred to as statistical learning (SL), a powerful mechanism that explains
85 how humans can acquire knowledge of the environment through observation (Perruchet &
86 Pacton, 2006). SL skills broadly refer to the ability to detect regularities in continuous sensory
87 input, and have been demonstrated empirically across sensory modalities and across the lifespan
88 (Conway & Christiansen, 2005; Fiser & Aslin, 2005; Kirkham et al., 2007; Saffran et al., 1996;
89 Slone & Johnson, 2015). A few recent studies have shown that both infants and adults are also
90 sensitive to the statistical regularities in continuous human actions (Ahlheim et al., 2014;
91 Baldwin et al., 2008; Monroy et al., 2017; Stahl et al., 2014). For instance, Baldwin and
92 colleagues (2008) investigated whether observers can parse action streams according to the

93 transitional probabilities between action steps. In their experiment, adult participants observed an
94 action stream made of 3-step action elements presented continuously, such as ‘pour-poke-clink’
95 or ‘peek-clink-rattle’. Participants were next shown ‘action’ sequences (the original 3-step
96 sequences, such as ‘pour-poke-clink’) and ‘part-action’ sequences (which spanned the
97 boundaries of two actions, such as ‘poke-clink-peek’). Adults accurately discriminated action
98 from part-action sequences, which could only be based on the transitional probabilities within
99 these 3-step sequences (Baldwin et al., 2008). Infants from seven months of age demonstrate
100 similar segmentation skills for familiar action sequences such as cleaning a kitchen (Baldwin,
101 Baird, & Saylor, 2001), and for novel, abstract movement sequences (Stahl et al., 2014).

102 Building upon these studies, which measured sensitivity to action structure post-
103 observation, Ahlheim and colleagues (2014) examined neural responses to statistical structure
104 during observation of action sequences. Results showed that increases in neural activation
105 corresponded to the probability of the occurrence of the next action step in the sequence. These
106 findings confirm that adults can exploit statistical structure while processing continuous human
107 action. They also suggest that observers use statistical learning skills to inform their predictions
108 of upcoming action steps.

109 The current study tested the hypothesis that new action knowledge, acquired via
110 observation, can be ‘fed’ into the motor system and result in a motor prediction of an observed
111 action based on visual statistical learning. Infants, who have a limited knowledge base for many
112 of the actions they observe—in terms of observational and motoric experience—present an ideal
113 opportunity for investigating this question. A developmental approach allowed us to directly test
114 the effect of introducing naïve participants to novel perceptual information about action
115 sequences, and whether this new knowledge is used to generate predictions in their motor

116 system. In a previous study, we showed that 18-month-old infants can learn statistical
117 regularities in continuous action sequences and predict upcoming actions (Monroy et al., 2017).
118 Importantly, infants correctly anticipated more frequently when they observed sequences
119 performed by a human actor, relative to infants who observed a non-action event sequence. This
120 finding supports the hypothesis that the motor system is involved in the perception and
121 prediction of observed actions. Building upon this prior work, we conducted a combined training
122 and EEG study with 18-month-old infants. Infants were first trained over three days by observing
123 videos of action sequences in which one action pair was deterministic: the second action always
124 followed the first action of this pair and was thus 100% predictable. The remaining actions in the
125 sequence were random and thus less predictable. Following this training phase, infants
126 participated in an EEG test session in which they observed a novel sequence featuring the same
127 statistical structure as the training phase.

128 A decrease in power of the mu rhythm overlaying motor regions is an established index
129 of anticipatory activation occurring prior to the onset of an observed action in infants and adults
130 (Marshall & Meltzoff, 2011; Southgate, Johnson, Osborne, & Csibra, 2009). The mu rhythm,
131 also sometimes referred to as sensorimotor alpha, features reduced power during both action
132 execution and observation (Fox et al., 2016; Vanderwert et al., 2012). In infants, this suppression
133 is also observed prior to the onset of an observed action, suggesting that the mu rhythm reflects
134 predictive activity in the human mirror neuron system (Southgate et al., 2009). We hypothesized
135 that the mu rhythm would be suppressed over the motor cortex, reflecting an increase in motor
136 activity, in anticipation of upcoming actions infants could predict based on statistical regularities
137 learned through observation. Conversely, we hypothesized that infants would show no such
138 anticipatory activity for actions which occurred at random and that they could thus not predict.

139

2.0 Method

2.1 Participants

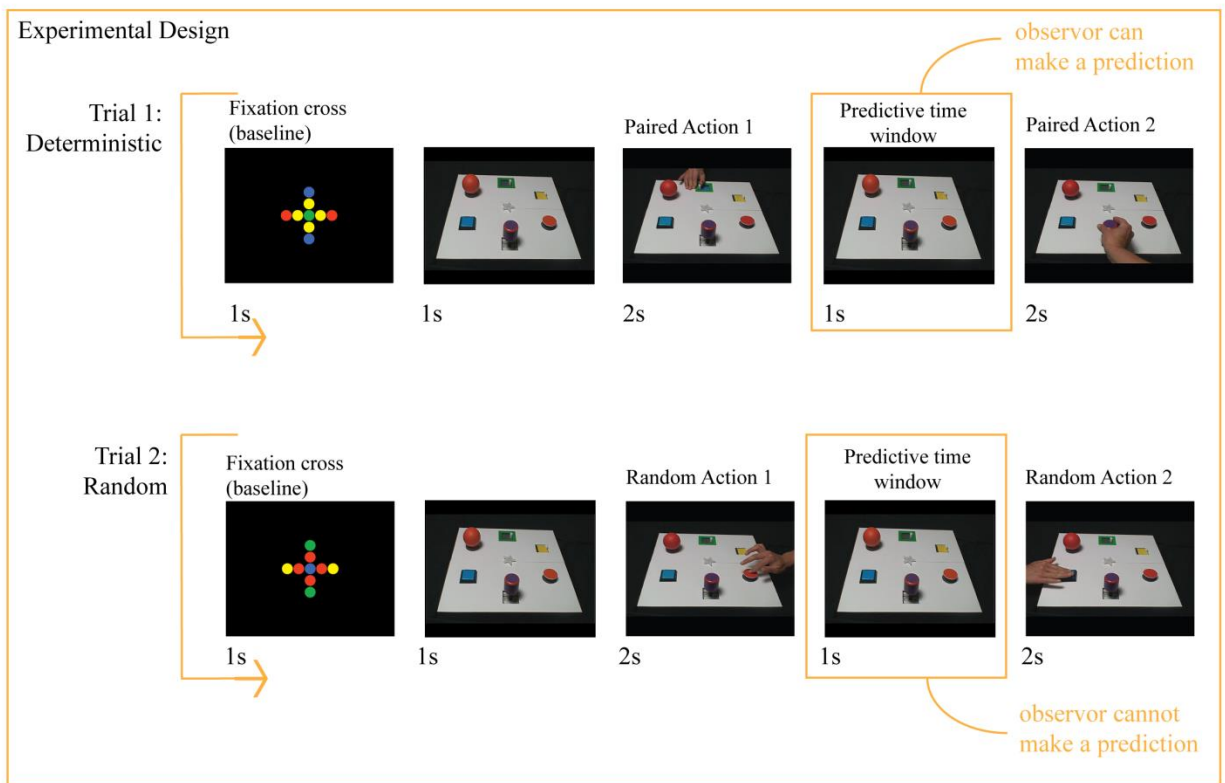
141 Twenty-eight infants (mean age = 18.55 months, $SD = .41$, 17 males) were included in
142 the final sample. Our predetermined target sample size of approximately 25 infants was based on
143 conventional standards for studies that measure the mu rhythm in infants (Gerson et al., 2015;
144 Marshall, et al., 2011; Southgate et al., 2009). Sixteen infants were tested but excluded from the
145 final analysis due to refusal to wear the EEG cap ($n = 4$), insufficient artifact-free trials given a
146 minimum requirement of 3 trials per condition ($n = 9$), not completing the required 3 days of
147 home training ($n = 1$), or experimenter error ($n = 2$). This attrition rate is not atypical in infant
148 EEG studies (Stets et al., 2012). All parents gave written consent, and families received a small
149 gift or 20 euros for participation. Participants were recruited from a database of interested
150 families from the surrounding region of Nijmegen, a middle-sized city in the Netherlands. All
151 procedures were approved by the local ethics committee.

