

1 Sensorimotor mu rhythm during action observation changes across the lifespan
2 independently from social cognitive processes

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4 Victoria E. A. Brunsdon*

5 Elisabeth E. F. Bradford

6 Heather J. Ferguson

7 University of Kent

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10 Corresponding Author:

11 Victoria E. A. Brunsdon

12 School of Psychology

13 Keynes College

14 University of Kent

15 Canterbury

16 CT2 7NP

17 Phone: 01227 824240, Fax: 01227 827030

18 v.e.a.brunsdon@kent.ac.uk

19

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22 Author Contribution

23 All authors contributed to study design, data collection, data analysis and
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25

26 Conflicts of Interest

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Abstract

The observation of actions performed by another person activates parts of the brain as if the observer were performing that action, referred to as the 'mirror system'. Very little is currently known about the developmental trajectory of the mirror system and related social cognitive processes. This experimental study sought to explore the modulation of the sensorimotor mu rhythm during action observation using EEG measures, and how these may relate to social cognitive abilities across the lifespan, from late childhood through to old age. Three-hundred and one participants aged 10- to 86-years-old completed an action observation EEG task and three additional explicit measures of social cognition. As predicted, findings show enhanced sensorimotor alpha and beta desynchronization during hand action observation as compared to static hand observation. Overall, our findings indicate that the reactivity of the sensorimotor mu rhythm to the observation of others' actions increases throughout the lifespan, independently from social cognitive processes.

Keywords: EEG; mu rhythm; mirror system; sensorimotor processes; social cognition; developmental trajectories

49 The observation of actions performed by someone else can activate neurons in the
50 sensorimotor cortex, and this apparent mirroring of observed actions in the brain has led to
51 the term ‘mirror neurons’. Mirror neurons were first termed after single unit studies reported
52 cells in the premotor cortex of macaque monkeys that discharged both when performing
53 actions and when observing actions (Dipellegrino, et al., 1992). There is abundant evidence
54 for a mirror neuron system in humans (Fox, et al., 2016; Gallese, et al, 2004; Kilner & Lemon,
55 2013), wherein observed actions are integrated with the person’s motor repertoire to
56 understand actions (Calvo-Merino, et al., 2005). The mirror system is thought to be configured
57 through sensorimotor learning, i.e., through the repeated co-occurrence between a sensory
58 input and motor output (Catmur & Heyes, 2013; Catmur et al., 2007, 2008, 2009; Cook et al.,
59 2014; Heyes, 2001). However, very little is known about how this mirror system develops
60 across the lifespan as most studies in humans have focussed exclusively on infants, young
61 adults, or those with autism spectrum disorder. Therefore, it is not known whether and how
62 the mirror system changes over typical development, or whether a comparably functioning
63 mirror system is present in older adults. We address this gap in the literature by exploring for
64 the first time how the mirror system develops across the lifespan, from late childhood through
65 to old age, and how social cognitive processes are related to the functioning of the mirror
66 system.

67 Electroencephalography (EEG) methods have been used to assess the modulation of
68 the sensorimotor mu rhythm during both action execution and observation as a proxy of the
69 mirror system (Arnstein et al., 2011; Fox et al., 2016). The mu rhythm is an EEG oscillation
70 between 8 and 13 Hz (Hari et al., 1997) recorded from central areas overlying the
71 sensorimotor cortex. There has been recent debate regarding the distinction between the mu
72 rhythm and alpha activity, since both are composed of the same frequency bands (Bowman
73 et al., 2017; Fox et al., 2016; Hobson & Bishop, 2016). Mu and alpha have largely been
74 distinguished based on their topography, with mu originating from central areas (overlying the
75 sensorimotor cortex) and alpha originating from occipital areas (overlying the occipital lobe).
76 Mu desynchronization studies have also considered beta oscillations from 13 to 35 Hz
77 (Hobson & Bishop, 2017), as the mu rhythm appears to consist of two spectral peaks at ~10
78 Hz and ~20 Hz (Hari, 2006). At rest, the sensorimotor cortex activity is synchronous, but

79 during both action execution and observation the sensorimotor cortex activity becomes
 80 desynchronized, reflecting changes in cortical activity (Fox et al., 2016). Typically, EEG mu
 81 desynchronization studies compare mu power in a baseline condition (e.g., static hands or
 82 kaleidoscope videos, Puzzo et al., 2011; Hobson & Bishop, 2017) with an experimental
 83 condition (e.g., performing and/or observing hand actions, Puzzo et al., 2011). A reduction in
 84 mu power over central regions in the experimental condition as compared to the baseline
 85 condition indicates that the mu rhythm has desynchronized to the performance/observation of
 86 actions, reflecting changes in the activation of the sensorimotor cortex.

87 Mu desynchronization studies have been expanded to investigate whether the mirror
 88 system is an important mechanism for social cognition, such as for imitation (e.g., Braadbaart,
 89 Williams, & Waiter, 2013), theory of mind (e.g., Pineda & Hecht, 2009), and empathy (e.g.,
 90 Woodruff, Martin, & Bilyk, 2011), as well as to investigate whether a 'faulty' mirror system
 91 underlies autism spectrum disorder (Oberman et al., 2005). However, there are a growing
 92 number of studies that dispute the role of the mirror system in understanding others' actions
 93 and intentions (see Hickok 2009; 2013). For example, individuals unable to execute actions
 94 due to congenital upper limb dysplasia were still able to understand and interpret those
 95 actions, undermining the view that the sensorimotor cortex mirrors observed actions to allow
 96 understanding and interpretation of others' behaviour (Vannuscorps & Caramazza, 2016).
 97 There is abundant evidence of sensorimotor cortex activation to action observation, but the
 98 function of this observation-related sensorimotor activity is therefore unclear. More recently,
 99 Catmur et al. (2018) demonstrated that 'counter-mirror' sensorimotor training (associative
 100 training in which the observation of one action is paired with the performance of another
 101 action) significantly reduced action understanding, providing support for the role of the mirror
 102 system in action understanding. We extend this work by investigating the developmental
 103 relationship between the mirror system and higher-order social cognitive processes.

