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6	The infant motor system predicts actions based on visual statistical learning
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25	
26	Abstract
27	Motor theories of action prediction propose that our motor system combines prior
28	knowledge with incoming sensory input to predict other people's actions. This prior knowledge
29	can be acquired through observational experience, with statistical learning being one candidate
30	mechanism. But can knowledge learned through observation alone transfer into predictions
31	generated in the motor system? To examine this question, we first trained infants at home with
32	videos of an unfamiliar action sequence featuring statistical regularities. At test, motor activity
33	was measured using EEG and compared during perceptually identical time windows within the
34	sequence that preceded actions which were either predictable (deterministic) or not predictable
35	(random). Findings revealed increased motor activity preceding the deterministic but not the
36	random actions, providing the first evidence that the infant motor system can use knowledge
37	from statistical learning to predict upcoming actions. As such, these results support theories in
38	which the motor system underlies action prediction.
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40	Keywords: mu rhythm, EEG, infants, statistical learning, action prediction
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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 in very different outcomes. As a consequence, predictions cannot always be made on the basis of 61 62 the current ongoing action alone (Jacob & Jeannerod, 2005). Motor accounts of action prediction have been criticized for failing to explain how action predictions can be generated for cases in 63 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 sensory input to determine the most likely action outcome (Kilner et al., 2007; Ondobaka et al., 68 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 how humans can acquire knowledge of the environment through observation (Perruchet & 85 Pacton, 2006). SL skills broadly refer to the ability to detect regularities in continuous sensory 86 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.

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

system. In a previous study, we showed that 18-month-old infants can learn statistical

117 <u>regularities in continuous action sequences and predict upcoming actions (Monroy et al., 2017).</u>

118 <u>Importantly, infants correctly anticipated more frequently when they observed sequences</u>

119 performed by a human actor, relative to infants who observed a non-action event sequence. This

120 <u>finding supports the hypothesis that the motor system is involved in the perception and</u>

121 <u>prediction of observed actions. Building upon this prior work</u>, 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

sequence were random and thus less predictable. Following this training phase, infants

participated in an EEG test session in which they observed a novel sequence featuring the same
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 that the mu rhythm would be suppressed over the motor cortex, reflecting an increase in motor 135 136 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

140 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.

152 **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

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

Fig. 1 illustrates the presentation of an action pair. There were 60 total pairs in each video featuring 10 deterministic pairs and 50 random pairs for a total of 120 observed actions. Thus, during the learning phase, infants were presented with a maximum of 360 total actions and 30 repetitions of the deterministic pairs over the three days. <u>All actions were presented an identical</u> 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

194 videos to their infants in a quiet setting with minimal distraction and to maintain identical

(video links are provided in the Supplementary materials). We instructed parents to play the

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.

193

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.

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

241 2.4.2 Identification of the mu rhythm.

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

Video recordings from the action execution phase were coded offline and epochs were selected 244 245 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.



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

- layout depicted on the right; selected channels corresponding to motor regions are outlined inred. 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 <u>Mean number of artifact-free trials during the test phase (SD).</u>

	$\frac{\text{Baseline Condition}}{(\text{max} = 60)}$	$\frac{\text{Deterministic Condition}}{(\text{max} = 10)}$	$\frac{\text{Random Condition}}{(\text{max} = 50)}$	Action Execution phase	
	17.64 (11.08)	4.54 (1.75)	<u>16.39 (10.25)</u>	<u>12.93 (11.39)</u>	
	<u>Range: 3-52</u>	<u>Range: 3-8</u>	<u>Range: 4-41</u>	<u>Range: 3-45</u>	
274 275	Following	g artifact rejection, we p	performed a fast Fo	ourier transform using a	a multitaper
276	method (Hanning	taper) to estimate pow	ver values between	7-9Hz (see Identificati	on of the Mu
277	Rhythm). Based of	on visual inspection of t	the data (Fig. 2), w	e also analyzed the me	an 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). <u>A one-sample Kolmogorov-Smirnov test</u>
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.
1	



291	<i>Figure 3.</i> (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

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

303 Table 2.

Paired t-test comparisons of mean normalized power for the mu rhythm (7-9Hz) over central
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

Based on previous literature (Vanderwert et al., 2012), we expected mu suppression to reflect activation of the motor cortex and thus be specific to channels over motor regions. To investigate the topographical specificity of the observed mu suppression, we also examined 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
- a within-subjects factor yielded a main effect of Condition, F(1,43) = 6.34, p < .01, $\eta_p^2 = .19$
- (Fig. 4). <u>Time-resolved power plots for central and occipital regions are depicted in the</u>
- 316 <u>Supplementary file (S4).</u>



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 anticipation of deterministic relative to random actions was specifically observed over motor, 333 334 and not visual, regions.

335

4.0 Discussion

The current study is the first to examine whether new knowledge learned through observation in infancy can be 'fed' into the motor system and thereby used for predicting upcoming actions. Until now, research on action perception has focused on the role of statistical learning in action segmentation and prediction, or on the role of the motor system in generating 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.
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