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2 Title: Developmental profile of slow hand movement oscillation coupling in humans

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4 Running head: Movement oscillation coupling development

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6 Authors: Katherine M. Deutsch¹, John A. Stephens¹ and Simon F. Farmer^{1,2}

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9 ¹Department of Physiology, University College London, The Rockefeller Building, University
10 Street, London WC1E 6BT

11 ²The National Hospital for Neurology & Neurosurgery, Queen Square, London, WC1N 3BG

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17 Corresponding author:

18 Katherine M. Deutsch

19 PO Box 1867, Doylestown, PA 18901

20 Phone: 814-404-7942

21 Fax: 301-402-7010

22 Email: kmdeutsch@yahoo.com

23

24 **Abstract**

25 In adults, slow hand and finger movements are characterized by 6-12 Hz
26 discontinuities visible in the raw records and spectra of motion signals such as acceleration.
27 This pulsatile behavior is correlated with motor unit synchronization at 6-12 Hz as shown by
28 significant coherence at these frequencies between pairs of motor units and between the motor
29 units and the acceleration recorded from the limb part controlled by the muscle, suggesting
30 that it has a central origin. In this study, we examined the correlation between this 6-12 Hz
31 pulsatile behavior and muscle activity as a function of childhood development. Sixty-eight
32 participants aged 4-25 years performed static wrist extensions against gravity or slow wrist
33 extension and flexion movements while extensor carpi radialis (ECR) muscle
34 electromyographic (EMG) and wrist acceleration signals were simultaneously recorded.
35 Coherence between EMG and acceleration within the 6-12 Hz frequency band was used as an
36 index of the strength of the relation between central drive and the motor output. The main
37 findings of the study are 1) EMG-acceleration coherence increased with increases in age, with
38 the age differences being greater under movement conditions, and the difference between
39 conditions increasing with age, 2) the EMG signal showed increases in normalized power with
40 increases in age under both conditions, 3) coherence under movement conditions was
41 moderately positively correlated with manual dexterity. These findings indicate that the
42 strength of the 6-12 Hz central oscillatory drive to the motor output increases through
43 childhood development and may contribute to age-related improvements in motor skills.
44
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46 Keywords: motor control, children, EMG

47 **Introduction**

48

49 In humans, muscle contractions during static limb posture and movement contain
50 oscillations with a frequency between 6-12 Hz (Elble & Randall, 1976; Vallbo & Wessberg,
51 1993). Coherence between acceleration and muscle activity and synchronization between
52 motor units within this frequency band are evident during static contraction (Elble & Randall,
53 1976; Farmer et al., 1993; Halliday et al., 1999; Mayston et al., 2001) and movement (Kakuda
54 et al., 1999; Wessberg & Kakuda, 1999) of wrist and finger muscles, pointing to a central
55 origin. Importantly, coherence and motor unit synchronization is increased during movement,
56 suggesting that movement-related 6-12 Hz oscillations may be ‘injected’ by the central
57 nervous system over the 6-12 Hz oscillations present during static muscle contraction. The
58 oscillations have been proposed to reflect an organizational principle of motor control (Vallbo
59 & Wessberg, 1993) whereby muscle contractions are driven by a central oscillatory command
60 dependent on oscillations within cortical, spinal and cerebellar networks (Gross et al., 2002).
61 A number of studies have produced evidence that 6-12 Hz oscillations are driven by central
62 nervous system processes supported by peripheral feedback (Conway et al., 2004; Elble &
63 Randall, 1976; Erimaki & Christakos, 2008; Gross et al., 2002; Halliday et al., 1998; Mayston
64 et al., 2001; Raethjen et al., 2002; Vallbo & Wessberg, 1993).

65 Neurophysiological changes within the motor system occur up through adolescence
66 (Cavallari et al. 2001; Eyre et al., 1991; Gibbs et al., 1997; Issler & Stephens, 1983).
67 However, oscillatory contributions to the motor output in children have not been studied
68 extensively. It has been shown that children exhibit similar 6-12 Hz but slower ~20 Hz
69 oscillations in the motor output (acceleration) during static limb posture in comparison to

70 young adults (Deutsch & Newell, 2006). However, it is unknown whether the 6-12 Hz
71 oscillations in the motor output are coherent with muscle activity and whether there are
72 developmental changes associated with the 6-12 Hz oscillations observed during movement.
73 It was recently shown that there is an increase in the amplitude of the ~20 Hz oscillatory drive
74 from the motor cortex to the muscle during isometric muscle contraction, as indicated by an
75 increase in oscillatory synchronization between the electromyographic (EMG) signal from co-
76 active muscles and between the sensori-motor cortex and EMG (Farmer et al., 2007; Graziado
77 et al., 2010; James et al., 2008).