104 Thus far, the majority of mu desynchronization studies in healthy individuals have
 105 focussed on the emergence of mirror system activity in infancy (~9 months old; Lepage &
 106 Theoret, 2006), or on averaged data from younger adults derived from student populations
 107 (e.g., 18-33 years old: Hobson & Bishop, 2016; 18-34 years old: Perry & Bentin, 2009; 21-41
 108 years old: Muthukumaraswamy, et al, 2004). To our knowledge, there have been no

109 developmental studies of sensorimotor mu rhythm across the lifespan, with a paucity of
 110 research in both adolescence and older age, meaning that very little is known about its
 111 development beyond childhood. The limited research that has addressed this developmental
 112 trajectory has observed changes across the mirror system network in early childhood (Shaw
 113 et al., 2012); children aged 10 years old elicit comparable brain activation during action
 114 observation as adults (Biagi et al., 2016), which suggests that mirror system development
 115 may reach maturity by mid/late-childhood. However, adolescence is a period of substantial
 116 development of certain areas of the brain involved in social cognitive processes (Blakemore,
 117 2008), thus it is possible that the mirror system continues to change beyond mid/late-
 118 childhood. Crucially, it remains unknown whether and how the mirror system continues to
 119 develop across adolescence and into adulthood (Kilner & Blakemore, 2007).

120 To our knowledge, there have been no sensorimotor mu rhythm studies investigating
 121 action observation in healthy aging. However, research has reported behavioral declines in
 122 related social abilities in older age, including theory of mind (Henry et al., 2013), action
 123 learning (Coats, et al., 2013), and imitation (Maryott & Sekuler, 2009). Moreover, functional
 124 imaging has revealed that motor-related areas in the brain are susceptible to aging, leading to
 125 compensatory over-activation in the motor cortices during action execution tasks (Hutchinson
 126 et al., 2002; Riecker et al., 2006; Ward & Frackowiak, 2003). EEG studies that have
 127 investigated aging effects on action execution using the go/no-go paradigm have reported
 128 greater beta desynchronization for response suppression, movement preparation and
 129 execution in older adults (Schmiedt-Fehr et al., 2016), leading to the suggestion that
 130 additional brain networks are recruited in older age (Hong et al., 2016). The current study
 131 examines whether the reactivity of the sensorimotor mu rhythm during action observation
 132 shows a comparable increase with age.

133 The aim of the current study was to explore the functioning of the mirror system
 134 across the lifespan, from late childhood through to old age, to obtain a comprehensive picture
 135 its development. In addition, we investigated how behavioral changes in social cognitive
 136 processes map onto the functioning of the mirror system across the lifespan. As a proxy of
 137 mirror system functioning, we investigated the modulation of the sensorimotor mu rhythm to
 138 the observation of other's hand actions. It was predicted that, across all ages, there would be

139 greater sensorimotor mu and beta desynchronization during hand action observation
 140 compared to static hand observation, replicating previous findings (Puzzo et al., 2010).
 141 Moreover, in line with research that has shown increased beta desynchronization in older
 142 adults during action execution (Hutchinson et al., 2002; Riecker et al., 2006; Ward &
 143 Frackowiak, 2003), we expected to observe a greater action-static difference in mu/alpha and
 144 beta desynchronization for older adults compared to young adults. Importantly, we also
 145 explored whether increasing age and higher social cognitive processes, including empathy
 146 (Empathy Quotient; EQ), emotion recognition (Reading the Mind in the Eyes Task; RMET),
 147 and theory of mind (ToM; Strange Stories), are related to the functioning of the mirror system.

148 **Method**

149 **Participants**

150 In total, 354 participants completed the larger CogSoCoAGE study. The final
 151 CogSoCoAGE sample consisted of 350 participants, as two participants were excluded due to
 152 low IQ (<70), one participant was excluded due to being a non-native English speaker, and
 153 one participant's data was lost due to computer failure. All participants were native English-
 154 speakers, had normal or corrected-to-normal vision, had no known neurological disorders,
 155 and had no mental health or autism spectrum disorder diagnoses. The participants' consent
 156 was obtained according to EU legislation, and the Ethical Committee of the School of
 157 Psychology, University of Kent, approved the study.

158 From the original sample, 14 participants did not complete the EEG task, 11
 159 participants were excluded due to excessive noise on the EEG recordings, nine participants
 160 were excluded due to too few segments for the EEG analysis (less than two-thirds of
 161 segments remaining), three participants were excluded due to computer error on the EEG
 162 task, three participants were excluded due to outliers in the EEG data, one participant did not
 163 complete the Reading the Mind in the Eyes Task, one participant was excluded due to
 164 computer error on the Strange Stories, and seven participants did not complete the Empathy
 165 Quotient. Thus, the final sample consisted of 301 participants in total, aged 10 to 86 years old
 166 (207 females, 94 males).

167 **Measures**

168 **Action Observation EEG Task.** This task was adapted from a previous study (Puzzo
 169 et al., 2011) and was used to measure sensorimotor mu/alpha and beta desynchronization
 170 during hand action observation compared to static hand observation as a proxy of the hMNS.
 171 First, participants performed a resting EEG for 2 minutes, which involved fixating on a central
 172 cross on a grey screen. After a self-directed break, participants performed the action
 173 observation task that contained 60 experimental trials. Stimuli consisted of seven different
 174 video clips depicting a static hand or various hand actions: cutting a piece of paper with
 175 scissors, ringing a bell, dialling a number on a mobile phone, clicking fingers, locking a door
 176 with keys, and crumpling a piece of paper. Trials consisted of a 1000ms fixation cross, then a
 177 3000ms video clip, ending with a 1000-3000ms blank screen (the inter-trial interval was
 178 variable to prevent expectancy effects on mu rhythm). Each of the six hand action video clips
 179 was shown five times with a total of 30 hand action trials. The static hand video clip was
 180 shown 30 times with a total of 30 static hand trials. Trials were presented in a randomised
 181 order. There was a break halfway through the observation task, the duration of which was
 182 directed by the participant.

