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The relationship between prior night's sleep and measures of infant imitation

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Abstract: We examined whether sleep quality during the night and naps during the day preceding a learning event are related to memory encoding in human infants. Twenty-four 6- and twenty-four 12-month-old infants' natural sleeping behavior was monitored for 24 hours using actigraphy. After the recording period, encoding was assessed using an imitation paradigm. In an initial baseline phase, infants were allowed to interact with the stimulus to assess spontaneous production of any target actions. Infants then watched an experimenter demonstrate a sequence of three target actions and were immediately given the opportunity to reproduce the demonstrated target actions to assess memory encoding. Analyses revealed significant correlations between nighttime sleep quality variables (sleep efficiency, sleep fragmentation) and immediate imitation in 6-month-olds, but not in 12-month-olds. High sleep quality in the preceding night was positively associated with next day's memory encoding in 6-month-old infants.

Keywords: infancy, sleep, encoding, memory, learning, imitation, actigraphy

1 “If sleep does not serve an absolutely vital function, then it is the biggest mistake the
2 evolutionary process ever made.”

3 Allan Rechtschaffen, 1978

4 University of Chicago Sleep Laboratory

5 In older children and adults, sleep is crucial for cognitive functioning, particularly for
6 a multitude of memory processes (Diekelmann & Born, 2010; Rasch & Born, 2013). Sleep
7 enhances both the quantity and quality of declarative and non-declarative memories, and
8 facilitates the application of existing knowledge to new situations (e.g., Ellenbogen, Hu,
9 Payne, Titone, & Walker, 2007; Gais & Born, 2004; Wagner, Gais, Haider, Verleger, &
10 Born, 2004). Although it has been proposed that sleep may be particularly important during
11 periods of enhanced plasticity (such as adolescence; Dahl, 2004; Dahl & Spear, 2004),
12 surprisingly little research has focused on the effects of sleep on cognitive functioning in
13 infancy (for a discussion, see El-Sheikh & Sadeh, 2015). Two recent empirical studies have
14 shown that sleeping is associated with strengthened declarative memory consolidation in 6-
15 and 12-month-olds (Seehagen, Konrad, Herbert, & Schneider, 2015) and semantic
16 generalization in 9- to 16-month-old infants (Friedrich, Wilhelm, Born, & Friederici, 2015).
17 However, the relation between infant sleep and the learning process, memory encoding, has
18 yet to be explored. In addition, although young infants spend the majority of their time
19 asleep, sleeping behavior rapidly changes throughout the first year of life and there are large
20 inter-individual as well as intra-individual day-to-day differences in sleeping patterns (Acebo
21 et al., 2005; Galland, Taylor, Elder, & Herbison, 2012; Goodlin-Jones, Burnham, Gaylor, &
22 Anders, 2001; Hoppenbrouwers, Hodgman, Arakawa, Geidel, & Serman, 1988; Scher,
23 Epstein, & Tirosh, 2004). Thus, in the present study we assessed whether sleep quantity and
24 quality prior to a learning event is related to subsequent memory encoding in 6- and 12-
25 month-old infants.

26 So far, research exploring the relations between infant sleep and general cognitive
27 development has focused on habitual sleep (e.g., Freudigman & Thoman, 1993; Gibson,
28 Elder, & Gander, 2012; Scher, 2005). Habitual sleep is a measure of how the infant usually
29 sleeps and is defined by sleep data that is averaged over several nights (often 5-7) for each
30 individual infant. Sleep data is typically collected via parent completed sleep logs/diaries, or
31 with objective techniques (e.g., actigraphy, polysomnography; for review of method strengths
32 and limitations see Sadeh, 2015). In these studies, cognitive development is often assessed
33 with the Mental Scale of the Bayley Scales of Infant Development (Bayley, 1993). The
34 Bayley Scales provides a global score of general cognitive functioning and has been used to
35 show normal sleep development is associated with favorable cognitive development (Ednick
36 et al., 2009).

37 A handful of studies have also specifically considered which facets of sleep quality
38 might be related to higher levels of general cognitive development in infancy (Ednick et al.,
39 2009; Freudigman & Thoman, 1993). One indicator of sleep quality found to be positively
40 associated with cognitive development is sleep efficiency (Gibson et al., 2012; Scher, 2005).
41 Sleep efficiency is defined as the percentage of time spent asleep within the total sleep period
42 (i.e., time the infant is put to bed until final wake up), and there is a temporal increase in
43 sleep efficiency during the first year of life (De Marcas, Soffer-Dudek, Dollberg, Bar-Haim,
44 & Sadeh, 2015). Another indicator of sleep quality is sleep fragmentation, which can be
45 measured through the number or duration of night wakings. Number of night wakings, for
46 example, has been found to be negatively related to the cognitive scores on the Bayley Scales
47 (Scher, 2005). Total sleep duration per se is not an indicator of sleep quality in infants
48 (Sadeh, 2015) and seems unrelated to their cognitive development at a given age (Bernier,
49 Carlson, Bordeleau, & Carrier, 2010; Scher, 2005). However, sleep duration can be regarded
50 as a marker of maturation as with increasing age infants spend less time asleep and more of
51 their sleep time occurs at night relative to the day (Bernier et al., 2010; Gibson et al., 2012;

52 Scher, 2005). Thus, age and developmental status of an infant are related to their sleeping
53 behavior (Acebo et al., 2005).