78 The present study explores the childhood developmental progression of the 6-12 Hz
79 oscillatory drive during static postural and *dynamic* slow wrist muscle activation, with a
80 particular emphasis on the correlation between muscle activity and the motor output during
81 dynamic conditions. Specifically, we used frequency and time domain techniques to examine
82 age differences in the strength of the relation between EMG and acceleration signals during
83 static postural wrist extensions in comparison to slow wrist movements in participants aged 4-
84 25 years; we also examined whether the strength of the EMG-acceleration correlation was
85 related to manual dexterity. In contrast to previous studies of EMG-EMG and EEG-EMG
86 coherence which have highlighted developmental change in centrally derived beta and gamma
87 rhythms (Farmer et al., 2007; James et al., 2008; Hvass-Petersen et al., 2010), in the present
88 study we focus on peripheral oscillations in the frequency range 6-12 Hz.

89 We hypothesized 1) age-related increases in the 6-12 Hz oscillatory drive to
90 motoneurones as detectable by an increase in the strength of the EMG-acceleration correlation
91 (coherence) within the 6-12 Hz frequency band during both static and movement conditions,
92 2) greater age differences in EMG-acceleration coherence under movement than static

93 conditions, and 3) a positive correlation between EMG-acceleration coherence and manual
94 dexterity. These results have been presented in abstract form (Deutsch et al., 2008; Farmer et
95 al., 2009).

96

97

98 **Materials and Methods**

99

100 **Motor task and data recording**

101

102 Experiments were performed in accordance with the declaration of Helsinki. We
103 obtained data with ethical permission (University College London) and consent from adults,
104 parents and children (68 participants total, aged 4 to 25 years). We recorded simultaneously
105 surface EMG from the belly of the extensor carpi radialis (ECR – interelectrode distance 2-2.5
106 cm) and acceleration from the center of the dorsal surface of the hand (band pass filter 4-256
107 Hz; sampling rate 512 Hz; recorded digitally - Oxford instruments medical systems, Old
108 Woking, Surrey, UK).

109 Participants were seated upright in a comfortable chair with their forearm supported on
110 the arm of the chair in the pronated position and their wrist and hand free to move vertically.
111 They were asked to perform 2 tasks with visual feedback of performance available: 1) slow
112 wrist extension and flexion movements (30 degrees extension and flexion, total range 60
113 degrees) at a rate of 0.5 Hz/cycle (paced with a metronome) and 2) maintain a static postural
114 wrist extension against gravity at a joint angle of zero degrees. For each condition, two runs,
115 each lasting for 1 minute, were obtained. The order of conditions was randomized across
116 participants.

117 In addition, 63 of the participants (18 subjects aged 4-6 years, 16 subjects aged 7-9
118 years, 11 subjects aged 10-14 years, 18 subjects aged 19-25 years) performed a timed motor
119 task comprised of sequential finger-to-thumb oppositions (Denkla et al., 1973) in order to
120 provide a measure of dexterity and speed of movement. Although the task did not involve the

121 wrist, it was chosen because it is simple enough for the younger children to perform and has
122 been previously validated as a measure of age-related changes in dexterity (Denkla, 1973) and
123 used in other studies of motor unit synchronization during disease (Farmer et al., 1993) and
124 development (Gibbs et al., 1997). Participants were asked to oppose each finger to the thumb
125 in a sequential order starting with and returning to the index finger (touching the little finger
126 only once) accurately and as fast as possible. The sequence was repeated five times (total 35
127 individual finger taps per trial) and 2 trials of the task were performed with each hand (order
128 of hands randomized across subjects). The run was repeated if the participant made visible
129 errors; therefore, an error score was not part of the data analysis. Prior to recording, the
130 experimenter demonstrated the task and a brief practice was allowed.

131

132 **Data analysis**

133

134 The EMG and acceleration signals from each of the two runs of the static wrist
135 extension and slow wrist movement conditions were combined to create a 2-min time series
136 for each condition for each participant. Full wave rectification of surface EMG signals was
137 adopted. This approach has been shown to maximize the information regarding timing of
138 motor unit action potentials whilst suppressing information regarding waveform shape
139 (Myers et al. 2003). Analysis of individual records between paired EMG and acceleration
140 signals was based on record lengths of 120 s of data. The method of autospectral and cross
141 spectral estimation was that of averaging over disjoint sections of data using 1-s window
142 lengths and a Hanning window giving a basic frequency resolution of 1 Hz (Halliday et al.,

143 1995). This number of sections was sufficient to produce 95% confidence levels on individual
144 coherence estimates that were below 0.05.

145 For each 2-min time series, estimates of the autospectra of the EMG and acceleration
146 signals, $f_{xx}(\lambda)$ and $f_{yy}(\lambda)$, and of two functions that characterize their correlation structure:
147 coherence, $|R_{xy}(\lambda)|^2$, and cumulant density, $q_{xy}(u)$, were calculated. Coherence analysis
148 provides frequency domain information on the neurogenic contribution to postural tremor and
149 the relationship between EMG and movement pulsatility (Elble & Randall, 1976; Halliday et
150 al., 1999; Kakuda et al., 1999; Wessberg & Kakuda, 1999). The cumulant density allows
151 examination of the EMG-acceleration correlation in the time domain.