183 **Social Cognition Tasks.** Three explicit measures were used to examine higher
 184 social cognitive processes, including emotion recognition, theory of mind and empathy (see
 185 supplementary materials for more detail [S1]).

186 A computerised version of the Reading the Mind in the Eyes Task (RMET) was
 187 completed using 28 items for the child version (10-15 years old) or 36 items for the adult
 188 version (Baron-Cohen et al., 2001). Participants' response accuracy was recorded ($M =$
 189 73.75%, range = 44.44 – 94.44%).

190 A computerised version of the Strange Stories was completed, in which participants
 191 verbally responded to questions about eight theory of mind, eight physical and eight nature
 192 stories (White et al., 2009). A ToM score was calculated from the theory of mind stories ($M =$
 193 13.51, range = 2 – 16) and a non-ToM control score was calculated from the physical stories
 194 ($M = 13.74$, range = 4 – 16).

195 The parent-report (10-15 years old; Auyeung et al., 2012) or the self-report (16+
 196 years old; Baron-Cohen et al., 2004) version of the Empathy Quotient (EQ) was completed.
 197 The questionnaires were scored to gain a total empathy score (maximum = 80) with a low

198 score indicating low levels of empathy and a high score indicating high levels of empathy ($M =$
 199 46.24, range = 7 – 76).

200 **Procedure**

201 Participants (or their parents if aged 10-15 years old) completed the EQ (plus
 202 additional questionnaires) before attending testing sessions. Participants completed one or
 203 two visits to the university as part of a larger study, which lasted approximately 5 hrs in total.
 204 The RMET and Strange Stories were included in a larger task battery with tasks administered
 205 in a counterbalanced order. The action observation EEG task was always completed at the
 206 end of the testing session. The Acticap was first applied and set up for recording. Participants
 207 then completed the action observation EEG task while EEG activity was recorded.

208 **EEG Recording and Analysis**

209 Electroencephalographic (EEG) activity was recorded during the action observation
 210 task from 30 active electrodes using a Brain Vision Quickamp amplifier system with an
 211 ActiCap cap referenced to FCz. Vertical electro-oculogram (VEOG) activity was recorded
 212 from one extra electrode (below right eye), and horizontal electro-oculogram (HEOG) activity
 213 was recorded from one extra electrode (to the left of the left eye). EEG and EOG recordings
 214 were sampled at 1000 Hz, and electrode impedance was kept below 10k Ω .

215 Prior to segmentation, a vertical ocular calculation was applied ($1*Fp2+(-1*VEOG)$).
 216 All data were re-referenced to a common average reference. EEG and EOG activity were
 217 band-pass filtered (0.1-70 Hz, notch filter at 50Hz). Data were visually inspected for noisy
 218 sections or channels, and for other general artifacts. EEG activity containing blinks was
 219 corrected using a semi-automatic ocular ICA correction approach (Brain Vision Analyzer 2.1).
 220 An average of 3 ICA components were removed per individual dataset.

221 The 2-minute resting EEG data was then cut in to 2s epochs (starting 0-2000ms).
 222 Semi-automatic artifact detection software (Brain Vision Analyzer 2.1) was run, to identify and
 223 discard segments with non-ocular artifacts (drifts, channel blockings, EEG activity exceeding
 224 $\pm 50\mu V$). A fast-fourier transformation, with 10% Hanning window, was then applied to each
 225 segment. The average alpha (8-13 Hz) and beta power (13-35 Hz) at rest was then calculated
 226 across all artifact-free segments for each electrode of interest. There was an overall data loss

227 of 5.24% for the resting EEG, with an average of 57 (out of 60) baseline segments retained
 228 per participant.

229 The action observation EEG task trial data segments (hand action and static hand)
 230 were cut into 2s epochs (500-2500ms from stimulus onset). Semi-automatic artifact detection
 231 software (Brain Vision Analyzer 2.1) was run, to identify and discard segments with non-
 232 ocular artifacts (drifts, channel blockings, EEG activity exceeding $\pm 50\mu\text{V}$). A fast-fourier
 233 transformation, with 10% Hanning window, was then applied to each segment, and the signal
 234 was averaged for each condition and electrode. There was an overall data loss of 6.02% for
 235 the hand action trials and 6.49% for the static hand trials, with an average of 28 (out of 30)
 236 trial segments retained per participant.

237 The average mu/alpha (8-13Hz) and beta (13-35Hz) power for each condition was
 238 calculated for the electrodes of interest over the central (C3, Cz, C4) and occipital electrodes
 239 (O1, Oz, O2). This allowed us to test whether changes in mu and beta desynchronization over
 240 central sites were distinct from alpha and beta desynchronization over occipital sites (Hobson
 241 & Bishop, 2017). A measure of the percentage change in power for each condition (test: hand
 242 action or static hand) and the resting EEG as a reference period (reference) was calculated
 243 for each electrode of interest for both alpha and beta bands, using the formula: (reference-
 244 test/reference) x 100 (Puzzo et al., 2011). Any outlier data points were excluded for both
 245 alpha and beta desynchronization values ($\pm 3\text{SD}$ from the mean). Data from electrodes C3,
 246 Cz and C4 were averaged for the central electrode site, and data from electrodes O1, Oz and
 247 O2 were averaged for the occipital electrode site. Positive values indicate alpha and beta
 248 desynchronization and negative values indicate alpha and beta synchronization.

249 **Statistical Analysis**

250 All statistical analyses were conducted in R version 3.5.0. The data and code are
 251 available at osf.io/z2ndf. To investigate alpha and beta desynchronization during the action
 252 observation EEG task, two 2 x 2 repeated measures ANOVAs were performed, with condition
 253 (hand action, static hand) and electrode site (central, occipital) as within-subject variables,
 254 and alpha and beta desynchronization values as the dependent variables. Post-hoc paired-
 255 samples t-tests (two-tailed) were conducted to investigate the source of significant
 256 interactions.