2.2 Stimuli and Materials

153 Three training videos and one test video were created, which were identical in length
154 (7m) and statistical structure. Videos featured an adult performing an action sequence on a box-
155 shaped toy which afforded six unique object-directed actions (Fig. 1). Action sequences
156 consisted of deterministic and random action pairs, which were presented with a brief fixation
157 cross between each pair. Deterministic pairs consisted of two pre-selected actions occurring in
158 the same order, such as ‘slide’ always followed by ‘bend’, and repeated 10 times throughout the
159 sequence. Random pairs were comprised of any other combination of the six objects on the toy.
160 The order of all pairs was shuffled pseudo-randomly in each of the four videos. Thus, infants
161 observed a novel video on each training day and during the test phase. Three sets of stimulus

162 videos were created, in which the two actions comprising the deterministic pair were uniquely
 163 selected from the six possible actions. These three video conditions were counterbalanced across
 164 infants.

165 Fig. 1 illustrates the presentation of an action pair. There were 60 total pairs in each video
 166 featuring 10 deterministic pairs and 50 random pairs for a total of 120 observed actions. Thus,
 167 during the learning phase, infants were presented with a maximum of 360 total actions and 30
 168 repetitions of the deterministic pairs over the three days. All actions were presented an identical
 169 number of times (i.e. 20) to ensure that infants received equal exposure to all six actions.



170
 171 *Figure 1.* (A) Example frames from video stimuli illustrating two successive trials. Trials began
 172 with a static fixation cross, followed by four successive clips played continuously (7s total). EEG
 173 markers were time-locked to the onset of each clip. Yellow boxes indicate the two condition time
 174 windows used for comparison in the EEG analysis: both conditions are perceptually identical (a

175 1s still frame with no action occurring), but in the Deterministic condition, infants can make a
176 prediction about the subsequent action based on statistical likelihood, whereas in the Random
177 condition they cannot make a prediction better than chance. The fixation cross was used as a
178 baseline condition in the analyses.

179
180 Videos were divided into four blocks, with the orientation of the toy relative to the
181 camera rotated in each block. This ensured that infants could not simply learn the physical
182 location on the screen where each action occurred, as the objects' spatial locations were
183 dissociated from their temporal position in the action sequence. In addition, we imposed the
184 following constraints: all actions occurred with equal frequency (20 times); no pair could occur
185 more than two times consecutively, random pairs could not consist of the same action twice, and
186 deterministic pairs were evenly distributed among the four blocks of the videos. Lastly, no sound
187 was played during any of the videos.

188 **2.3 Procedure**

189 *2.3.1 Training phase.*

190 Parents were asked to show each of the three learning videos to their infants at home once
191 per day over the three days immediately prior to their lab appointment. These videos were made
192 available to parents via links on YouTube (www.youtube.com) which were sent to them by email
193 (video links are provided in the Supplementary materials). We instructed parents to play the
194 videos to their infants in a quiet setting with minimal distraction and to maintain identical
195 viewing conditions each day if possible. They were further instructed to watch the videos with
196 their infant seated on their lap approximately one meter from the viewing screen, to mimic the
197 conditions in the laboratory they would experience during the EEG session.

198 Parents were asked to fill out a detailed diary at home containing information about each
199 video session, including the number of minutes the child watched the movie and their own rating
200 of their infant's average attention to the screen on a scale from 1 to 5. In addition, they were
201 asked to record the type of device they used to watch the videos (e.g., laptop, television screen,
202 or tablet), the time of day, and any additional notes about each training day. The aim of the diary
203 was to assess whether parents complied with the instructions and to measure potential individual
204 differences in infants' exposure to the training videos. All parents but one brought completed
205 diaries with them to the EEG lab session. The mean number of minutes that infants watched the
206 three training videos at home was 13.06 minutes ($SD = 5.9$; $range = 1-21$), which yielded an
207 average of 18.44 observations of the Deterministic pair. Mean rating of attention on the five-
208 point scale was 3.07 ($SD = 1.21$, median = 3.33). [Additional data and analyses from the training](#)
209 [phase can be found in the Supplementary materials \(S1 and S2\).](#)

210 2.3.2 EEG session (test phase).

211 Test sessions took place on the day following the final training day and consisted of an
212 action observation phase followed by an action execution phase. Infants were first familiarized
213 with the environment while the procedure was explained to the parent. Experimenters then fitted
214 an infant-sized EEG cap to the infant (ActiCap, Brain Products, Munich, Germany) with 32
215 active electrodes arranged according to the standard 10-20 configuration. Following capping,
216 EEG was recorded continuously while infants sat on a caretaker's lap in a shielded testing room.
217 The EEG signal was referenced online to FCz and re-referenced offline to the average of all
218 electrodes after excluding noisy channels. The mean number of channels included in the average
219 reference was 22 ($SD = 3$). During measurement, the signal was amplified using a Brain-Amp
220 amplifier, band-pass filtered (0.1–125 Hz) and digitized at 500Hz.