152 Coherence estimates are bounded measures of association defined over the range [0, 1]
153 and cumulant density estimates are unbounded. For the present data, coherence estimates the
154 fraction of the activity in the acceleration signal that can be predicted by the activity in the
155 EMG signal. The reference signal for phase and cumulant density estimates was EMG from
156 the forearm extensor carpi radialis (ECR). For two uncorrelated signals the coherence and
157 cumulant have an expected value of zero; significant deviations from zero indicate a
158 correlation between the EMG and acceleration signals at a particular phase $\Phi_{xy}(\lambda)$, for
159 coherence, or time (u), for the cumulant. The analyses were performed on a personal
160 computer within the Matlab 7.0 (MathWorks, Natick, MA) environment using NeuroSpec 2.0
161 (David M. Halliday, University of York, UK).

162 For comparisons of the spectra across age and condition, we normalized each
163 individual spectrum by calculating the proportion of the total power from 1-30 Hz that was
164 contained within each 1-Hz frequency bin between 1 and 30 Hz (Deutsch & Newell, 2001).
165 We chose this frequency band because it contains most of the frequency content of the power

166 spectral signals of the tasks used in this study and, because it is commonly used in studies
167 comparing various conditions and/or age groups, to allow for comparisons with existing
168 literature. However, because of the possibility that the movement task may introduce low
169 frequency (<1 Hz) components into the power spectra, we re-analyzed the data using 5-30 Hz
170 normalization. Since the results did not differ between the two normalization procedures, we
171 report those using the former (1-30 Hz). Subsequently, the peak frequency (frequency with
172 the maximum normalized power) within the frequency band of interest, 6-12 Hz, and the
173 magnitude of the normalized power at the peak frequency were each determined for the EMG
174 and acceleration signals for each condition for each participant. The Chi² difference of
175 coherence test (see also Farmer et al., 2007) was calculated to evaluate the magnitude of the
176 difference in coherence between the movement and static conditions at each frequency of the
177 spectrum.

178 For the purpose of statistical analyses, the data were grouped into 4 age ranges: 4-6
179 years (n=21), 7-9 years (n=16), 10-14 years (n=11) and adults (19-25 years, n= 20).
180 Significant differences as a function of age group and condition for the peak frequency and
181 magnitude of normalized power at the peak frequency for each signal (acceleration, EMG)
182 and coherence between the two signals were determined with a 4 (Age Group) x 2 (Condition)
183 two-way ANOVA. A one-way ANOVA was used to determine significant age group
184 differences for the Chi² difference of coherence values. The relation between peak coherence
185 within the 6-12 Hz range from each condition (static wrist extension and slow wrist
186 movement) and finger dexterity and age, as well as the relation between finger dexterity and
187 age, were determined with Pearson's Product Moment correlations. The significance level for
188 all statistical analyses was set at p<.05.
189

190 **Results**

191

192 Figure 1 shows raw and analyzed data from 2 participants, an adult aged 20 years (A-
193 C) and a child aged 4 years (D-F). The EMG-acceleration coherence is shown in Figures 1 A
194 and D for the static wrist extension condition and in Figures 1 B and E for the slow wrist
195 movement condition. The raw EMG and acceleration data are shown as inserts. Figures 1 C
196 and F show the Chi² difference between the EMG-acceleration coherence of the static and
197 movement conditions for the same two participants. The adult data shows higher coherence
198 values in both conditions and compared to the child a much greater increase in EMG-
199 acceleration coherence when comparing the static and movement conditions in the frequency
200 range 6-12 Hz (maximal difference at 9 Hz).

201

202 (Figure 1 near here – please use an entire page for this figure)

203

204 **Power spectral analysis of EMG and acceleration signals**

205

206 Figure 2 shows the mean normalized power spectrum (normalized to the total power
207 contained between 1 and 30 Hz) of the acceleration and EMG data for the static wrist
208 extension and slow wrist movement conditions for each age group. Note that, with increases
209 in age, the spectral profile of the acceleration signal appears more peaked under static
210 conditions but broader under movement conditions (Figures 2 A and C, respectively). In
211 addition, the EMG spectral profile of the adult but not children data exhibits a discernible
212 peak in the 6-12 Hz frequency band under both conditions (Figures 2 B and D).

213

214 (Figure 2 near here)

215

216 These age-related changes observed in the spectral profiles of the EMG and
217 acceleration signals were confirmed by 4 (Age Group) x 2 (Condition) ANOVAs on the peak
218 frequency within the 6-12 Hz band and magnitude of the normalized power at the peak
219 frequency (see Table 1). The analyses of the peak frequency of both the EMG and
220 acceleration spectra showed significant Age Group ($F_{3,128}=12.52$, $p<0.01$ and $F_{3,128}=5.98$,
221 $p<0.01$, for EMG and acceleration, respectively) and Condition ($F_{1,128}=18.90$, $p<0.01$ and
222 $F_{1,128}=32.35$, $p<0.01$ for EMG and acceleration, respectively) main effects but no interaction.