257 To investigate relationships with age, a series of regression models tested linear and
 258 curvilinear relationships between alpha/beta desynchronization to hand actions versus static
 259 hands during the action observation EEG task and age, and for each social cognition
 260 measure and age. The first series of models specified the outcome variable as the action-
 261 static difference in power across the central electrodes in the alpha or beta band and the
 262 predictor variable as age using linear, quadratic, cubic, or quartic terms. The best fitting model
 263 was deduced by comparing the simpler model against the more complex model using an
 264 ANOVA (i.e., linear vs. quadratic, quadratic vs. cubic, cubic vs. quartic; see supplementary
 265 materials [S2]). If the p-value was greater than .05, then the simpler model was selected as
 266 the best fitting model. The best fitting model was then re-run with the addition of the action-
 267 static difference in power across the occipital electrodes as a covariate. If a curvilinear
 268 relationship with age was determined, follow-up linear regressions were performed by
 269 subsetting the data into appropriate age bands to further describe any increases or decreases
 270 across certain periods of age. This sequence of model fitting was then repeated separately for
 271 each of the following outcome variables: (1) percentage correct for RMET, (2) ToM score and
 272 (3) physical score for Strange Stories, and (4) total score in the EQ. If a curvilinear model
 273 provided the best fit, then the curve was examined with a series of linear regressions to
 274 further describe the relationship with age. Finally, two multiple regression models were
 275 conducted to examine whether age and the social cognitive measures are related to the alpha
 276 and beta desynchronization during the action observation EEG task. These models specified
 277 alpha/beta desynchronization across the central electrodes as the outcome variables, and
 278 age, RMET, ToM and physical score in Strange Stories, EQ total as predictor variables, and
 279 alpha/beta desynchronization across the occipital electrodes as a covariate.

280 **Results**

281 **Action Observation**

282 Figure 1 shows the mean percentage change in power from baseline during static
 283 hand observation and hand action observation over the central and occipital electrodes for
 284 both alpha and beta bands.

285 A 2 (condition) x 2 (electrode) repeated measures ANOVA revealed a significant main
 286 effect of condition in both the alpha ($F(1, 300) = 335.60, p < .001, \eta^2 = .528$) and beta band
 287 ($F(1, 300) = 439.40, p < .001, \eta^2 = .594$), showing significantly greater desynchronization
 288 during hand action observation (alpha $M = 20.38\%$; beta $M = 15.55\%$) compared to static
 289 hand observation (alpha $M = -1.52\%$; beta $M = -0.30\%$). A significant main effect of electrode
 290 site was found for both the alpha ($F(1, 300) = 9.75, p = .002, \eta^2 = .032$), and beta band ($F(1,$
 291 $300) = 7.92, p = .005, \eta^2 = .026$), indicating greater power over the occipital electrodes (alpha
 292 $M = 11.63\%$; beta $M = 9.03\%$) compared to the central electrodes (alpha $M = 7.23\%$; beta M
 293 $= 6.21\%$). There was also a significant 2-way interaction between condition and electrode in
 294 the beta band ($F(1, 300) = 79.77, p < .001, \eta^2 = .210$). To examine this 2-way interaction,
 295 follow up analyses compared the magnitude of the action-static difference in power across the
 296 central versus occipital electrode sites. The action-static difference in power was significantly
 297 greater over the central site ($M = 19.65\%$) compared to the occipital site ($M = 12.05\%$) for the
 298 beta band ($t(300) = 7.60, p < .001$).

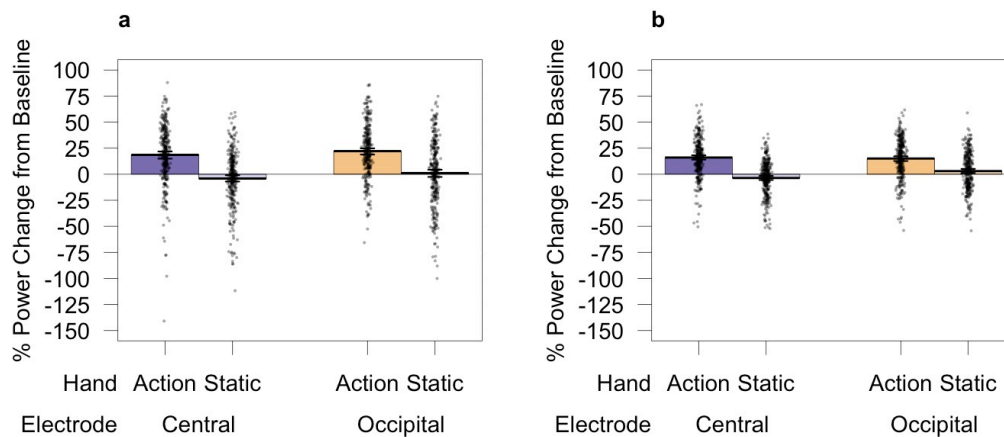


Figure 1. Mean percentage change in power from baseline for static hand observation and hand action observation over the central and occipital electrodes in alpha (a) and beta (b) bands. The bold horizontal line indicates the group mean and the bars indicate the 95% confidence intervals. The points show the raw data. Positive values indicate alpha and beta desynchronization and negative values indicate alpha and beta synchronization.

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300 Relationship with Age and Social Cognition

301 To more closely examine changes in the modulation of sensorimotor mu
 302 desynchronization to action observation over the lifespan, a series of regression models
 303 tested linear and curvilinear relationships between alpha/beta desynchronization and age

304 (see Table A for model comparisons). This was repeated for each social cognition measure to
 305 further examine social cognition across the lifespan. Finally, a multiple regression was
 306 conducted to investigate the relationship between alpha/beta desynchronization, age, and
 307 social cognition, whilst accounting for activity over the occipital electrodes.