221 Infants were next shown the test video displayed on a monitor at approximately 50cm
222 distance from the infant and caretaker. An experimenter monitored a live video feed of infants'
223 behavior from an adjacent room and initiated attention-grabbers (brief, salient cartoons)
224 whenever necessary to regain the infant's attention. Trials containing or following attention-
225 grabbers were excluded from further analyses. After all trials were completed or when infants
226 lost interest, an action execution phase began. The purpose of this phase was to identify the
227 sample-specific mu frequency range, as defined by a decrease in power during overt movement
228 relative to baseline (Meyer et al., 2016). The experimenter turned off the video monitor and
229 placed the toy stimulus in front of the infant. Infants were allowed to play with the toy for
230 several minutes or until they began to lose interest. The entire testing session was video-recorded
231 for offline movement and behavior analysis.

232 **2.4 Data Analysis.**

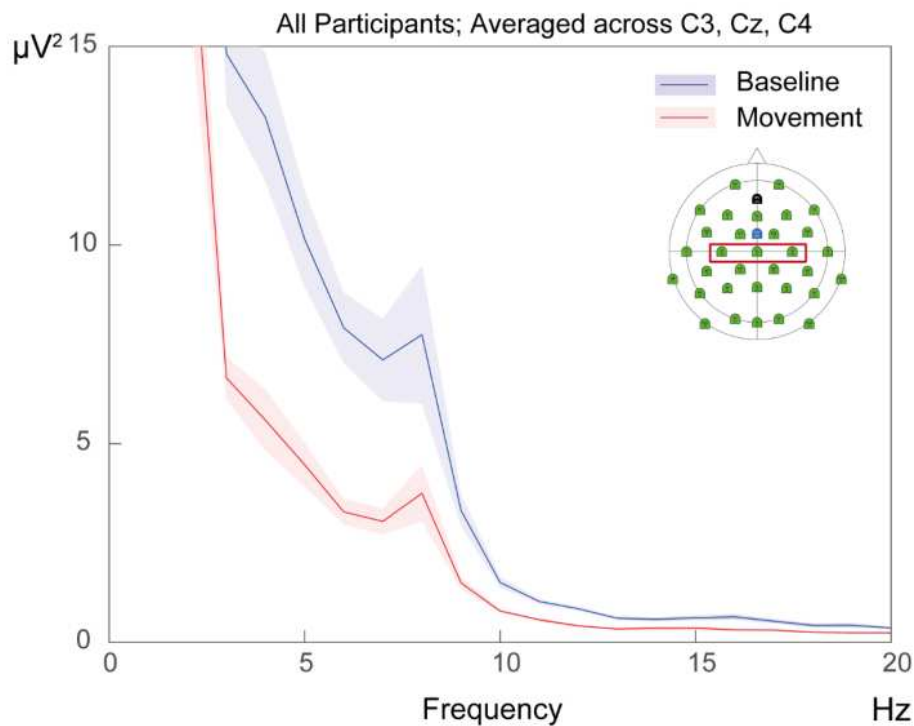
233 *2.4.1 Coding for movement artifacts and visual attention.*

234 Video recordings of the action observation phase were coded offline frame-by-frame for
235 infant movement. Trials that contained any whole body (e.g., kicking) or single-limb (e.g.,
236 moving one arm) movement were marked as invalid and removed from analyses to eliminate
237 motor activity related to overt motor movements during action observation. Trials in which the
238 infant was not looking at the screen were marked as invalid and removed from analyses as well.
239 Across infants, 32.41% of all trials were removed from analyses based on these criteria. These
240 coding procedures are commonly used for infant EEG studies (Hoehl & Wahl, 2012).

241 *2.4.2 Identification of the mu rhythm.*

242 To investigate differences in motor activity during anticipation of deterministic and
243 random actions, we first identified the mu rhythm in the current sample of 18-month-old infants.

244 Video recordings from the action execution phase were coded offline and epochs were selected
 245 in which the infant reached for or manipulated one of the objects on the toy. These epochs were
 246 segmented into 1s trials for data processing (see *EEG processing*). To verify that the frequency
 247 range in our sample was within the expected range for this age (Marshall et al., 2002), the mean
 248 power spectrum was inspected in the 2–50Hz range during baseline and action execution
 249 conditions across central channels (C3, Cz and C4; Fig. 1). Consistent with the literature (e.g.,
 250 Marshall et al., 2011; Nyström et al., 2011), data inspection indicated a clear alpha peak around 8
 251 Hz (+/-1Hz) in which power during action execution was lower compared to baseline, despite
 252 broadband differences. Consequently, a sample-specific frequency range of 7-9Hz was used to
 253 compare our conditions of interest in the action observation phase.



254
 255 *Figure 2.* (A) Power values as a function of frequency (Hz) for the action execution and
 256 baseline trials. The mu rhythm is clearly visible as a sharp peak between 7 and 9Hz. Electrode

257 layout depicted on the right; selected channels corresponding to motor regions are outlined in
 258 red. Shaded areas represent the standard error of the mean.

259

260 *2.4.3 EEG processing.*

261 Data were analyzed using Fieldtrip, an open source toolbox for Matlab (Oostenveld et al.,
 262 2011). Each action pair was divided into two trials: the 1-second fixation cross (Baseline
 263 condition) and the 1-second time window of still-frame preceding the second action, which
 264 became the Deterministic and Random conditions depending on the pair (Fig. 1). Trials were de-
 265 trended, corrected by the mean of the entire segment, and a DFT filter was applied to remove
 266 line noise. They were then visually inspected for artifacts such as noisy channels or muscle
 267 artifacts (Marshall et al., 2011; Meyer et al., 2016). Segments in which infants were not attending
 268 to the screen based on video recordings of the session were rejected. Based on prior work,
 269 participants were required to have at least three artifact-free trials per experimental condition (to
 270 be included in further analyses (Kaduk et al., 2016; Monroy et al., 2017). Table 1 contains the
 271 mean number of trials included in the analysis for each condition after artifact rejection.

272 Table 1.

273 Mean number of artifact-free trials during the test phase (SD).

<u>Baseline Condition</u> (max = 60)	<u>Deterministic Condition</u> (max = 10)	<u>Random Condition</u> (max = 50)	<u>Action Execution phase</u>
<u>17.64 (11.08)</u> <u>Range: 3-52</u>	<u>4.54 (1.75)</u> <u>Range: 3-8</u>	<u>16.39 (10.25)</u> <u>Range: 4-41</u>	<u>12.93 (11.39)</u> <u>Range: 3-45</u>