223 Post hoc tests of the Condition main effects for the peak frequency within the 6-12 Hz
224 band of the acceleration and EMG signals indicated a significantly lower peak frequency
225 under movement than static conditions. Post hoc tests of the Age Group main effects for the
226 peak frequency within this band for the two signals indicated that the 4-6-year-old and 7-9-
227 year-old groups showed a significantly lower peak frequency than the 10-year-old and adult
228 groups in the EMG signal and the adult group in the acceleration signal.

229 The ANOVAs on the magnitude of the normalized power at the peak frequency within
230 the 6-12 Hz band for the EMG and acceleration data both revealed significant main effects for
231 Age Group ($F_{3,64}=29.65$, $p<0.01$ and $F_{3,64}=7.00$, $p<0.01$ for the EMG and acceleration,
232 respectively) and Condition ($F_{1,128}=19.01$, $p<0.01$ and $F_{1,128}=62.82$, $p<0.01$, for the EMG and
233 acceleration, respectively), and an Age Group x Condition interaction ($F_{3,128}=6.22$, $p<0.01$
234 and $F_{3,128}=14.73$, $p<0.01$ for the EMG and acceleration, respectively).

235 Post hoc tests of the main effects for the normalized power at the peak frequency
236 within the 6-12 Hz band of the EMG signal showed a significantly lower magnitude of
237 normalized power for all the children's groups than the adult group and for the movement than
238 static condition. However, post hoc tests of the interaction revealed that only the adult group
239 exhibited a significantly lower magnitude of normalized power in the EMG signal during the
240 movement versus static condition. In addition, although all the children's groups exhibited a
241 significantly lower magnitude of normalized power at the peak frequency within this band
242 than the adult group under the static condition, only the 7-9-year-old group did so under the
243 movement condition.

244 For the acceleration signal, post hoc tests of the main effects on the normalized power
245 at the peak frequency showed a significantly lower magnitude of power for the 4-6-year-old
246 group than the adult group and for the movement than static condition. However, post hoc
247 tests of the interaction indicated that, under the static condition, the 4-6-year old group
248 exhibited a significantly lower magnitude of normalized power at the peak frequency than the
249 10-14-year-old and adult groups and the 7-9-year-old group a significantly lower magnitude
250 of normalized power than the adult group. Post hoc tests of the interaction also showed that
251 both the 10-14-year-old and adult groups (but not the younger age groups) exhibited a
252 significantly lower magnitude of power at the peak frequency under movement than static
253 conditions.

254 In sum, all age groups exhibit a lower peak frequency and reduced normalized power
255 at the peak frequency within the 6-12 Hz frequency band of the power spectra of the EMG and
256 acceleration signals under movement than static conditions. With the exception of the
257 acceleration signal during movement, the normalized power at the peak frequency increases

258 with increases in age. The difference in the magnitude of normalized power at the peak
259 frequency between conditions increases with increases in age for both EMG and acceleration
260 signals.

261

262 (Table 1 near here)

263

264 **Correlation between EMG and acceleration signals**

265

266 Figure 3 A and B show the EMG-acceleration coherence for the static wrist extension
267 and slow wrist movement conditions, respectively, as a function of age and frequency. Figure
268 4 A and B show the mean (\pm SEM) coherence magnitude and frequency of maximum
269 coherence, respectively, for the 6-12 Hz band for the two conditions for each group. A 4 (Age
270 Group) x 2 (Condition) two-way ANOVA on the peak coherence within the 6-12 Hz
271 frequency band revealed main effects for Age Group, $F_{3,64}=20.62$, $p<.01$, and Condition,
272 $F_{1,128}=16.59$, $p<.01$, and a significant Age Group x Condition interaction, $F_{3,128}=2.79$, $p<.05$.
273 Post hoc tests of the main effects revealed significantly greater peak coherence in the 6-12 Hz
274 frequency band for the adults than children and under movement than static conditions. Post
275 hoc tests of the interaction indicated that the difference in peak coherence between the static
276 and movement conditions reached significance only for the adult group. In addition, the adult
277 group exhibited a significantly greater coherence than all the children's groups under
278 movement conditions and the two younger age groups under static conditions.

279 A 4 (Age Group) x 2 (Condition) ANOVA on the frequency of the peak coherence
280 between the acceleration and EMG signals within the 6-12 Hz frequency band revealed a

281 significant Age Group main effect only ($F_{3,64}=3.56$, $p<0.05$). Post hoc tests showed a
282 significantly lower frequency for the peak coherence of the 4-6-year-old group than the 10-
283 year-old group.