308 To examine changes in alpha/beta desynchronization, a difference score was
 309 calculated for each participant by subtracting the percentage change in power for the static
 310 hand condition from the percentage change in power for the action hand condition in the
 311 action observation task, separately for alpha and beta power bands, across the central
 312 electrodes. Mean difference scores per participant are displayed in Figure 2a, showing age as
 313 a continuous variable.

314 A linear model provided the best fit of the data for the relationship between the action-
 315 static difference in alpha power and age (alpha: $R^2 = .14$, $F(1, 299) = 48.93$, $p < .001$) and a
 316 cubic model provided the best fit of the data for the relationship between the action-static
 317 difference in beta power and age ($R^2 = .29$, $F(3, 297) = 40.44$, $p < .001$). Age significantly
 318 explained the variance in the action-static difference over the central electrodes in both the
 319 alpha and beta power bands (alpha: $\beta = .37$, $p < .001$; beta: $\beta = .79$, $p < .001$; $\beta^2 = -.17$, $p =$
 320 $.005$; $\beta^3 = -.18$, $p = .006$). In the alpha band, desynchronization to hand actions versus static
 321 hands increased linearly from 10 to 86 years of age. To further describe the curvilinear
 322 relationship with age in the beta band, linear regressions on certain age periods were
 323 conducted; β estimates and p -values are presented to indicate significant relationships for
 324 each age period. In the beta band, desynchronization to hand actions versus static hands did
 325 not change between 10 to 17 years old ($\beta = .13$, $p = .372$), but increased from 18 to 60 years
 326 of age ($\beta = .44$, $p < .001$), then decreased from age 60 onwards ($\beta = -.27$, $p = .013$). These
 327 relationships remained when accounting for the action-static difference over the occipital
 328 electrodes (alpha: $R^2 = .35$, $F(2, 298) = 83.32$, $p < .001$; beta: $R^2 = .48$, $F(4, 296) = 68.52$, $p <$
 329 $.001$).

330 A cubic model provided the best fit of the relationship between RMET and age ($R^2 =$
 331 $.09$, $F(3, 297) = 9.54$, $p < .001$). Age was significantly associated with RMET scores (all beta
 332 coefficient $ps < .012$), indicating an increase in RMET scores from 10 to 35 years of age ($\beta =$

333 .34, $p < .001$), a decrease from 35 to 70 years old ($\beta = -.22$, $p = .009$), and a plateau from 70
 334 years old ($\beta = -.13$, $p = .395$; Figure 2b).

335 A linear model provided the best fit of the relationship between EQ and age ($R^2 = .02$,
 336 $F(1, 299) = 7.07$, $p = .008$). Age was significantly associated with EQ ($\beta = .15$, $p = .008$)
 337 indicating an increase in levels of empathy with increasing age (Figure 2c).

338 A cubic model provided the best fit of the relationship between Strange Stories ToM
 339 scores and age (cubic $R^2 = .05$, $F(3, 297) = 5.59$, $p < .001$). Age was significantly associated
 340 with Strange Stories ToM scores (all beta coefficient $ps < .002$), indicating an initial increase
 341 in ToM scores from 10 years to 30 years of age ($\beta = .26$, $p = .008$), a decrease from 30 to 70
 342 years old ($\beta = -.17$, $p = .028$), and a plateau from 70 years of age onwards ($\beta = -.13$, $p = .395$;
 343 Figure 2d). Strange Stories control scores were not significantly associated with age ($\beta = .07$,
 344 $p = .257$; linear $R^2 = .004$, $p = .257$; Figure 2e).

345 Crucially, to explore the relationship between sensorimotor activity, age, and social
 346 cognition, a multiple linear regression was calculated to predict the action-static difference in
 347 alpha/beta desynchronization over the central electrodes based on age, RMET scores,
 348 Strange Stories ToM and control scores, and EQ score, accounting for the action-static
 349 difference over the occipital electrodes. The regression model was significant for both alpha
 350 ($R^2 = .37$, $F(6, 294) = 28.39$, $p < .001$) and beta power ($R^2 = .47$, $F(6, 294) = 44.04$, $p < .001$)¹.
 351 This analysis revealed that the action-static difference over the central electrodes was
 352 significantly predicted by the action-static difference over the occipital electrodes (alpha $\beta =$
 353 $.49$; beta $\beta = .48$), age (alpha $\beta = .23$; beta $\beta = .38$), and Strange Stories ToM score for beta
 354 power only (beta $\beta = .10$). None of the other predictors were significant (all $ps > .211$).

¹ A second multiple regression was conducted to include the quadratic and cubic terms for age due to the curvilinear relationship for the action-static difference at the central electrodes and age in the beta band. The results of this analysis were similar ($R^2 = .49$, $F(7, 293) = 40.04$, $p < .001$), with identical predictors of the action-static difference at the central electrodes in the beta band.