54 The Bayley Scales only provides a global score of general cognitive functioning and
55 are thus not suitable for exploring relations between sleep and specific memory processes.
56 The only infant study which has assessed the relation between habitual sleep and specific
57 memory processes, rather than general cognitive development, used an elicited imitation
58 paradigm (Lukowski & Milojevich, 2013). In this paradigm, infants are first allowed to
59 explore the stimuli in a baseline control phase that is child-controlled rather than fixed in
60 duration. A series of target actions are then modeled to the infant and the infant is presented
61 with the stimuli again immediately and/or after a delay and is prompted verbally to imitate
62 the actions (Bauer, 1996). Imitation tasks can provide a measure of the amount of information
63 encoded into memory, and also the structure of the memory, by examining how many actions
64 are reproduced by the infant and whether the actions are produced in the same order as they
65 were shown. In Lukowski and Milojevich's (2013) sample of 10-month-old infants, the
66 duration of daytime napping was positively associated with encoding of the correct temporal
67 order of target actions but not with the total number of actions encoded. The percentage of
68 sleep in 24 hours that was obtained at night was negatively associated with the correct
69 temporal order. The authors suggested that habitual napping might be especially important
70 for encoding of the correct temporal order of actions. In that study, habitual sleep was
71 assessed using a parental-report questionnaire regarding their infants' sleeping behavior
72 averaged over the past week (Brief Infant Sleep Questionnaire (BISQ), Sadeh, 2004). Since
73 parents systematically underestimate the frequency and duration of night wakings in their
74 infants (Sadeh, 2008; Werner, Molinari, Guyer, & Jenni, 2008), it remains unclear whether
75 any associations between sleep fragmentation and infant imitation might be detected when
76 sleep is assessed objectively.

77 A further unanswered question relates to the role of night sleep immediately preceding
78 a learning event. On the one hand, research on sleep inertia (i.e., “the transitional state of
79 lowered arousal occurring immediately after awakening from sleep”, Tassi & Muzet, 2000, p.
80 341) in adults indicates that prior sleep can lead to a diminished learning performance up to
81 four hours after sleep occurred (Tassi & Muzet, 2000). On the other hand, sleep deprivation
82 studies with adults show that sufficient sleep is essential for encoding (e.g., Harrison &
83 Horne, 2000) and recent studies indicate that prior sleep can also have enhancing effects on
84 subsequent encoding (Antonenko, Diekelmann, Olsen, Born, & Mölle, 2013; Mander,
85 Santhanam, Saletin, & Walker, 2011). For example, adults who are well rested exhibit better
86 encoding of episodic memories than adults in a sleep deprivation condition who had not slept
87 for one night before the encoding session (Yoo, Hu, Gujar, Jolesz, & Walker, 2007). In
88 children, some studies have examined the effect of night sleep restriction on cognitive
89 functioning (Carskadon, Harvey, & Dement, 1981; Kopasz et al., 2010; Könen, Dirk, &
90 Schmiedek, 2015; Randazzo, Muehlbach, Schweitzer, & Walsh, 1998; Sadeh, 2007). Sleep
91 restriction negatively affects encoding in children, particularly in tasks that tap into higher-
92 order cognitive processes such as creative thinking (Randazzo et al., 1998). In contrast, at
93 least mild sleep restriction does not influence encoding ability of lower cognitive tasks, such
94 as learning of short word lists (Biggs et al., 2010).

95 Only one study has so far examined the effect of prior daytime naps on the encoding
96 of novel actions in infants (Seehagen et al., 2015). In this study, 6- and 12-month-old infants
97 were randomly assigned to either take or to not take a naturally-occurring extended nap
98 within 4 hours preceding participation in an imitation task (Barr, Dowden, & Hayne, 1996).
99 Sleeping behavior was monitored using actigraphy. In the imitation task, a within-subject
100 procedure was used such that infants first participated in a baseline phase during which they
101 interacted with the stimuli for 90 s to assess spontaneous production of any target actions.
102 Then, the experimenter modeled three target actions. In the test phase immediately

103 afterwards, the infants were allowed to interact with the stimuli again to assess encoding of
104 the target actions. Infants in both the nap and in the no-nap condition produced a significantly
105 higher number of target actions in the test phase than in the baseline phase and this increase
106 did not differ between the two conditions. Thus, infants in the nap and in the no-nap
107 condition encoded the target actions equally well.

108 In Seehagen et al. (2015), only the effect of daytime sleep during the 4 hours
109 preceding a learning event was measured. Previous research in adults and children has shown
110 that night sleep might be especially important for subsequent encoding (Gomez, Newman-
111 Smith, Breslin, & Bootzin, 2011; Walker, 2009). Therefore, in the present study we focused
112 on the association between infants' sleep during the night and subsequent memory encoding.
113 The primary question of interest was whether there was a relation in 6- and 12-month-old
114 infants between their sleep quality in the preceding night and their encoding performance. We
115 were interested in investigating two different age-groups as there are complex relations
116 between sleep and cognitive functioning such that specific findings obtained with one age-
117 group can often not be generalized to different developmental periods (Ednick et al., 2009).
118 Using an objective technique to monitor sleep behavior (i.e., actigraphy) for 24-hours, we
119 assessed the role of prior sleep/wakefulness for infants' learning of novel actions in an
120 imitation task, controlling for the infants' overall developmental status, parental education,
121 and breastfeeding. Parental characteristics such as socio-economic status have been shown to
122 be associated with a child's sleeping patterns (Acebo et al., 2005; Zhang, Li, Fok, & Wing,
123 2010). For example, 12- to 60- month-old infants of parents with a lower socio-economic
124 status (SES) have a higher variability in bed times, spend more time awake at night and rise
125 later in the morning than infants of parents with higher SES (Acebo et al., 2005).
126 Furthermore, breastfeeding is associated with longer night waking episodes, at least in 3-
127 month-old infants (Tikotzky et al., 2015).