284

285 (Figures 3 and 4 near here)

286

287 The difference in coherence between static and movement conditions as a function of
288 age is further exemplified in Figure 3 C, which illustrates the mean difference in coherence
289 between the movement and static conditions (movement minus static) for each age group as a
290 function of frequency. The one-way ANOVA on the calculations of the maximum Chi²
291 difference in coherence between conditions within the frequency band of interest, 6-12 Hz,
292 revealed a significantly greater difference for the adult group than the 4-6-year-old and 7-9-
293 year-old groups, $F_{3,64}=6.21$, $p<.01$, but no significant age differences in the frequency of the
294 maximum Chi² difference (see Table 2).

295

296 (Table 2 near here)

297

298 Figure 5 A and B show the mean (\pm SEM) cumulant and lag, respectively, of the time
299 domain correlation analyses between the EMG and acceleration signals as a function of age.
300 The 4 (Age Group) x 2 (Condition) ANOVA on the lag of the acceleration signal relative to
301 the EMG signal indicated that the lag between the signals was significantly smaller during the
302 static than movement condition ($F_{1,128}=7.29$, $p<.01$) but did not differ significantly as a
303 function of age. The ANOVA on the peak amplitude of the cumulant revealed a significantly

304 larger peak amplitude for the adult group than the 4-6-year-old group ($F_{3,128} = 10.67$, $p < .01$),
305 but no other significant effects.

306

307 (Figure 5 near here)

308

309 In sum, the analyses of the correlation between EMG and acceleration signals show
310 that with increases in age the peak EMG-acceleration coherence within the 6-12 Hz frequency
311 band increases, as does the difference in peak coherence between the movement and static
312 conditions (larger under the movement than static condition). However, the degree to which
313 the EMG signal leads the acceleration signal does not differ as a function of age under either
314 static or movement conditions, with all groups exhibiting a greater lag under movement than
315 static conditions.

316

317 **Relations between dexterity, coherence, and age**

318

319 Finger dexterity (i.e., speed, indicated by taps/s in the finger-to-thumb tapping task)
320 and age were positively correlated ($r = .86$, $p < .01$) and each was also positively correlated
321 with the maximum EMG-acceleration coherence within the 6-12 Hz frequency band under
322 both static ($r = .30$, $p < .05$ and $r = .41$, $p < .01$, for the correlations with finger dexterity and
323 age, respectively) and movement ($r = .49$, $p < .01$ and $r = .66$, $p < .01$, for the correlations with
324 finger dexterity and age, respectively) conditions (see Figure 6 A-E). Taking age into
325 consideration in the calculations of the correlations between finger dexterity and EMG-
326 acceleration coherence under each condition reduced the correlations to non-significant levels,

327 suggesting that other aspects related to developmental age also play a role in the strength of
328 these correlations. However, this does not remove completely the possibility that dexterity
329 and EMG-acceleration coherence are related. Correlations can be highly influenced by
330 between subject variability and the correlation between the EMG-acceleration coherence
331 under the movement condition and dexterity came close to reaching significance ($p = .06$),
332 suggesting that a larger sample size may have resulted in a significant relation between these
333 two variables. Note that the correlation of finger dexterity with the maximum EMG-
334 acceleration coherence is greater for the movement than the static condition.

335

336 (Figure 6 near here – please use 1/3 or 1/2 a page for this figure)

337

338

339 **Discussion**

340

341 Previous studies have shown age-related changes during *static* muscle contraction in
342 the power spectral profile of acceleration and EMG signals, and in EMG-EMG and EEG-
343 EMG coherence with particular focus on centrally derived 16-32 Hz beta oscillations (Deutsch
344 & Newell 2006; Farmer et al., 2007; Gibbs et al., 1997; Graziado et al., 2010; James et al.,
345 2008). Here, we show age-related differences in the 6-12 Hz frequency band in EMG and
346 acceleration and coherence between the two during static muscle contraction *and* movement.
347 Critically, we show that the difference between static and movement EMG-acceleration
348 coherence increases with increases in age. We suggest that motor development includes
349 changes in the neurogenic contribution to the motor output that may contribute to
350 improvements in motor skills.

351

352 **Development of 6-12 Hz oscillations**

353 We focused our study on discontinuities in the 6-12 Hz frequency band which, in
354 adults have been shown to be due to motor unit synchronization and coherent modulation of
355 motor unit activity, respectively, for static muscle contraction and movement (Elble &
356 Randall, 1976; Halliday et al., 1995, 1999; Kakuda et al., 1999; McAuley et al., 1997;
357 Wessberg & Kakuda, 1999). These oscillations have been suggested reflect an organizational
358 principle of motor control (Vallbo & Wessberg, 1993) and, therefore, may provide significant
359 information with respect to the typically observed age-related improvements in movement
360 production. We found coherence between the EMG and acceleration signals within the 6-12
361 Hz frequency band to be greater during movement than static contraction, in accordance with

362 previous studies (Kakuda et al., 1999; Wessberg & Kakuda, 1999). Importantly, the
363 difference between conditions increased with increases in age, an effect largely attributable to
364 greater age differences under the movement condition (see Figures 3 and 4). We also found
365 the normalized power (proportion of power) of the peak frequency of the EMG signal within
366 the 6-12 Hz frequency band to increase with age under both movement and static conditions.
367 These findings suggest that the oscillatory drive to the motoneurons within this band increases
368 and becomes more tightly tuned and more strongly synchronized with motor output through
369 childhood development. We speculate that an increase in 6-12 oscillatory influences on motor
370 output contributes to movement production and that it may play a role in improvements in
371 movement performance through childhood.