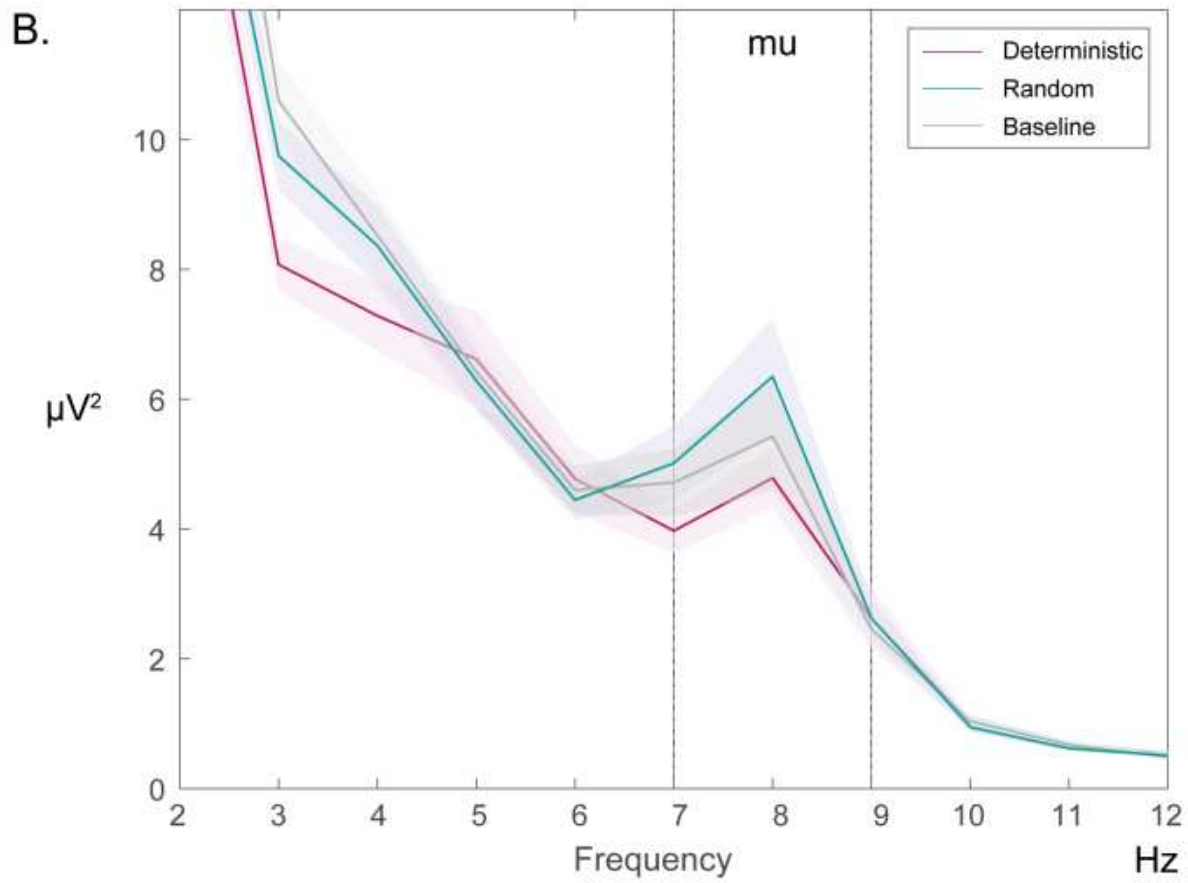
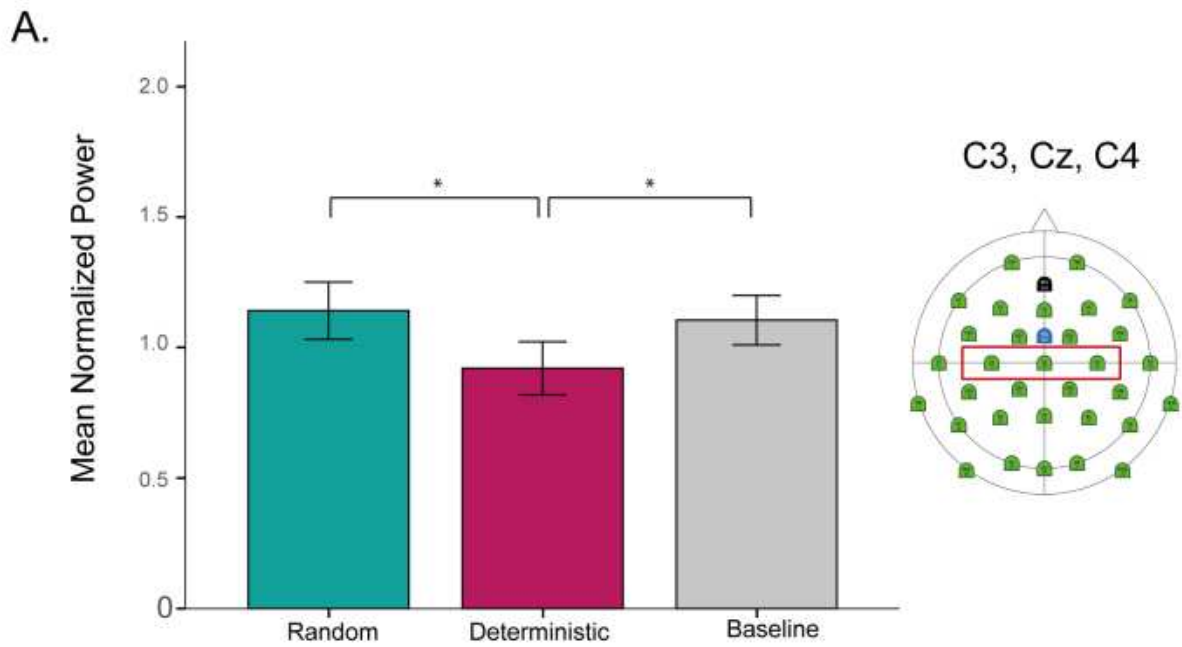
274

275 Following artifact rejection, we performed a fast Fourier transform using a multitaper
 276 method (Hanning taper) to estimate power values between 7-9Hz (see *Identification of the Mu*
 277 *Rhythm*). Based on visual inspection of the data (Fig. 2), we also analyzed the mean log-

278 transformed in the theta rhythm (3–6Hz). Results from this post-hoc analysis are described in the
279 Supplementary file (S3).

280 **3.0 Results**

281 We first conducted a repeated-measures ANOVA with mean normalized power of the mu
282 rhythm over central sites (C3, Cz, and C4) as the dependent variable and Condition
283 (Deterministic, Random, Baseline) as a within-subjects factor. This revealed a main effect of
284 Condition, $F(2.54) = 5.22, p < .01, \eta_p^2 = .16$ (Fig. 3). A one-sample Kolmogorov-Smirnov test
285 revealed the Random condition in the occipital region, $p = .03$, differed significantly from a
286 normal distribution. No other dependent measures differed from a normal distribution, $ps > .20$.
287 There was one outlier (+/- 3SD from the mean) in the Baseline condition over central channels;
288 however, as results did not change when this participant was excluded, we included all
289 participants in our analyses.