128 We hypothesized that encoding performance would be positively associated with
129 sleep quality (sleep efficiency, sleep fragmentation) of the preceding night. As sleep duration
130 does not seem to be an indicator of sleep quality in infants (Sadeh, 2015), our second
131 hypothesis was that prior night's sleep duration would not be associated with encoding
132 performance on the next day. Third, we predicted that, in accordance with previous findings
133 (Seehagen et al., 2015), there would be no relation between preceding daytime sleep and
134 encoding performance. We made no specific assumptions for differences between age-
135 groups.

136

137 **Method**

138 **Participants**

139 The final sample consisted of twenty-four 6-month-old and twenty-four 12-month-old
140 full-term infants (50% girls). All infants participated within two weeks of turning 6 or 12
141 months, respectively (6-month-olds: M age = 186 days, SD = 7 days; 12-month-olds: M age =
142 365 days, SD = 8 days). Ten additional infants were tested but excluded from the final sample
143 due to actiwatch failure (n = 4), fussiness (n = 3), experimenter error (n = 2), or refusal to
144 remain seated during the test phase (n = 1).

145 The families were initially recruited from local birth registers from the city of
146 Bochum. Part of the sample derived from a bigger study on sleep-dependent memory in
147 infants (Seehagen et al., 2015). Except for one, all infants were living with both parents.
148 Sixty-seven percent of the infants were first born; the maximum number of siblings an infant
149 had was three. Twelve 6-month-olds and six 12-month-olds were breastfed when they
150 participated in the study; three parents in each age-group did not provide this information. On
151 average, mothers of the 6-month-old infants were 32 (SD = 5) years old and had 16 years of
152 education. Fathers were 35 (SD = 5) years old on average and had 16 years of education.
153 Mothers of the 12-month-old infants were 34 (SD = 4) years old and had 16 years of

154 education. Fathers were 35 (SD = 5) years old on average and had 16 years of education; one
155 father did not provide this information.

156 **Measures**

157 **Sleep records.**

158 **Actigraphy.** Sleep was recorded using Micro Motionlogger® Actiwatches
159 (Ambulatory Monitoring inc.). Actiwatches (devices similar in appearance to a wristwatch)
160 record the frequency of movement with the aid of a piezo-electric beam, which produces a
161 voltage each time the actiwatch is moved. Actigraphy is a valid and accurate method for
162 assessing sleep-wake patterns in infants (Müller, Hemmi, Wilhelm, Barr, & Schneider, 2011;
163 Sadeh, Acebo, Seifer, Aytur, & Carskadon, 1995). An algorithm which was specifically
164 developed for the differentiation of sleep and wake states in infants (Sadeh Infant algorithm,
165 Sadeh et al., 1995) was used to calculate for each minute whether the infant was awake or
166 asleep.

167 **Sleep diary.** Parents were asked to complete a sleep diary to document their infant's
168 sleeping (i.e., exact nap times, the time they put their infant to bed at night, wake up times at
169 night, and final wake up time in the morning). Additionally, parents noted the exact start and
170 end times of periods when the actiwatch was removed (e.g., while changing diapers) as well
171 as times when the infant was moved externally (e.g., being pushed in a pram). Since
172 actigraphy is exclusively based on motion, the data it produces during periods of external
173 movement can be distorted. During these times, the sleep diary was used to calculate sleep
174 durations.

175 **Stage of development.** To control for infants' general development, parents
176 completed a German translation of the Ages and Stages Questionnaire (ASQ, Bricker &
177 Squires, 1999) for infants aged 6 months or 12 months, respectively. The questionnaires
178 contain six questions for each of the following five developmental areas: communication,
179 gross motor, fine motor, problem solving, and personal social. Parents rate on a 3-point scale

180 (yes, sometimes, not yet) whether their infant is able to perform described activities. Infants
181 score 10 points for every activity parents rate with “yes”, 5 points for every activity parents
182 rate with “sometimes”, and 0 points for every activity parents rate with “no”. A score for each
183 developmental domain is calculated by summing up the points from the relevant items. A
184 total score across developmental domains is calculated by summing up the scores from the
185 five domains. The ASQ shows good to acceptable internal consistency, strong two week test-
186 retest reliability and moderate agreement between parent and a trained examiner within
187 developmental areas, as well as concurrent validity (Squires, Twombly, Bricker, & Potter,
188 2009). The total ASQ-Scores were used in our analyses to control for overall developmental
189 status. In the present sample, the 6-month-olds’ ASQ scores ranged from 115 to 295 ($M =$
190 225 , $SD = 41$) and the 12-month-olds’ scores ranged from 165 to 300 ($M = 226$, $SD = 36$).