372 In a previous study, a direct measure of the efficacy of tibialis anterior muscle
373 activation has been shown to correlate positively with gamma band (~40 Hz) tibialis anterior
374 EMG-EMG coherence during walking at a self-selected pace (Petersen et al., 2010). In our
375 study, we were not able to derive a direct measure of movement efficiency because of the
376 constrained nature of the flexion-extension task used to assess EMG-acceleration coherence
377 and the power spectra of the respective signals; that is, subjects were externally cued to
378 complete each iteration of flexion and extension. However, we were able to detect a positive
379 (although moderate) correlation between a measure of manual dexterity (in terms of speed)
380 and EMG-acceleration coherence within the 6-12 Hz frequency band. This supports the idea
381 that oscillations within this band may play a role in the efficiency of movement production.

382 However, whether the increase in synchronization between EMG and acceleration
383 within the 6-12 Hz particular frequency band with increasing age actually contributes
384 mechanistically to age-related improvements in movement performance (e.g., faster, more

385 accurate, consistent) still remains to be determined. Clearly, a multitude of
386 maturation/practice-related factors are likely to influence movement performance
387 improvements through childhood (Deutsch & Newell, 2005). Nonetheless, it should be noted
388 that a motor system network in which timing is constrained by oscillation frequency allows
389 for more robust inter-muscle co-ordination and rapid and accurate limb movement (see also
390 McAuley et al., 1999). Oscillations might convey an advantage through affecting the
391 linearization of muscle properties affecting the execution timing and speed of movement (see
392 Bernstein, 1967). A model of fast single joint human arm movements based on the
393 equilibrium point hypothesis with intermittent control signals (at 10 Hz) resulted in faster limb
394 movements than one with continuous control signals (Kistemaker et al., 2006).

395 Age related improvement in motor output *quality* are reflected in the spectrum of the
396 acceleration signal. A previous study found age-related improvements in the performance of a
397 constant isometric force task, particularly reductions in variability, accompanied by reductions
398 in the normalized power at the peak frequency and a broadening of the spectral profile of the
399 motor output signal (Deutsch & Newell, 2001). These authors proposed that increases in the
400 range of frequencies included in the motor output signal plays a role in reducing performance
401 variability and increasing the smoothness of movements with increases in age through
402 childhood. In this study, we also found an albeit non-significant reduction with increased age
403 in the normalized power (which provides an index of the relative contribution of individual
404 frequencies to the total power of the spectrum) at the peak frequency of the acceleration signal
405 during movement (see Figure 2 and Table 1). The acceleration signal showed a similar
406 pattern as a function of age to the EMG signal under the static condition (increasing with
407 increases in age), in agreement with Deutsch and Newell (2006). Importantly, the difference

408 in normalized power at the peak acceleration frequency within the 6-12 Hz frequency band
409 between the movement and static conditions increased with increases in age (becoming
410 significant for the two older groups).

411 Taken together, the age-related changes in coherence and power spectra suggest that
412 two different types of modifications in the oscillatory contributions to the motor output may
413 play a role in movement production improvements through childhood. One is an increase in
414 the influence of the 6-12 Hz oscillatory drive, which may contribute to improvements in
415 movement efficiency, execution timing and speed. The other is a modification in the relative
416 contributions of oscillations to the motor output, which may contribute to increasing the
417 smoothness of movements.

418 The cumulant density analysis did not indicate a change in the timing relations
419 between EMG and acceleration with age in either the static or dynamic conditions. This
420 suggests that the motor units exert a consistent effect over age on the timing of limb forcing.
421 However, the magnitude of the EMG-acceleration cumulant increased with age in keeping
422 with increases in EMG-acceleration synchrony/coherence.