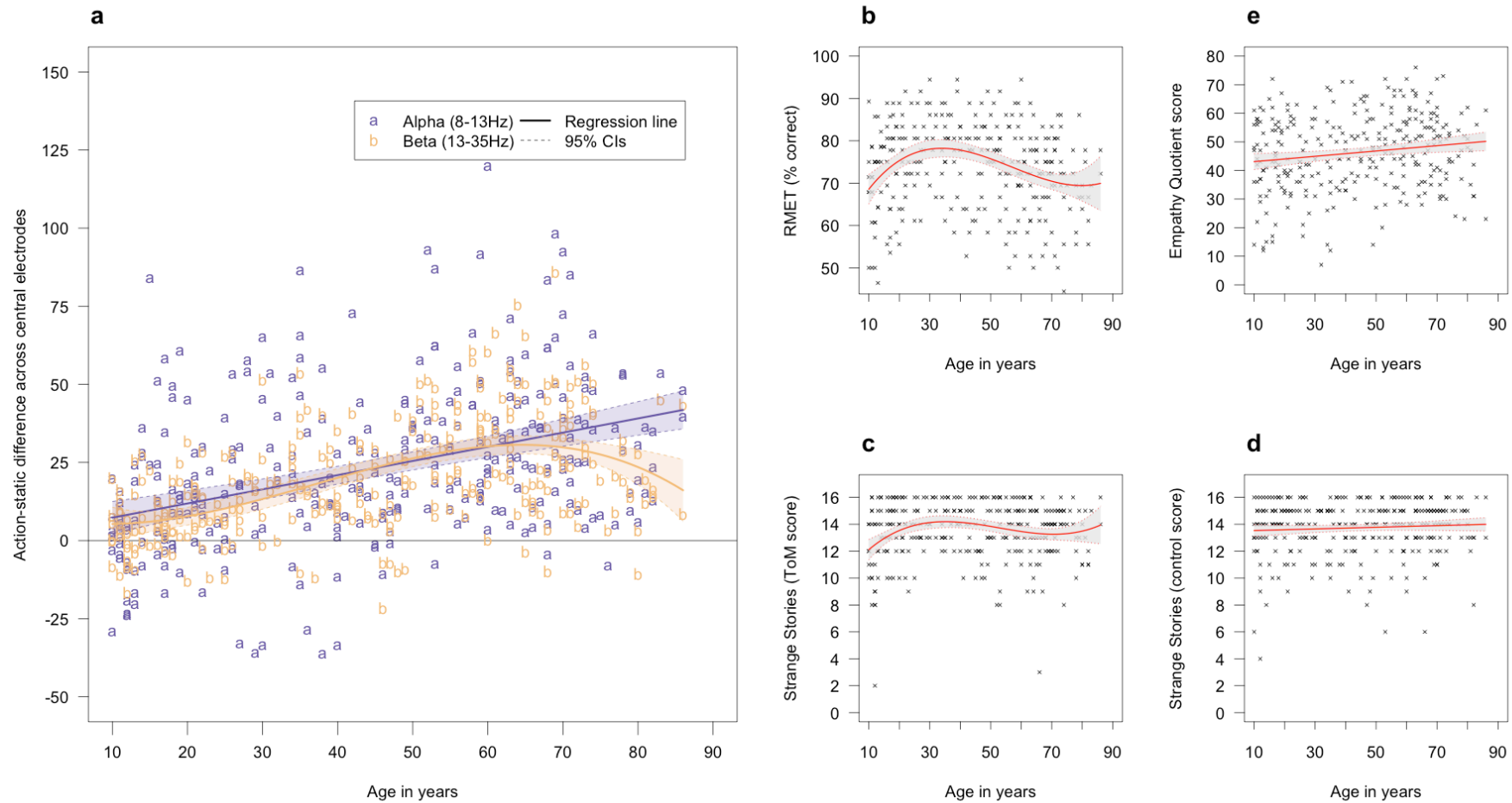


Figure 2. Relationship between age (in years) and a) the mean percentage change in alpha and beta power in the central electrodes from static hand observation to hand action observation in the action observation task, b) percentage correct in Reading the Mind in the Eyes Task (RMET), c) Empathy Quotient (EQ) total score, d) Strange Stories Theory of Mind (ToM) score, and e) Strange Stories control score. The bold line indicates the best-fitting regression line and the dashed line indicates the 95% confidence intervals (CIs).

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Discussion

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The present study is the first to explore sensorimotor mu rhythm during action observation from late childhood through to old age. Three-hundred and one individuals aged 10- to 86-years-old observed short video clips depicting hand actions or a static hand, and mu/alpha (8-13Hz) and beta (13-35Hz) desynchronization were used as an EEG marker of mirror system activity across the sensorimotor cortex. Results revealed greater alpha and beta desynchronization across the sensorimotor cortex during hand action observation compared to static hand observation, in support of our predictions.

Importantly, our study is the first to explore the developmental trajectory of the mirror system from 10 years old through to 86 years old in a sizable sample. Analyses revealed a greater percentage change in the alpha power band over the central electrodes to hand action observation from 10 to 86 years old. In contrast, the percentage change in beta power over the central electrodes to hand action observation did not change through adolescence, but increased from 18 to 60 years old, then decreased in older age. These differential patterns over age for sensorimotor alpha and beta rhythms to observing actions suggest that these rhythms have distinct developmental trajectories. These distinct developmental trajectories likely reflect the dissociable, but complementary, processes underlying the two rhythms, with the alpha rhythm suggested to be related more to sensory processing and beta rhythm related more to motor processing (Ritter et al., 2009). These patterns therefore highlight the importance of measuring both alpha and beta power bands in EEG studies of action observation.

These age-related changes in the sensorimotor mu rhythm during action observation are a novel finding; the few existing studies that have examined aging and action execution/observation have generally compared a dichotomous sample of younger versus older adults (Hutchinson et al., 2002; Riecker et al., 2006; Schmieft-Fehr et al., 2016), which does not allow the investigation of developmental trajectories from adolescence and through middle age. The overall action-static desynchronization effect found here shows that a functioning mirror system is present in late childhood and adolescence. However, in line with studies showing continued development of the 'social brain' during adolescence (Blakemore, 2008), our results reveal that the mirror system has not reached full maturity by adolescence;

385 sensorimotor alpha desynchronization increased between adolescence and into adulthood,
 386 and sensorimotor beta rhythm remained the same during adolescence but increased into
 387 adulthood.