191 **Stimuli.** Four different hand puppets were used in the imitation task (counterbalanced
192 across age and gender) which were specifically made for research purposes and not
193 commercially available. The puppet stimuli have been successfully used in a number of
194 deferred imitation studies with 6- and 12- month-old infants (e.g., Barr et al., 1996; Hayne,
195 MacDonald, & Barr, 1997; Brito & Barr, 2014; Seehagen et al., 2015). There were two
196 puppets resembling a mouse and two resembling a rabbit, one of each being grey and one
197 pink. A removable felt mitten matching the color of the puppet was placed over each puppet’s
198 right hand. Only one puppet was used for each infant.

199 **Procedure**

200 All families were visited in their own homes twice, with a 24-hour delay between the
201 sessions. The visits occurred at a convenient time for the parents when the infant was likely
202 to be alert and playful. The time of the visits varied from 8.45 am to 6.15 pm with a mean
203 time of 11.50 am. On the first visit, the experimenter obtained informed consent from the
204 parents and handed out the ASQ and a sleep diary to chart infant’s sleeping behavior. An
205 actiwatch was attached to the infant’s left ankle. On the second visit, the actiwatch was

232 GmbH, Arnstorf, Germany). Each infant received an imitation score from 0 to 3 for both the
233 baseline and the test phase. A second independent coder, who was blind to the hypotheses of
234 the study, coded 50% of the videos. Inter-rater reliability was very good, kappa = .91.

235 **Analyses of sleep measures.** All analyses of the infant's night sleep (defined as time
236 the infants were put to bed at night until final wake up in the morning) were conducted solely
237 using the actigraphy data. The following actigraphy variables for the night sleep were used
238 for computation: total sleep duration, number of night wakings exceeding 5 minutes, total
239 wake duration, and sleep efficiency (i.e., the percentage of sleep within the total sleep period
240 from the time the infant is put to bed until final wake up). Night wakings are usually defined
241 as period of wakefulness of more than 5 minutes in actigraphy studies with infants since the
242 number of long wake episodes that seriously disrupt sleep are of particular interest (e.g.,
243 Sadeh, 1994; Scher & Cohen, 2015; Tikotzky & Shaashua, 2012). Actigraphy records may be
244 somewhat distorted when infants co-sleep with their parents due to the movement of the
245 parents. However, only a minority of infants regularly co-slept around the time of study
246 participation (n = 5 six-month-olds and n = 4 twelve-month-olds, two caregivers did not
247 provide this information). We did not specifically assess sleeping arrangements during the
248 night preceding the learning event.

249 For daytime naps during the 24-h recording period, two sleep variables were
250 calculated: number of naps and total nap duration . The times indicated as sleep during the
251 day in the sleep diary were used to identify naps initially. The actigraphy data was used for
252 68% of all recorded naps to calculate sleep duration. The durations for the remaining naps
253 were extracted from the sleep diary entries as these naps occurred during periods when the
254 infant was moved externally. Additionally, the total sleep duration within 24-hours was
255 calculated.

256 **Preliminary Analyses**

257 There were no differences in maternal and paternal education between age-groups,
258 $t(46) = 0.37, p = .710$, and $t(45) = 0.85, p = .402$, respectively. Furthermore, the mean ASQ
259 score did not differ between age-groups, $t(46) = -0.15, p = .878$.

260 **Sleep parameters.** In the 6-month-olds, there were no significant differences in
261 nighttime and daytime sleeping behavior (see Table 1 for sleep variables) between males and
262 females, Wilks' $\lambda = .759, F(6, 17) = 0.90, p = .517, \eta_p^2 = .24$, between infants with and
263 without siblings, Wilks' $\lambda = .590, F(6, 17) = 1.97, p = .127, \eta_p^2 = .41$, between infants who
264 were or were not breastfed, Wilks' $\lambda = .892, F(6, 15) = 0.30, p = .925, \eta_p^2 = .11$, or between
265 infants who regularly did or did not co-sleep with their parents, Wilks' $\lambda = .770, F(6, 15) =$
266 $0.75, p = .621, \eta_p^2 = .23$.

267 In the 12-month-olds, there were no significant differences in nighttime and daytime
268 sleeping behavior between males and females, Wilks' $\lambda = .821, F(6, 17) = 0.62, p = .713, \eta_p^2$
269 $= .18$, between infants with or without siblings, Wilks' $\lambda = .728, F(6, 17) = 1.06, p = .424,$
270 $\eta_p^2 = .27$, or between infants who were or were not breastfed, Wilks' $\lambda = .708, F(6, 15) =$
271 $1.03, p = .442, \eta_p^2 = .29$. However, a MANOVA revealed a significant multivariate main
272 effect of co-sleeping status on nighttime and daytime sleeping behavior, Wilks' $\lambda = .491, F$
273 $(6, 16) = 2.77, p = .049, \eta_p^2 = .51$. A significant univariate main effect of co-sleeping status
274 was obtained for the number of naps during the 24-h recording period, $F(1, 21) = 11.57, p =$
275 $.003, \eta_p^2 = .36$, indicating that infants who regularly co-slept with their parents took more
276 naps than infants who did not co-sleep. In addition, a significant univariate main effect of co-
277 sleeping status was obtained for the number of night wakings exceeding 5 minutes, $F(1, 21)$
278 $= 6.17, p = .022, \eta_p^2 = .23$, indicating that infants who regularly co-slept woke up more often.