423

424

425 **Neural contributions to 6-12 Hz oscillations**

426 Afferents may play a role in the 6-12 Hz oscillations observed during movements.
427 Wessberg & Vallbo (1995, 1996) showed that during slow finger movements Group Ia, Ib and
428 II reflex afferents are modulated by 6-12 Hz discontinuities. However, 6-12 Hz movement-
429 induced oscillations appear to primarily involve the central nervous system (Evans & Baker,
430 2003; Kakuda et al., 1999; McAuley et al., 1999; Vallbo & Wessberg, 1993; Wessberg &

431 Kakuda, 1999; Wessberg & Vallbo, 1996). Although central nervous system oscillators are
432 pivotal, peripheral feedback is crucial to the maintenance of 6-12 Hz motor unit synchrony,
433 (Christakos et al., 2006; Erimaki & Christakos, 2008). Welsh et al. (1995) have described
434 units in the inferior olive of the rat cerebellum that show 6-10 Hz synchronous oscillations
435 with activation patterns that depend on the phase of a repetitive movement. There is evidence
436 of 6-9 Hz oscillatory coupling between contralateral primary motor cortex and muscle activity
437 during slow index finger flexion-extension movements (Gross et al., 2002) as well as 6-12 Hz
438 oscillatory coupling between sensorimotor cortex and muscle activity during rapid wrist
439 movements (Conway et al., 2004).

440 Through dynamic imaging of coherent sources, Gross et al. (2002) suggested that the
441 primary motor cortex displays efferent directionality and is the source of 6-9 Hz oscillatory
442 drive to motor neurons during movements and that the 6-9 Hz oscillations detected by
443 peripheral receptors are fed back as an afferent signal to the sensory cortex. Schnitzler &
444 Gross (2005) suggested that 6-12 Hz oscillations either facilitate or result from a pulsatile
445 integration process in which sensory feedback is integrated with an efference copy. It has
446 also been recently proposed that out of phase spinal cord oscillations can dampen the ~10 Hz
447 oscillations in the central drive to motor neurons and thus enhance movement precision
448 (Williams et al., 2010).

449 We are unable to identify the components underlying 6-12 Hz oscillations that undergo
450 age-related changes through childhood in order for oscillations to provide a more prominent
451 driving role in the motor output. Based on human and primate studies it is clear that the
452 sensorimotor cortex forms part of an extensive oscillatory movement network with multiple
453 interactions between contralateral primary motor cortex, pre-motor cortex, thalamus and

454 ipsilateral cerebellum, spinal cord and periphery each of which may display intrinsic
455 oscillatory behaviours (Christakos et al., 2006; Erimaki & Christakos, 2008; Gross et al.,
456 2002; Williams et al., 2009). Any number of these networks, oscillators and interaction
457 mechanisms may change with development to produce stronger and more tuned oscillatory
458 drive to motor neurons. It may be speculated that the nervous system becomes capable
459 through maturation and/or learns through experience that particular oscillations are best suited
460 for specific tasks and then internalizes these oscillatory components into neural networks and
461 communicates with the periphery via oscillatory synchronization.

462

463 **Experimental considerations**

464 Because of the problems of extracting reliable data from young children the
465 experimental paradigm was necessarily very simple. We chose slow (0.5 Hz) wrist
466 flexion/extension movements with visual feedback because they are easy to perform for all
467 age groups. The experimenters paid careful attention to the performance of the task to ensure
468 that it was similar across subjects.

469 Movement related 6-12 Hz EMG-acceleration coherence in the current study is
470 unlikely to be influenced by differences in hand mass between adults and children. Previous
471 studies have shown similarly strong coherence between muscle activity and kinematic signals
472 within this frequency band during slow movements of limb segments of greatly differing
473 mass, i.e. finger, wrist and elbow movements in adults (Conway et al., 1997; Kakuda et al.,
474 1999; Wessberg & Kakuda, 1999). In addition, we found the largest age differences in the
475 power spectral profile of the EMG signal and in the EMG-acceleration coherence, measures

476 that reflect the neurogenic contribution to tremor and are not influenced by mechanical factors
477 (Halliday et al., 1999).

478

479 In summary, we found with increases in age an increase in the normalized power of
480 the EMG signal within the 6-12 Hz frequency band along with increased coherence between
481 muscle activity and acceleration within this frequency band (with the increase being greater
482 during movement), and a significant, though moderate, relation between the strength of the
483 EMG-acceleration coherence during movement and manual dexterity. These results suggest
484 that the 6-12 Hz oscillatory drive to the motor output becomes stronger through childhood
485 development and may contribute to motor skill improvements through childhood.

486

487

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489

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496

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500

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602

603 **Figure Legends**

604

605 Figure 1. Data of 2 participants, an adult aged 20 years (*A-C*) and a child aged 4 years (*D-F*).

606 *A* and *D*: coherence between the electromyography (EMG) and acceleration signals for the

607 static wrist extension condition. *B* and *E*: coherence between the EMG and acceleration

608 signals for the slow wrist movement condition. Inserts in *A*, *B*, *D*, and *E* are raw acceleration

609 (top) and EMG (bottom) data. *C* and *F*: χ^2 difference in coherence between the static and

610 movement conditions. Dashed horizontal lines represent the 95% confidence interval.