291 *Figure 3.* (A) Mean log-transformed power depicted for the two experimental conditions
 292 (Deterministic, Random) and the baseline condition (a fixation cross) over central channels
 293 overlaying motor regions (electrode layout depicted on the right; selected channels are outlined
 294 in red). Error bars represent the standard error of the mean. (B) Power values as a function of
 295 frequency (Hz). Shaded areas represent the standard error of the mean. Gray dotted lines indicate
 296 the selected mu frequency range (7–9 Hz).

297
 298 Pairwise comparisons confirmed that power in the mu rhythm over central channels was
 299 lower in the Deterministic condition relative to both the Random and Baseline conditions ($p <$
 300 $.02$; see Table 2). There was no significant difference between the Random and Baseline
 301 conditions ($p = .56$). These findings show that motor activity selectively increased in anticipation
 302 of the deterministic actions and not prior to random actions.

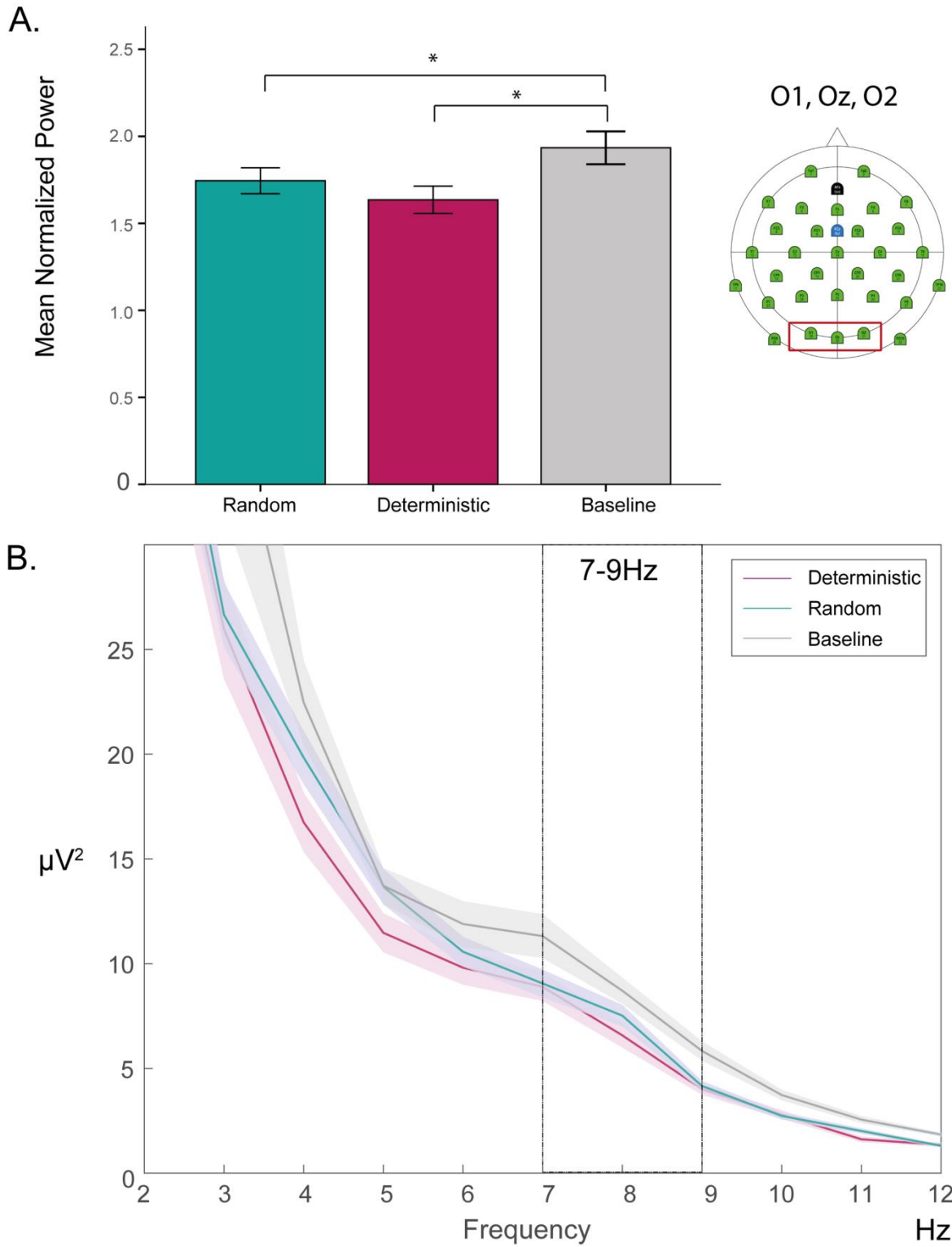
303 Table 2.

304 *Paired t-test comparisons of mean normalized power for the mu rhythm (7-9Hz) over central*
 305 *channels (N = 28).*

Paired sample t-tests	Mean Difference (SD)	$t(27)$	p-value	95% CI
Random - Deterministic	.22 (.44)	2.64	0.01	[0.05, 0.39]
Baseline - Random	-.04 (.32)	-0.59	0.56	[-0.16, 0.09]
Baseline - Deterministic	.18 (.39)	2.51	0.02	[0.03, 0.34]

306
 307 Based on previous literature (Vanderwert et al., 2012), we expected mu suppression to
 308 reflect activation of the motor cortex and thus be specific to channels over motor regions. To
 309 investigate the topographical specificity of the observed mu suppression, we also examined
 310 activity in the 7-9Hz range over occipital channels (O1, Oz, and O2) located over the visual

311 cortex. We did not expect visual activity to differ between Deterministic and Random conditions
312 because the input was perceptually identical. A repeated-measures ANOVA with mean
313 normalized power as the dependent variable and Condition (Deterministic, Random, Baseline) as
314 a within-subjects factor yielded a main effect of Condition, $F(1,43) = 6.34, p < .01, \eta_p^2 = .19$
315 (Fig. 4). [Time-resolved power plots for central and occipital regions are depicted in the](#)
316 [Supplementary file \(S4\).](#)



318 *Figure 4.* (A) Mean log-transformed power depicted for the two experimental conditions
319 (Deterministic, Random) and the baseline condition (a fixation cross) over occipital channels
320 corresponding to visual regions (electrode layout depicted on the right; selected channels
321 outlined in red). Error bars represent the standard error of the mean. (B) Power values as a
322 function of frequency (Hz). Shaded areas represent the standard error of the mean. Gray dotted
323 lines indicate the selected mu frequency range (7–9 Hz).