279 Furthermore, 12-month-old infants who co-slept imitated significantly fewer target
280 actions than infants who did not co-sleep, $t(21) = 2.17, p = .042$. This was not the case for the
281 6-month-olds, $t(20) = 0.53, p = .603$. Co-sleeping status was thus controlled in further

282 correlations between night sleep variables and adjusted imitation scores for the 12-month-old
283 infants.

284 Mean starting time of the night sleep period (i.e., when the infant was put to bed) was
285 08.01 pm for the 6-month-olds and 07.35 pm for the 12-month-olds. Mean wake up time in
286 the morning was 07.14 am for the 6-month-olds and 07.21 am for the 12-month-olds. Sleep
287 measures of infants' sleep within the assessed 24-hours are displayed in Table 1 for each age-
288 group separately. A MANOVA revealed a significant multivariate main effect of age-group
289 on nighttime and daytime sleeping behavior, Wilks' $\lambda = .677$, $F(6, 41) = 3.26$, $p = .010$, $\eta_p^2 =$
290 $.32$. A significant univariate main effect for age-group was obtained for the number of naps ,
291 $F(1, 46) = 17.34$, $p < .001$, $\eta_p^2 = .27$, indicating that 6-month-old infants took significantly
292 more naps than 12-month-old infants.

293

294 ---- Insert Table 1 about here ----

295

296 **Imitation task.** There were no significant differences in adjusted imitation scores
297 between males and females at 6 or 12 months, so data was collapsed across gender in the
298 following analyses, $t(22) = -0.30$, $p = .770$, and $t(22) = -1.16$, $p = .260$, respectively. To
299 assess encoding performance, a 2 (Phase: baseline, test) x 2 (Age: 6 months, 12 months)
300 mixed-model ANOVA was conducted. There was a main effect of phase, indicating that
301 infants produced a significantly higher number of target actions during test than during
302 baseline, $F(1, 46) = 16.94$, $p < .001$, $\eta_p^2 = .27$ (see Figure 1 for imitation scores). Thus, as a
303 group, infants showed evidence of having encoded the target actions after having watched the
304 demonstration. There was no significant main effect of age and no age x phase interaction
305 effect, biggest $F(1, 46) = 0.61$, $p = .440$, $\eta_p^2 = .01$.

306 **Willingness to interact with the puppet and sleep parameters.** To assess whether
307 prior sleep was associated with general willingness or interest to interact with the puppet

308 stimuli, we conducted Pearson's correlations between all sleep variables (as shown in Table
309 1) and the time infants spent touching the puppet during the baseline and the test phase for
310 both age-groups. From these 28 correlations, only one reached significance which we
311 therefore regarded as a chance finding: at 12 months, the time infants touched the puppet
312 during baseline phase was negatively associated with the total duration of naps during the
313 day, $r = -.43$, $p = .038$. Overall, these results therefore suggest that prior sleep was not related
314 to infants' willingness to interact with the stimuli.

315

316 ----- Insert Figure 1 about here -----

317

318 **Main Analyses**

319 **Prior daytime sleep, total sleep and imitation performance.** To relate individual
320 encoding performance to sleep variables, an adjusted imitation score was created by
321 subtracting each infant's baseline score from the infant's imitation score at test (Lukowski &
322 Milojevich, 2013; Sheffield, 2004). The adjusted imitation score could thus range from -3 to
323 +3. In the present sample, it ranged from -1 to 3 in the 6-month-olds and from -2 to 3 in the
324 12-month-olds.

325 As expected, number of naps, total sleep duration during the day, and total sleep
326 within 24 hours were not significantly related to the adjusted imitation score at 6 and 12
327 months, biggest $r = .25$, $p = .245$. Furthermore, time of the visit and length of time the infant
328 had been awake before participating in the imitation task did not significantly correlate with
329 the adjusted imitation score at 6 and 12 months, biggest $r = .19$, $p = .371$.

330

331 ----- Insert Table 2 about here -----

332

Discussion

359
360 The goal of the present study was to examine whether sleeping behavior during the
361 night is related to next day's memory encoding in the first year of life. The results support the
362 hypotheses that sleep quality, but not sleep duration per se, is critical for next day's memory
363 encoding in 6-month-old infants. Hence, having a good night's sleep in the preceding night
364 appears not only to be associated with memory encoding in children and adults (Gomez et al.,
365 2011; Walker, 2009), but already in young infants. The same variables that underlie the
366 relations between habitual sleep quality (i.e., sleep fragmentation and sleep efficiency) and
367 general cognitive development (Gibson et al., 2012; Scher, 2005) appear to be important for
368 the association between immediately preceding night sleep and memory encoding. It is
369 unlikely that these associations can be explained by a third variable such as general
370 developmental status of the infants or socioeconomic background as the associations held
371 when controlling for parent's education and ASQ scores. In addition, sleep quality seems to
372 be the underlying factor for associations with imitation performance: the 12-month-old
373 infants who regularly co-slept with their parents in our sample also showed poorer sleep
374 quality. This might be the reason they had lower imitation scores than infants who did not co-
375 sleep in our sample. The third hypothesis could also be confirmed: in accordance with
376 previous findings (Seehagen et al., 2015) daytime sleep was unrelated to encoding
377 performance.