388 Crucially, our findings also suggest that the reactivity of the sensorimotor mu rhythm
 389 to action observation continues to change beyond adolescence, throughout adulthood and
 390 into older age. This enhanced sensorimotor alpha/beta rhythm into older age parallels that
 391 seen in previous research that has found over-activation of motor areas during action
 392 execution in older adults (Heinrichs-Graham et al., 2018; Rossiter et al., 2014; Schmiedt-Fehr
 393 et al., 2016; Vallesi & Stuss, 2010). We have provided novel evidence that this change
 394 emerges incrementally *throughout* adulthood, and is not tied specifically to the onset of old
 395 age (typically considered 65 years old plus). This related research interprets the increased
 396 activation in older age either as a compensatory aging mechanism, or as detrimental in
 397 nature (Ward, 2006). The compensatory account proposes that advancing age leads to
 398 increasing compensatory activity to maintain task performance, whereas the detrimental
 399 account proposes that advancing age leads to greater activity that causes poorer task
 400 performance. Our findings suggest that while sensorimotor mu desynchronization during
 401 action observation clearly increases through adulthood and into older age in the alpha band,
 402 activity in the beta band actually decreases from 60 years onwards. As such, the current data
 403 only provides partial support for these existing accounts, and suggests that any
 404 compensatory or detrimental activity reaches a peak around the onset of old age. It is also
 405 interesting to note that the static or declining mu desynchronization observed here in older
 406 age would have been occluded in a group comparison design (e.g., 19-26-year-olds vs. 55-
 407 71-year-olds; Schmiedt-Fehr et al., 2016), or in studies that only test a linear relationship
 408 between beta desynchronization and age (Ritter et al., 2009).

409 An interesting alternative to these existing compensatory/detrimental accounts is that
 410 the increasing sensorimotor mu desynchronization across adulthood to action observation
 411 reflects *enhanced* specialization of the mirror system. This novel proposal is supported by
 412 previous research showing effects of expertise, where motor areas show greater activity while
 413 observing an action that is part of the observer's motor repertoire (Calvo-Merino et al., 2006).
 414 Moreover, mu suppression has been shown to increase after active experience with actions,

415 indicating that action expertise modulates the sensorimotor mu rhythm (Cannon et al., 2014;
 416 Marshall et al., 2009; Quandt et al., 2011). It is therefore possible that the increasing
 417 sensorimotor activation seen across adulthood might reflect individuals' increasing
 418 experience/expertise with the observed motor actions. This possibility is particularly relevant
 419 in the current study since the observed videos depicted everyday hand actions (e.g. unlocking
 420 a door, dialling on a phone), meaning that participants' experience with those actions was
 421 likely to increase with age due to more frequent encounters in everyday life. An expertise
 422 account would therefore be compatible with the continuously increasing effect seen across
 423 adulthood in the current study. Crucially, this account would suggest that the human brain
 424 continues to develop and specialize not just through adolescence and young adulthood (as
 425 previously documented by Blakemore, 2015), but well into middle age.

426 This study also explored the developmental trajectories of higher social cognitive
 427 processes. Participants completed three additional measures purported to assess complex
 428 emotion understanding, theory of mind ability and empathic capacity. Complex emotion
 429 understanding (as measured by the RMET) improved from adolescence through to adulthood
 430 with a peak at 35 years old, and a decline through middle age to 70 years old, and no change
 431 in older age. Empathy capacity (as measured by the EQ) showed a linear increase from
 432 adolescence into old age. Finally, theory of mind ability (as measured by the Strange Stories)
 433 showed an improvement from adolescence through to adulthood with a peak at 30 years old,
 434 a decline to 70 years old, and no further change in old age. In contrast, the control stories
 435 from the Strange Stories did not show a relationship with age, suggesting that age effects in
 436 this task are specific to social inferences and do not simply reflect a general decline in
 437 memory. Taken together, our social cognitive findings support research that has reported
 438 behavioral declines in older age in the understanding of complex emotions and mental states
 439 (Henry et al., 2013) and contrasts with research that has reported no age-related differences
 440 in empathy capacity (Beadle et al., 2012; Grühn, et al., 2008). Therefore, this study adds to
 441 the literature as we demonstrate distinct developmental trajectories of different social
 442 cognitive processes that is occluded in past research that has used group comparison
 443 designs.

444 Importantly, we also explored whether increasing age and these higher social
 445 cognitive processes are related to the functioning of the mirror system. Increasing alpha
 446 desynchronization to action observation was related to increasing age, but was not related to
 447 any measure of social cognition, after controlling for desynchronization over the occipital
 448 cortex. Increasing beta desynchronization over the sensorimotor cortex to action observation
 449 was related to increasing age and theory of mind ability, after controlling for
 450 desynchronization over the occipital cortex. This indicates that there is an age-related change
 451 in alpha desynchronization that does not map onto a behavioral change in the social cognitive
 452 components tested here. In addition, this finding suggests that sensorimotor processes and
 453 social cognitive processes may be underpinned by distinct neural mechanisms, each with
 454 different developmental trajectories. This suggestion is consistent with a meta-analysis of
 455 more than 200 fMRI studies of the mirror and mentalizing systems (Van Overwalle & Baetens,
 456 2009). This meta-analysis indicated that the mirror and mentalizing systems are both involved
 457 in the processing of sensory or verbal information about other people. However, the mirror
 458 and the mentalizing systems are rarely concurrently activated, with the mirror system
 459 activated by the observation of moving body parts when no active inferential processing is
 460 required and the mentalizing system activated when this input is not available (Brass et al.,
 461 2007; Van Overwalle & Baetens, 2009). In line with the conclusions of Brass et al. (2007), the
 462 distinction between mirror processes and social cognitive processes in the current study may
 463 be due to the degree of inferential processing needed to understand the actions, i.e., the
 464 familiar actions used here would be automatically mapped on to the person's motor repertoire
 465 to understand the actions with little to no input from the mentalizing system, whereas the
 466 mirror system may be dependent on the mentalizing system when inferring the purpose of an
 467 action is more difficult, such as for understanding unfamiliar hand actions. One challenge for
 468 future work is to identify the degree of inferential processing needed to understand different
 469 types of actions, particularly from an aging perspective. For example, we find that mentalizing
 470 abilities decrease throughout adulthood, and as such, we would predict increased difficulties
 471 with age in action understanding for actions with greater levels of inferential processing (e.g.,
 472 unfamiliar versus familiar actions).