611

612 Figure 2. Mean normalized power spectra (normalized to the total power between 1-30 Hz) of

613 the acceleration signal during (*A*) static wrist extension and (*B*) slow wrist movement, and the

614 EMG signal during (*C*) static wrist extension and (*D*) slow wrist movement, for each of the 4

615 age groups. The normalized power at the peak frequency within the 6-12 Hz frequency band

616 of the acceleration data increased with increases in age for the static wrist extension condition

617 but decreased with increases in age for the slow wrist movement condition. The EMG data

618 shows a discernible peak in the 6-12 Hz frequency band only for the adult group under both

619 static wrist extension and slow wrist movement conditions.

620

621 Figure 3. Mean EMG-acceleration coherence as a function of frequency for each of the 4 age

622 groups during (*A*) static wrist extensions and (*B*) slow wrist movements. *C*: Difference in

623 coherence between the two conditions (movement minus static). Dashed horizontal lines in *A*

624 and *B* represent the 95% confidence interval. Coherence was greater under movement than

625 static conditions and increased with increases in age, with age differences being greater under

626 the slow wrist movement condition. The difference in coherence between conditions also
627 increased with age.

628

629 Figure 4. Mean (\pm SEM) of (A) peak EMG-acceleration coherence and (B) frequency of the
630 peak coherence within the 6-12 Hz frequency band, for each of the 4 age groups for the static
631 wrist extension and slow wrist movement conditions. *Significantly smaller than adult group
632 under movement conditions, $p < .01$. †Significantly smaller during the static than movement
633 condition, $p < .05$. ‡Significantly lower than 10-14-year-old group, $p < .05$. Note that only the
634 adult group exhibited a significant difference in peak coherence between conditions.

635

636 Figure 5. Mean (\pm SEM) of the time series correlation between the EMG and acceleration
637 signals for each of the 4 age groups for the static wrist extension and slow wrist movement
638 conditions. A: peak cumulant. B: Lag between EMG and acceleration at the peak cumulant.
639 *Significantly smaller than adult group ($p < .01$). †Significantly smaller under the static than
640 movement condition for all age groups ($p < .01$). Note the absence of age differences in the
641 lag between the EMG and acceleration signals.

642

643 Figure 6. Scatter plots of: (A) finger dexterity (finger tap speed in taps/s) versus age; peak
644 EMG-acceleration coherence within the 6-12 Hz frequency band during (B) static wrist
645 extension versus age, (C) slow wrist movement versus age, (D) static wrist extension versus
646 finger dexterity, and (E) slow wrist movement versus finger dexterity. Each data point
647 represents an individual subject. All correlations are significant at $p < .05$. Note that the

648 correlations of both age and finger dexterity with EMG-acceleration coherence are greater
649 under the movement than static condition.

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Table 1. *Peak EMG and acceleration frequencies within the 6-12 Hz frequency band and normalized power at the peak frequency for the static wrist extension and slow wrist movement conditions for each age group*

Age Group	Static		Movement	
	Peak Freq (Hz)*	Power	Peak Freq (Hz)	Power
<i>EMG</i>				
4-6 yrs	7.7 ± 1.8†	5.52 ± 1.57‡	6.7 ± 0.7†	4.85 ± 1.01
7-9 yrs	8.3 ± 2.2†	4.80 ± 1.37‡	7.1 ± 1.1†	4.05 ± 0.91‡
10-14 yrs	9.5 ± 2.0	4.69 ± 0.96 ‡	8.4 ± 2.1	4.44 ± 0.76
Adult	10.0 ± 1.6	8.89 ± 2.39*	8.9 ± 1.7	5.82 ± 1.78
<i>Acceleration</i>				
4-6 yrs	7.5 ± 0.9‡	15.89 ± 3.91†	6.4 ± 0.7 ‡	16.35 ± 3.66
7-9 yrs	7.6 ± 0.9‡	20.69 ± 5.66‡	6.8 ± 1.0 ‡	15.43 ± 3.63
10-14 yrs	8.4 ± 1.2	23.59 ± 6.95*	6.8 ± 1.3	13.24 ± 4.08
Adult	8.2 ± 1.2	28.30 ± 7.00*	7.6 ± 1.3	13.85 ± 5.09

Values are means ± SD. Normalized power represents the proportion of the total power between 1-30 Hz. * Significantly lower during the movement than static condition ($p < .01$); † Significantly lower than adult and 10-year-old groups ($p < .01$); ‡ Significantly lower than adult group ($p < .01$). Freq: Frequency.

Table 2. *Maximum Chi² difference and frequency of maximum Chi² difference of the peak EMG-acceleration coherence within the 6-12 Hz frequency band between the static wrist extension and slow wrist movement conditions for each age group*

Age Group	Chi ² Diff	Freq (Hz)
4-6 yrs	7.5 ± 6.3*	8.1 ± 2.0
7-9 yrs	9.0 ± 4.9*	8.1 ± 1.8
10-14 yrs	12.6 ± 7.9	8.6 ± 2.2
Adult	32.2 ± 36.0	8.8 ± 1.8

Values are means ± SD. *Significantly smaller than adult group (p <.01). Diff: difference; Freq: Frequency.

Adult 4 years