324

325 Pairwise comparisons revealed that normalized power during Deterministic and Random
326 conditions was lower than during the Baseline condition (mean difference_{Deterministic-Baseline} = -.30,
327 $t(27) = 4.34, p < .001$, mean difference_{Random-Baseline} = -.20, $t(27) = 2.62, p = .01$, respectively).
328 There was no significant difference in normalized power between Deterministic and Random
329 conditions (mean difference_{Deterministic-Random} = -.11, $t(27) = 1.78, p = .09$). Thus, power reduction
330 reflecting visual processing was greater during predictive time windows (displaying the toy
331 stimulus) than during the baseline (displaying the fixation cross), regardless of the upcoming
332 action's probability. These results confirm that the differential mu suppression during
333 anticipation of deterministic relative to random actions was specifically observed over motor,
334 and not visual, regions.

335

4.0 Discussion

336 The current study is the first to examine whether new knowledge learned through
337 observation in infancy can be 'fed' into the motor system and thereby used for predicting
338 upcoming actions. Until now, research on action perception has focused on the role of statistical
339 learning in action segmentation and prediction, or on the role of the motor system in generating
340 action predictions. Using a developmental approach, we investigated how these two systems

341 interact by examining whether infants make motor predictions about upcoming actions based
342 solely on visual statistical learning. In line with our hypothesis, findings revealed suppression of
343 the infant mu rhythm, an index of motor activity, during anticipation of upcoming actions that
344 were statistically deterministic, and not for random actions. Infants were not simply anticipating
345 that any action would occur; rather, the observed motor activated reflected anticipation of
346 specific actions based on their statistical likelihood. Moreover, as the videos used in the EEG
347 session had never been seen before, infants could only base their predictions on previously
348 learned transitional probabilities within action pairs. These findings provide the first evidence for
349 motor-based predictions based on information acquired through visual statistical learning.

350 Our findings are in line with recent frameworks which propose that prior action
351 knowledge is fed into generative models in the motor system (Kilner, 2011; Schubotz, 2007). In
352 the current study, infants learned the transitional probabilities between sequential actions from
353 observation alone. The motor system was then able to access this new knowledge and infer the
354 most likely upcoming action. In addition, the current study extends this framework from
355 predicting single action events (e.g., Kilner, et al., 2004) to predicting sequential action steps.

356 These results are also consistent with prior evidence for statistical learning as a
357 foundational mechanism underlying infants' developing understanding of their sensory
358 environment (for a review, see Krogh et al., 2013). Statistical learning is likely a core mechanism
359 that accounts for the human ability to build expectations about upcoming sensory events.

360 Statistical learning abilities may thus also be an important pathway through which infants
361 develop conceptual knowledge about observed actions (Ruffman et al., 2012). In the current
362 study, infants were not simply learning raw frequencies of occurrences, as each action was
363 presented an equal number of times. Rather, infants could only rely on the transitional

364 [probabilities between action events to form predictions, which is consistent with prior research](#)
365 [on infant SL abilities](#) (Stahl et al., 2014). [Future research could target the specific aspects of the](#)
366 [structure that infants were able to encode, such as joint or conditional probabilities.](#)

367 A separate line of evidence has shown that infants' own actions are another important
368 source of information linked to action processing (Hunnius & Bekkering, 2014). Infants can
369 acquire new sensorimotor associations between self-produced actions and the same actions when
370 they observe them performed by others (Gerson et al., 2015; Paulus et al., 2012). However, until
371 now these two sources of information—active and observational experiences—have been
372 considered complementary but separate from one another (e.g., Calvo-Merino et al., 2006). The
373 current findings challenge this notion by providing evidence that the motor system can predict
374 actions from observational experiences alone, suggesting that these two pathways are rather part
375 of one integrated mechanism.

376 In line with this notion, neuroimaging research in adults reveals that brain regions
377 relevant for statistical learning also overlap with regions of the action-observation network
378 (Ahlheim et al., 2014; Turk-Browne et al., 2008). [According to Kilner \(2009\) the action-](#)
379 [observation network relies on reciprocal connections with domain-general regions to generate](#)
380 [predictions. These regions are likely to include those involved in visual statistical learning, such](#)
381 [as the medial temporal lobe and the hippocampus, which are activated when statistical](#)
382 [regularities provide predictive cues of upcoming stimuli](#) (Turk-Browne et al., 2008, 2010).

383 [An alternative interpretation of our data could be that the observed power reduction in the](#)
384 [7-9Hz range reflects a more general suppression of the alpha rhythm, rather than the](#)
385 [sensorimotor mu rhythm. As the two rhythms share an overlapping frequency band, it is possible](#)
386 [that our findings reflect modulation of the 'classical' alpha rhythm which is thought to reflect](#)

387 general processing of visual stimuli (Bazanova & Vernon, 2014). The observed reduction in
388 alpha power prior to the predictable action might then reflect enhanced visual attention in
389 anticipation of a stimulus that is expected relative to one that is unknown, although if so this
390 should have been observed primarily in the occipital channels. However, our methodology was
391 designed to reliably separate the mu rhythm from the alpha rhythm as suggested in the literature
392 (Bowman et al., 2017; Fox et al., 2016). First, we included both action execution and observation
393 phases, which is crucial to identify the mu rhythm as it is characterized by a suppression over
394 motor regions during movement relevant to non-movement (Cuevas et al., 2014). Second, we
395 report findings from multiple electrode sites, including visual areas, which did not show the same
396 pattern of results. Third, we controlled for visual confounds by analyzing the predictive time
397 window prior to the actions themselves during which the stimuli were visually identical. Thus,
398 the observed activity was most likely related to the infants' anticipation of the forthcoming
399 stimulus rather than ongoing visual processing

400 Due to the limited number of trials included in our experimental conditions, findings
401 from the current study should be interpreted with caution and replicated in future work. Still, our
402 main findings regarding the mu rhythm are consistent with prior research in terms of both its
403 functional significance during action anticipation (e.g., Southgate et al., 2009) as well as the
404 location and frequency range in infants (Marshall et al., 2002; 2011, Nyström et al., 2011). In
405 addition, the current study is limited to the interpretation of neural data. Given the challenges of
406 simultaneous EEG and eye-tracking recordings in infants, we did not collect eye-tracking data,
407 which would have allowed us to examine anticipatory eye movements as an additional measure
408 of learning and prediction. Directly relating the current findings with behavioral findings from

409 [prior research \(e.g., Monroy et al., 2017\) using simultaneous recordings—for instance, with](#)
410 [adults—would be an interesting avenue for future research.](#)

411 [4.1 Conclusion](#)

412 In conclusion, we show that prediction of an upcoming action based on its statistical
413 likelihood elicits activation of the infant motor system. These results extend the functional role
414 of infants' statistical learning to the development of the human action-observation network.
415 Infants can acquire new knowledge of an upcoming action by using their powerful statistical
416 learning abilities, and subsequently use this knowledge to generate action predictions in their
417 motor system.

418 **Acknowledgments.**

419 We would like to thank Lorijn Zaadnoordijk, Ricarda Braukmann, Angela Khadar and
420 Birgit Knudsen for their generous help with recruitment and data collection. We would
421 especially like to thank Pascal de Water for invaluable help with programming the experiment.