473 The finding that theory of mind ability predicted beta desynchronization, but not alpha
 474 desynchronization, has interesting implications for the specificity of the relationship between
 475 mirror system development and social cognitive skills. Though we acknowledge that the effect
 476 size for the relationship is small even in the beta rhythm, we consider how this difference
 477 might relate to the different underlying processes that each rhythm is likely to reflect.
 478 Specifically, it has been suggested that beta desynchronization to the observation of an
 479 action reflects the activity of the motor cortex that guides motor preparation and selection,
 480 and supports the understanding of complex actions (Ritter et al., 2009). Therefore, a better
 481 understanding of other people (i.e., theory of mind) may be related to better understanding of
 482 goal-directed actions of other people, resulting in greater activity of the motor cortex during
 483 action observation. This is a tentative link that requires further investigation as we note that
 484 the current study mapped behavioral changes in a small set of general social cognitive
 485 processes using diverse measures and paradigms onto putative EEG markers of the mirror
 486 system. Future research should investigate how more specific motor skills map onto the
 487 functioning of the mirror system across the lifespan, preferably using a range of tasks that
 488 assess different components of social cognition, and elicit a behavioral response alongside
 489 the EEG measures. Some obvious candidates are imitation and grasp responses (Kumar et
 490 al., 2013), as both have been shown to modulate activity in the mirror system, which can be
 491 mapped onto changes at a behavioral level. We note that neither of these capacities have
 492 been explored in a lifespan context, meaning that significant open questions remain regarding
 493 whether and how changes in the mu desynchronization might predict decreasing motor
 494 control with advancing age (Seidler et al., 2011) or in clinical movement disorders (e.g.
 495 Parkinson's disease, Caligiore et al., 2017).

496 In this paper we interpret our findings with the view that sensorimotor mu
 497 desynchronization to action observation reflects the activation of the mirror system. However,
 498 there is a debate regarding the extent to which mu desynchronization reflects mirror system
 499 activity (see Bowman et al., 2017; Hobson & Bishop, 2017a; Hobson & Bishop, 2017b). For
 500 example, an alternative interpretation suggests that the central mu rhythm instead indexes
 501 somatosensory features of an action, rather than the motor features of an action (Coll et al.,
 502 2015; Cook et al., 2014), reflecting sensory processing rather than motor mirroring (Coll et al.,

2017). Hobson and Bishop (2017a) suggest that to show evidence of mirroring, mu desynchronization studies should include both action execution and observation conditions, report EEG activity from multiple electrode sites, and evaluate attentional confounds. Firstly, we note that the current study did not include an action execution condition. This would be an interesting future avenue of research to investigate whether a comparable age-related increase in mu desynchronization is seen during execution (Marshall & Meltzoff, 2011). Secondly, we report EEG activity from multiple electrode sites, including both central and occipital sites. We note that it is unlikely that the mu desynchronization effect in our study reflects differences in attentional demands between conditions (Bazanov & Vernon, 2014). In line with Hobson and Bishop (2017a), we compared mu/alpha and beta desynchronization over central and occipital electrode sites. Although there was an indication of occipital alpha suppression, a different pattern of results emerged for central mu suppression that corresponded with the results for beta desynchronization. In addition, increasing age remained related to the action-static difference in mu desynchronization over the central sites when accounting for the difference at occipital sites.

Finally, we acknowledge the possibility that the increase in mu desynchronization in the current study could be influenced by the observation of transitive actions in the hand action condition compared to no actions in the static hand condition, or the presence of objects in five out of six hand actions compared to the absence of objects in the static hand condition. However, we do not believe that these low-level differences are driving sensorimotor effects seen here for a number of reasons. Influential findings have indicated no difference in mirror system activation for transitive versus intransitive actions (e.g., Press, Bird, Walsh & Heyes, 2008), with no moderating effect on the mu rhythm for object versus non-object directed stimuli (Fox et al., 2016). Moreover, the mirror neuron system is activated during the observation, imitation and production of both object-directed and (non-object) communicative hand gestures (Montgomery, Isenberg & Haxby, 2007). The mere presence of objects does not lead to mu desynchronization (Perry & Bentin, 2009), and mu desynchronization has been shown to be greater when observing moving hands than when observing static hands, moving objects, or static objects (Pfurtscheller et al., 2007). Additionally, Papadourakis and Raos (2017) have recently shown that the mirror neurons of

533 rhesus macaque monkeys' respond to the observation of both transitive and intransitive
 534 actions, and these discharge differences are correlated with the kinematic differences of the
 535 actions, not with the objects' features. This suggests that mirror neurons code the kinematics
 536 of actions and can detect subtle differences, suggesting that they have a role in encoding the
 537 goals of actions.

538 **Conclusion**

539 We explored the developmental trajectory of the mirror system and social cognitive
 540 processes from 10 years old through to 86 years old in a large sample of healthy individuals.
 541 We show for the first time that sensorimotor activation to action observation continues to
 542 increase throughout adulthood, with additional changes in older age. A functional mirror
 543 system is apparent from adolescence through to older age, but this is still maturing during
 544 adolescence. Moreover, an increase in sensorimotor activation to observing actions across
 545 adulthood was observed, which may reflect increasing experience with hand actions,
 546 suggesting that the mirror system continues to specialize for action observation throughout
 547 adulthood. Emotion recognition, theory of mind and empathy showed distinct developmental
 548 trajectories; these behavioural changes did not map onto alpha desynchronization elicited
 549 during action observation, although beta desynchronization during action observation was
 550 shown to be related to theory of mind ability. These distinct patterns illustrate specificity in the
 551 relationship between mirror system development and social cognitive skills.

552 In general, studies have largely overlooked middle-aged participants when
 553 investigating sensorimotor processes related to the mirror system and social cognitive
 554 processes, with studies either focussing on infants and children, student populations, or
 555 comparing dichotomous groups of young versus older adults. The findings of the current
 556 study highlight the importance of studying this age group, with measurable changes in both
 557 sensorimotor activation and social cognitive processes throughout adulthood. Overall, our
 558 findings indicate that the activity of the mirror system increases throughout the lifespan with
 559 measurable changes into older age that are independent from social cognitive processes.

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563

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