378 In Lukowski and Milojevich's (2013) study, habitual sleep in 10-month-olds was only
379 related to more complex aspects in an imitation task like encoding of the temporal order of
380 actions. In the present study we found that, at least in the 6-month-olds, prior sleep was
381 associated with encoding of the number of target actions. Since different measurements of
382 sleep were used between studies (habitual sleep vs. objectively measured prior sleep), it is
383 possible that there are different associations between habitual sleep and prior sleep with
384 encoding.

385 It might seem surprising that in this sample, the 6- and 12-month-olds only differed
386 significantly in a single sleep variable that is, the number of naps. The literature suggests that
387 while sleep duration in a 24-h period and the nocturnal sleep duration remain relatively
388 constant between 6 and 12 months of age (Iglowstein, Jenni, Molinari, & Largo, 2003; Sadeh,
389 Mindell, Luedtke, & Wiegand, 2009; Scher, Epstein, & Tirosh, 2004; Spruyt et al., 2008), a
390 larger proportion of the total sleep occurs at night by 12 months. In addition, there is a
391 decrease of diurnal sleep (Spruyt et al., 2008). Due to considerable day-to-day variability of
392 sleep, studies examining sleep parameters in infants with objective measures like actigraphy
393 usually take measurements for 5-7 consecutive days and then use the means of these nights to
394 determine the infant's habitual or average sleeping behavior (Sadeh, 2015). As we were
395 especially interested in the effects of such variations in sleep, we only collected sleep data for
396 24 hours prior to the imitation task. It is thus likely that we did not measure each infant's
397 most representative day of their habitual sleeping behavior. Furthermore, many studies
398 examined sleep quality in large samples using questionnaires to assess sleep (e.g., over 5000
399 parents in Sadeh et al., 2009; over 2000 parents in Teng, Bartle, Sadeh, & Mindell, 2012).
400 Thus, even differences in sleep variables that were relatively small numerically may have
401 reached statistical significance. In sum, methodological differences to previous studies in
402 sample size, mode of sleep assessment, and length of sampling might explain the lack of age-
403 related differences in sleep parameters in the present study.

404 What could be the underlying mechanism connecting nighttime sleep quality and next
405 day's encoding performance? The present data are correlational in nature, precluding causal
406 interpretations. Yet, on the basis of experimental research in animals and human adults, it
407 could be speculated that sleep influences encoding performance early in life as well. In
408 previous studies, sleep deprived rats and adults show reduced activity in the hippocampus, a
409 brain region critically involved in learning, during encoding of new information (e.g., Guan,
410 Peng, & Fang, 2004; McDermott et al., 2003; Yoo et al., 2007). Thus, sleep appears to

411 prepare the brain for memory encoding during the next wake phase (Antonenko et al., 2013;
412 Van Der Werf et al., 2009). There are at least two possible hypotheses explaining this
413 function of restoring learning capacities of sleep which are not mutually exclusive and could
414 work hand in hand. The first one, the synaptic homeostasis hypothesis, explains this
415 restoration through the downscaling of synaptic strength during sleep (Tononi & Cirelli,
416 2006). During wakefulness, synapses become potentiated when new information is encoded
417 (Vyatovskiy, Cirelli, Pfister-Genskow, Faraguna, & Tononi, 2008). Sleep renormalizes
418 synaptic potentiation to a baseline level, saving energy and space in the brain (Tononi &
419 Cirelli, 2014; Vyatovskiy et al., 2008). Thus without sleep, the synapses would soon become
420 saturated and learning capacities would quickly reach a limit during wakefulness (Tononi &
421 Cirelli, 2006, 2014). Hence, it could be speculated that, as a result of synaptic downscaling,
422 the infants in our sample that had better sleep quality in the preceding night showed better
423 learning performance.

424 A second explanation, the active system consolidation hypothesis, can be derived
425 from the two-stage model of sleep-dependent memory consolidation (Diekelmann & Born,
426 2010; Frankland & Bontempi, 2005). According to this model, new information is encoded in
427 parallel in hippocampal and cortical networks (Frankland & Bontempi, 2005). The
428 hippocampus allows fast learning and acts as an intermediate buffer which retains
429 information for a limited time. Transfer into cortical networks occurs during sleep when
430 recently acquired information is reactivated in the hippocampal-neocortical network. This
431 “strengthening of cortico-cortical connections eventually allows new memories to become
432 independent of the hippocampus and to be gradually integrated with pre-existing cortical
433 memories” (Frankland & Bontempi, 2005, p. 122). An explanation for the reduced
434 hippocampal activity in sleep-deprived animals and adults can be derived from this model:
435 the previously learned information during wakefulness exceeds the hippocampal encoding
436 capacity and, due to the lack of sleep, the information cannot be consolidated into a long-term

437 store to free up space for new input (Diekelmann & Born, 2010; Frankland & Bontempi,
438 2005).