422
423 Funding: This project was funded by an Initial Training Network (ITN) of the People Marie
424 Curie Actions grant—Seventh Research Programme (FP7) of the European Union
425 (FP7ITN2011-289404).

432

433

References

434

Ahlheim, C., Stadler, W., & Schubotz, R. (2014). Dissociating dynamic probability and

435

predictability in observed actions-an fMRI study. *Frontiers in Human Neuroscience*, 8, 273.

436

<https://doi.org/10.3389/fnhum.2014.00273>

437

Baldwin, D., Andersson, A., Saffran, J., & Meyer, M. (2008). Segmenting dynamic human

438

action via statistical structure. *Cognition*, 106(3), 1382–1407.

439

<https://doi.org/10.1016/j.cognition.2007.07.005>

440

Baldwin, D., Baird, J., & Saylor, M. (2001). Infants parse dynamic action. *Child Development*,

441

72(3), 708–717. <https://doi.org/10.1111/1467-8624.00310>

442

Bazanov, O. M., & Vernon, D. (2014). Interpreting EEG alpha activity. *Neuroscience and*

443

Biobehavioral Reviews, 44, 94–110. <https://doi.org/10.1016/j.neubiorev.2013.05.007>

444

Becchio, C., Cavallo, A., Begliomini, C., Sartori, L., Feltrin, G., & Castiello, U. (2012). Social

445

grasping: From mirroring to mentalizing. *NeuroImage*, 61(1), 240–248.

446

<https://doi.org/10.1016/j.neuroimage.2012.03.013>

447

Bowman, L. C., Bakermans-Kranenburg, M. J., Yoo, K. H., Cannon, E. N., Vanderwert, R. E.,

448

Ferrari, P., ... Fox, N. A. (2017). The mu-rhythm can mirror: Insights from experimental

449

design, and looking past the controversy. *Cortex*.

450

<https://doi.org/10.1016/j.cortex.2017.03.025>

451

Calvo-Merino, B., Grèzes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or

452

doing? Influence of visual and motor familiarity in action observation. *Current Biology*,

453

16(19), 1905–1910. <https://doi.org/10.1016/j.cub.2006.07.065>

454

Conway, C. M., & Christiansen, M. H. (2005). Modality-constrained statistical learning of

- 455 tactile, visual, and auditory sequences. *Journal of Experimental Psychology*, 31(1), 24–39.
456 <https://doi.org/10.1037/0278-7393.31.1.24>
- 457 Fiser, J., & Aslin, R. (2005). Encoding multielement scenes: statistical learning of visual feature
458 hierarchies. *Journal of Experimental Psychology*, 134(4), 521–37.
459 <https://doi.org/10.1037/0096-3445.134.4.521>
- 460 Flanagan, J. R., & Johansson, R. S. (2003). Action plans used in action observation. *Nature*,
461 424(6950), 769–771. <https://doi.org/10.1038/nature01861>
- 462 Fox, N. A., Bakermans-Kranenburg, M. J., Yoo, K. H., Bowman, L. C., Cannon, E. N.,
463 Vanderwert, R. E., ... van IJzendoorn, M. H. (2016). Assessing human mirror activity with
464 EEG mu rhythm: A meta-analysis. *Psychological Bulletin*, 142(3), 291–313.
465 <https://doi.org/10.1037/bul0000031>
- 466 Friston, K. (2003). Learning and inference in the brain. *Neural Networks*, 16(9), 1325–1352.
467 <https://doi.org/10.1016/j.neunet.2003.06.005>
- 468 Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal
469 Society B: Biological Sciences*, 360(1456), 815–36. <https://doi.org/10.1098/rstb.2005.1622>
- 470 Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory. *Trends in
471 Cognitive Sciences*, 2(12), 493–501. [https://doi.org/10.1016/S1364-6613\(98\)01262-5](https://doi.org/10.1016/S1364-6613(98)01262-5)
- 472 Gerson, S. A., Bekkering, H., & Hunnius, S. (2015). Short-term motor training, but not
473 observational training, alters neurocognitive mechanisms of action processing in infancy.
474 *Journal of Cognitive Neuroscience*, 27(6), 1207–1214. <https://doi.org/10.1162/jocn>
- 475 Hobson, H., & Bishop, D. (2017). The interpretation of mu suppression as an index of mirror
476 neuron activity: past , present and future. *Royal Society Open Science*, 4(160662), 1–22.
477 <https://doi.org/10.1098/rsos.160662>

- 478 Hoehl, S., & Wahl, S. (2012). Recording Infant ERP Data for Cognitive Research.
479 *Developmental Neuropsychology*, 37(3), 187–209.
480 <https://doi.org/10.1080/87565641.2011.627958>
- 481 Hunnius, S., & Bekkering, H. (2014). What are you doing? How active and observational
482 experience shape infants' action understanding. *Philosophical Transactions of the Royal*
483 *Society B: Biological Sciences*, 369(1644), 20130490.
484 <https://doi.org/10.1098/rstb.2013.0490>
- 485 Jacob, P., & Jeannerod, M. (2005). The motor theory of social cognition: A critique. *Trends in*
486 *Cognitive Sciences*, 9(1), 21–25. <https://doi.org/10.1016/j.tics.2004.11.003>
- 487 Kaduk, K., Bakker, M., Juvrud, J., Gredebäck, G., Westermann, G., Lunn, J., & Reid, V. M.
488 (2016). Semantic processing of actions at 9 months is linked to language proficiency at 9
489 and 18 months. *Journal of Experimental Child Psychology*, 151, 96–108.
490 <https://doi.org/10.1016/j.jecp.2016.02.003>
- 491 Kilner, J. M. (2011). More than one pathway to action understanding. *Trends in Cognitive*
492 *Sciences*, 15(8), 352–357. <https://doi.org/10.1016/j.tics.2011.06.005>
- 493 Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). Predictive coding: An account of the mirror
494 neuron system. *Cognitive Processing*, 8(3), 159–166. [https://doi.org/10.1007/s10339-007-](https://doi.org/10.1007/s10339-007-0170-2)
495 [0170-2](https://doi.org/10.1007/s10339-007-0170-2)
- 496 Kilner, J. M., Vargas, C., Duval, S., Blakemore, S.-J., & Sirigu, A. (2004). Motor activation prior
497 to observation of a predicted movement. *Nature Neuroscience*, 7(12), 1299–1301.
498 <https://doi.org/10.1038/nn1355>
- 499 Kirkham, N. Z., Slemmer, J. A., Richardson, D. C., & Johnson, S. P. (2007). Location, location,
500 location: Development of spatiotemporal sequence learning in infancy. *Child Development*,