439 Although we did not find an association between night sleep quality and immediate
440 imitation in the 12-month-olds using the puppet task, it is possible that there is an association
441 between sleep quality and encoding at this age in general. Put differently, it seems somewhat
442 unlikely that associations between prior sleep quality and encoding exist in 6-month-old
443 infants as well as older children and adults, but not in 12 month-olds. More comprehensive
444 measures of sleep, like polysomnography, are needed to further investigate the relation
445 between sleep quality and encoding in infants. Polysomnography records body functions
446 during sleep, including electroencephalography to score sleep stages, sleep quality, eye
447 movements, muscle activity, and heart rhythm during sleep. However, complete
448 polysomnography has major disadvantages because it is an expensive procedure that requires
449 the infant to sleep in an unnatural laboratory environment (Sadeh, 2015). Other factors of
450 sleep quality should be considered as well, like disordered breathing during sleep (e.g.,
451 snoring). Snoring which can occur frequently in children and can be easily assessed with a
452 one-item screening indicating the frequency of snoring in the child rated by the parents (e.g.,
453 Montgomery-Downs, O'Brien, Holbrook, & Gozal, 2004). In addition, more fine-grained
454 analyses of encoding performance could be beneficial. Previous studies showed that there are
455 no differences in imitation performance in the first year of life when tested immediately after
456 the demonstrations (Barr et al., 1996; Herbert, Gross, & Hayne, 2006). In line with that, our
457 sample of 6- and 12-month-olds did not differ in immediate imitation performance even
458 though there are marked age-related changes in memory functioning across the first year of
459 life (Hayne, 2004). Thus, future studies investigating relations between encoding and sleep in
460 infants could benefit from including a wider range of encoding tasks and more
461 comprehensive assessments of sleep quality and architecture.

462 In a bigger picture, prior sleep could be one factor underlying day-to-day variances in
463 infants' performance in memory tasks. Rapid changes in cooperation, interest, and mood are
464 often an issue when assessing infant memory, especially when tasks involve multiple sessions
465 (Hayne, 2004). Furthermore, in the few studies that assessed test-retest reliabilities for infant
466 memory tasks, there was much variability in performance, leading to reliabilities that were
467 only medium in size (Goertz, Kolling, Frahsek, & Knopf, 2009; Goertz, Kolling, Frahsek,
468 Stanisch, & Knopf, 2008). Thus, it may be informative to collect data about prior sleep to
469 explain variance in performance on a specific day.

470 The present study shows that prior night sleep is related to memory encoding in young
471 infants. This relation should be investigated further in infants to better understand its
472 importance for cognitive development and to identify its physiological underpinnings.

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747

Tables

748

749 Table 1

	Sleep duration at night in min (SD)	Time awake at night in min (SD)	Number of night wakings exceeding 5 min (SD)	Sleep efficiency in % (SD)	Number of naps within 24h (SD)	Sleep duration during the day in min (SD)	Total sleep duration within 24h in min (SD)
6 months	626.8 (81.1)	35.1 (27.7)	1.9 (1.4)	93.2 (4.8)	3.0 (1.2)	130.3 (39.1)	757.1 (77.8)
12 months	657.2 (95.7)	31.2 (24.1)	1.8 (1.4)	93.1 (9.0)	1.8 (0.6)	124.2 (53.7)	781.4 (105.5)
p	.24	.60	.84	.98	.00	.66	.37

750

751 Note. P-values are provided for the comparison of sleep variables between age-groups.

752 Table 2

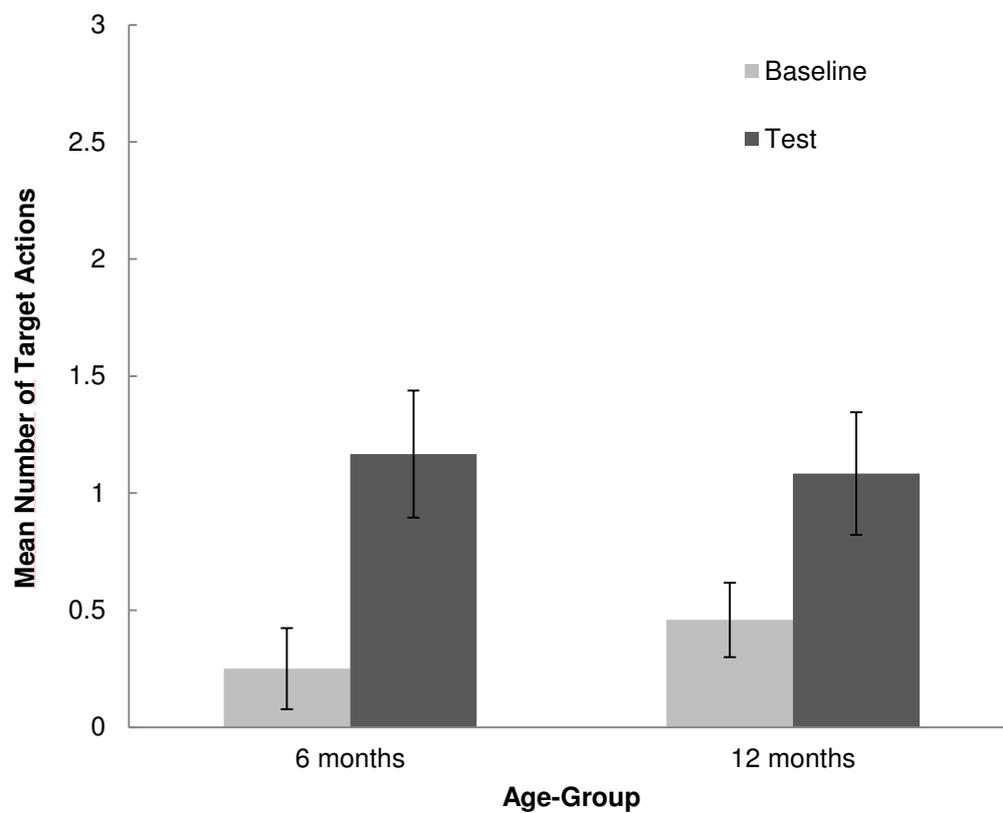
Age-group		Total sleep duration at night (min)	Time awake at night (min)	Number of night wakings exceeding 5 min	Sleep efficiency in %
6 months	Adjusted Imitation Score	.137	-.421*	-.391 [†]	.455*
12 months	Adjusted Imitation Score	.088	-.021	.108	.239