- 501 78(5), 1559–1571. <https://doi.org/10.1111/j.1467-8624.2007.01083.x>
- 502 Krogh, L., Vlach, H. A., & Johnson, S. P. (2013). Statistical learning across development:
503 Flexible yet constrained. *Frontiers in Psychology*, 3, 598.
504 <https://doi.org/10.3389/fpsyg.2012.00598>
- 505 Marshall, P. J., Bar-Haim, Y., & Fox, N. A. (2002). Development of the EEG from 5 months to 4
506 years of age. *Clinical Neurophysiology*, 113(8), 1199–1208. <https://doi.org/10.1016/S1388->
507 2457(02)00163-3
- 508 Marshall, P. J., & Meltzoff, A. N. (2011). Neural mirroring systems: Exploring the EEG mu
509 rhythm in human infancy. *Developmental Cognitive Neuroscience*.
510 <https://doi.org/10.1016/j.dcn.2010.09.001>
- 511 Marshall, P. J., Young, T., & Meltzoff, A. N. (2011). Neural correlates of action observation and
512 execution in 14-month-old infants: An event-related EEG desynchronization study.
513 *Developmental Science*, 14(3), 474–480. <https://doi.org/10.1111/j.1467-7687.2010.00991.x>
- 514 Meyer, M., Braukmann, R., Stapel, J. C., Bekkering, H., & Hunnius, S. (2016). Monitoring
515 others' errors: The role of the motor system in early childhood and adulthood. *British*
516 *Journal of Developmental Psychology*, 34(1), 66–85. <https://doi.org/10.1111/bjdp.12101>
- 517 Monroy, C. D., Gerson, S. A., Domínguez-Martínez, E., Kaduk, K., Hunnius, S., & Reid, V.
518 (2017). Sensitivity to structure in action sequences: An infant event-related potential study.
519 *Neuropsychologia*. <https://doi.org/10.1016/j.neuropsychologia.2017.05.007>
- 520 Monroy, C., Gerson, S., & Hunnius, S. (2017). Toddlers' action prediction: Statistical learning of
521 continuous action sequences. *Journal of Experimental Child Psychology*, 157, 14–28.
522 <https://doi.org/10.1016/j.jecp.2016.12.004>
- 523 Ondobaka, S., Lange, F. de, Wittmann, M., & Frith, C. (2015). Interplay between conceptual

- 524 expectations and movement predictions underlies action understanding. *Cerebral Cortex*,
525 25(9), 2566–2573.
- 526 Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: open source software
527 for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational*
528 *Intelligence and Neuroscience*, 2011(1), 1–9. <https://doi.org/10.1155/2011/156869>
- 529 Paulus, M., Hunnius, S., & Bekkering, H. (2013). Neurocognitive mechanisms underlying social
530 learning in infancy: Infants' neural processing of the effects of others' actions. *Social*
531 *Cognitive and Affective Neuroscience*, 8(7), 774–779. <https://doi.org/10.1093/scan/nss065>
- 532 Paulus, M., Hunnius, S., Elk, M. Van, Van Elk, M., & Bekkering, H. (2012). How learning to
533 shake a rattle affects 8-month-old infants' perception of the rattle's sound:
534 Electrophysiological evidence for action-effect binding in infancy. *Developmental*
535 *Cognitive Neuroscience*, 2(1), 90–96. <https://doi.org/10.1016/j.dcn.2011.05.006>
- 536 Perruchet, P., & Pacton, S. (2006). Implicit learning and statistical learning: one phenomenon,
537 two approaches. *Trends in Cognitive Science*, 10(5), 233–238.
538 <https://doi.org/10.1016/j.tics.2006.03.006>
- 539 Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of*
540 *Neuroscience*, 27(1), 169–192. <https://doi.org/10.1146/annurev.neuro.27.070203.144230>
- 541 Ruffman, T., Taumoepeau, M., & Perkins, C. (2012). Statistical learning as a basis for social
542 understanding in children. *British Journal of Developmental Psychology*, 30(1), 87–104.
543 <https://doi.org/10.1111/j.2044-835X.2011.02045.x>
- 544 Saffran, J., Aslin, R., & Newport, E. (1996). Statistical learning by 8-month-old infants. *Science*,
545 274(5294), 1926. <https://doi.org/10.1126/science.274.5294.1926>
- 546 Schubotz, R. I. (2007). Prediction of external events with our motor system: Towards a new

- 547 framework. *Trends in Cognitive Sciences*, 11(5), 211–218.
548 <https://doi.org/10.1016/j.tics.2007.02.006>
- 549 Sebanz, N., & Knoblich, G. (2009). Prediction in joint action: what, when, and where. *Topics in*
550 *Cognitive Science*, 1(2), 353–367. <https://doi.org/10.1111/j.1756-8765.2009.01024.x>
- 551 Slone, L. K., & Johnson, S. P. (2015). Infants' statistical learning: 2- and 5-month-olds'
552 segmentation of continuous visual sequences. *Journal of Experimental Child Psychology*,
553 133, 47–56. <https://doi.org/10.1016/j.jecp.2015.01.007>
- 554 Southgate, V., Johnson, M. H., Osborne, T., & Csibra, G. (2009). Predictive motor activation
555 during action observation in human infants. *Biology Letters*, 5(6), 769–772.
556 <https://doi.org/10.1098/rsbl.2009.0474>
- 557 Stahl, A. E., Romberg, A. R., Roseberry, S., Golinkoff, R. M., & Hirsh-Pasek, K. (2014). Infants
558 segment continuous events using transitional probabilities. *Child Development*, 85(5),
559 1821–1826. <https://doi.org/10.1111/cdev.12247>
- 560 Stets, M., Stahl, D., & Reid, V. M. (2012). A meta-analysis investigating factors underlying
561 attrition rates in infant ERP studies. *Developmental Neuropsychology*, 37(3), 226–252.
562 <https://doi.org/10.1080/87565641.2012.654867>
- 563 Turk-browne, N. B., Scholl, B. J., Chun, M. M., & Johnson, M. K. (2008). Neural evidence of
564 statistical learning: Efficient detection of visual regularities without awareness. *Journal of*
565 *Cognitive Neuroscience*, 1934–1945. <https://doi.org/10.1162/jocn.2009.21131>
- 566 Vanderwert, R. E., Fox, N. a, & Ferrari, P. F. (2012). The mirror mechanism and mu-rhythm in
567 social development. *Neuroscience Letters*, 540, 15–20.
568 <https://doi.org/10.1097/MPG.0b013e3181a15ae8>.Screening
- 569 Wolpert, D. D. M., Doya, K., & Kawato, M. (2003). A unifying computational framework for

570 motor control and social interaction. *Philosophical Transactions of the Royal Society B:*

571 *Biological Sciences*, 358(1431), 593–602. <https://doi.org/10.1098/rstb.2002.1238>

572