753

754 * $p < .05$ 755 [†] $p < .06$

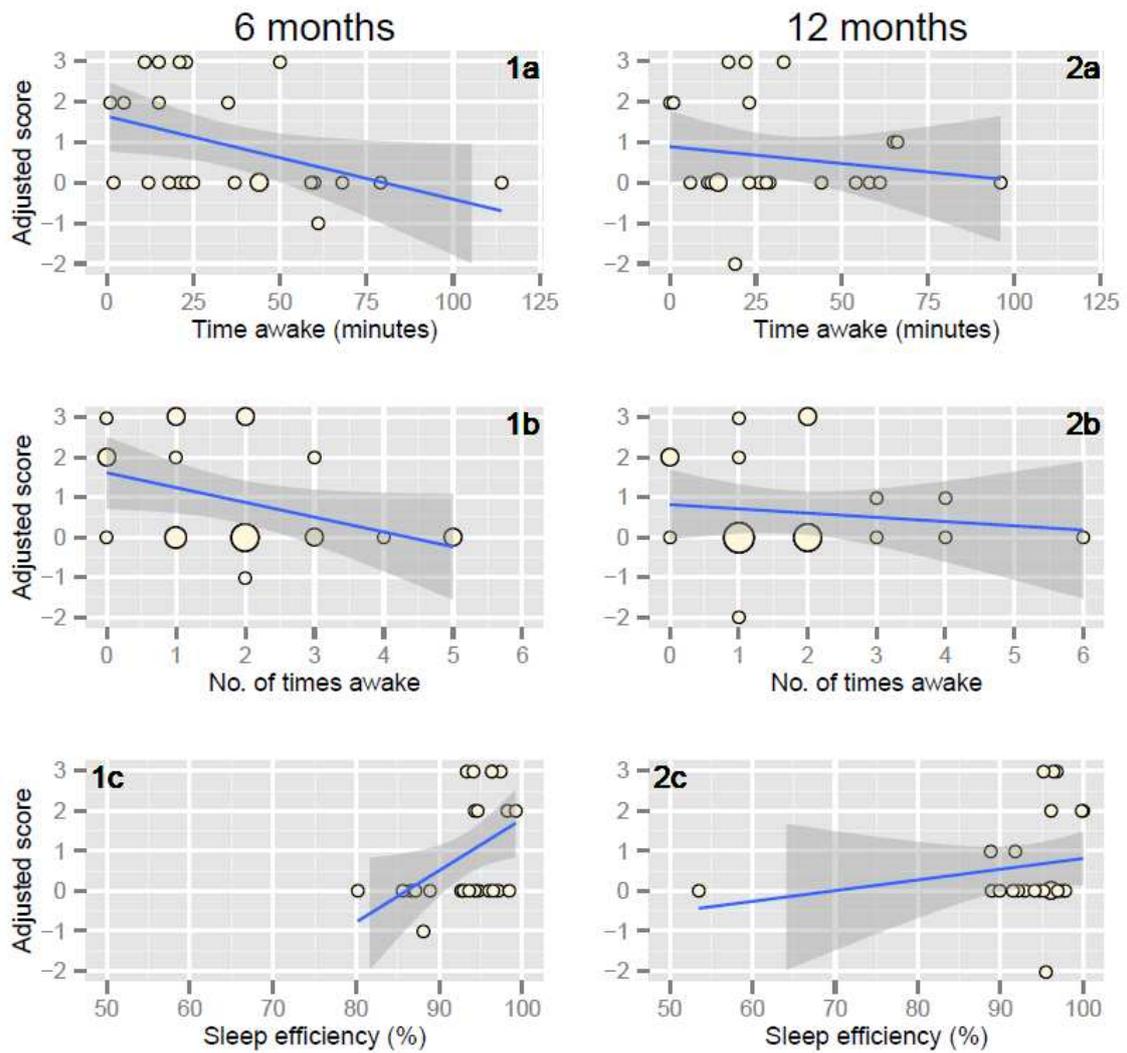
756 Note. Correlations in 12-month-olds are controlled for co-sleeping status.

757

Figures

758

759 Figure 1.



760

761 Figure 2.

762 Note. Column 1 displays the data for 6-month-olds, and column 2 the data for 12-month-

763 olds. Symbol areas are proportional to the number of data at each location. 95% confidence

764 bands about each regression line are also shown.

765

Captions

766 Table 1

767 Means, Standard Deviations and P-Values for Sleep Variables for each Age-Group.

768

769 Table 2

770 Correlations between Night Time Sleep Variables and Adjusted Imitation Score for each Age-

771 Group.

772

773 Figure 1. Mean imitation scores as a function of phase and age. Error bars represent SE of M.

774

775 Figure 2. Scatterplots and regression lines of adjusted imitation score against sleep quality

776 variables for each age group.

Running title: Prior sleep is related to infant imitation