

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

Running head: Movement oscillation coupling development

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Abstract

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

Keywords: motor control, children, EMG

Introduction

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

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

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

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

We hypothesized 1) age-related increases in the 6-12 Hz oscillatory drive to motoneurons as detectable by an increase in the strength of the EMG-acceleration correlation (coherence) within the 6-12 Hz frequency band during both static and movement conditions, 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).

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Materials and Methods

Motor task and data recording

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

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

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

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

Data analysis

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

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

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

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

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

spectral signals of the tasks used in this study and, because it is commonly used in studies comparing various conditions and/or age groups, to allow for comparisons with existing literature. However, because of the possibility that the movement task may introduce low frequency (<1 Hz) components into the power spectra, we re-analyzed the data using 5-30 Hz normalization. Since the results did not differ between the two normalization procedures, we report those using the former (1-30 Hz). Subsequently, the peak frequency (frequency with the maximum normalized power) within the frequency band of interest, 6-12 Hz, and the magnitude of the normalized power at the peak frequency were each determined for the EMG and acceleration signals for each condition for each participant. The χ^2 difference of coherence test (see also Farmer et al., 2007) was calculated to evaluate the magnitude of the difference in coherence between the movement and static conditions at each frequency of the spectrum.

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

Results

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

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

Power spectral analysis of EMG and acceleration signals

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

(Figure 2 near here)

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

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

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

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

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

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

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

(Table 1 near here)

Correlation between EMG and acceleration signals

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

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

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

(Figures 3 and 4 near here)

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

(Table 2 near here)

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

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

(Figure 5 near here)

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

Relations between dexterity, coherence, and age

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

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

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

Discussion

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

Development of 6-12 Hz oscillations

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

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

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

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

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

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

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

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

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

Neural contributions to 6-12 Hz oscillations

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

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

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

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

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

Experimental considerations

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

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

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

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

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488 **Acknowledgements**

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490 We gratefully thank the children their parents and their carers and the adult subjects for their
491 help. We are very grateful to Dr David Halliday for his help and advice on pooled coherence
492 analysis. We thank Ratheesh Vimalendran for his help with data collection and Leonardo G.
493 Cohen for his helpful comments on the manuscript. Katherine M. Deutsch is currently
494 affiliated with NINDS, NIH, Bethesda, MD.

495

496

497 **Funding**

498 Dr Simon Farmer was supported by University College London Comprehensive Biomedical

499 Research Center.

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Figure Legends

Figure 1. Data of 2 participants, an adult aged 20 years (*A-C*) and a child aged 4 years (*D-F*). *A* and *D*: coherence between the electromyography (EMG) and acceleration signals for the static wrist extension condition. *B* and *E*: coherence between the EMG and acceleration signals for the slow wrist movement condition. Inserts in *A*, *B*, *D*, and *E* are raw acceleration (top) and EMG (bottom) data. *C* and *F*: Chi^2 difference in coherence between the static and movement conditions. Dashed horizontal lines represent the 95% confidence interval.

Figure 2. Mean normalized power spectra (normalized to the total power between 1-30 Hz) of the acceleration signal during (*A*) static wrist extension and (*B*) slow wrist movement, and the EMG signal during (*C*) static wrist extension and (*D*) slow wrist movement, for each of the 4 age groups. The normalized power at the peak frequency within the 6-12 Hz frequency band of the acceleration data increased with increases in age for the static wrist extension condition but decreased with increases in age for the slow wrist movement condition. The EMG data shows a discernible peak in the 6-12 Hz frequency band only for the adult group under both static wrist extension and slow wrist movement conditions.

Figure 3. Mean EMG-acceleration coherence as a function of frequency for each of the 4 age groups during (*A*) static wrist extensions and (*B*) slow wrist movements. *C*: Difference in coherence between the two conditions (movement minus static). Dashed horizontal lines in *A* and *B* represent the 95% confidence interval. Coherence was greater under movement than static conditions and increased with increases in age, with age differences being greater under

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

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

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

Figure 6. Scatter plots of: (A) finger dexterity (finger tap speed in taps/s) versus age; peak EMG-acceleration coherence within the 6-12 Hz frequency band during (B) static wrist extension versus age, (C) slow wrist movement versus age, (D) static wrist extension versus finger dexterity, and (E) slow wrist movement versus finger dexterity. Each data point 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*

	Peak Freq (Hz)*	Power	Peak Freq (Hz)	Power
Age Group	Static		Movement	
EMG				
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
Acceleration				
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

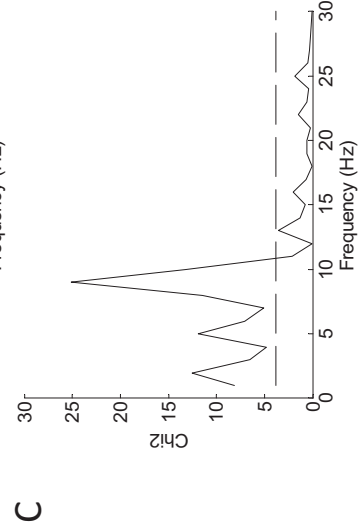
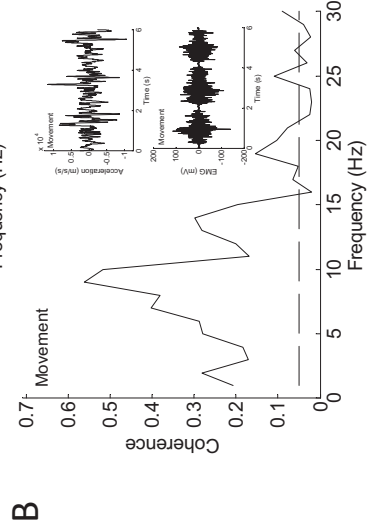
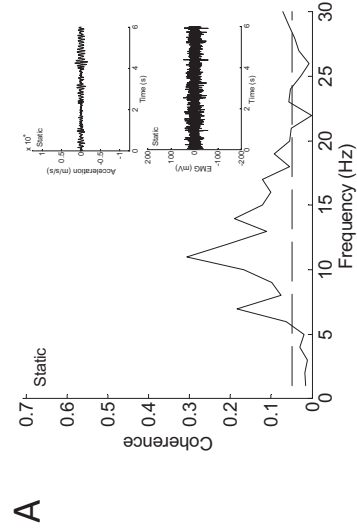
Values are means ± SD. Normalized power represents the proportion of the total power between 1-30 Hz. * Significantly lower during the movement than static condition (p <.01); † Significantly lower than adult and 10-year-old groups (p <.01); ‡ Significantly lower than adult group (p <.01). Freq: Frequency.

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*

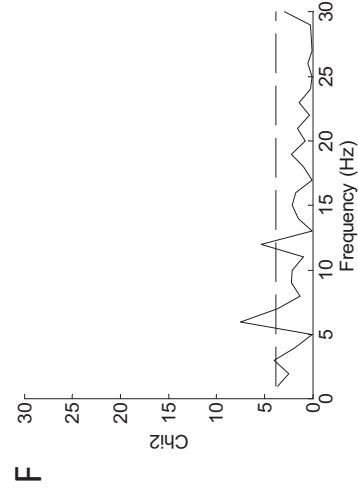
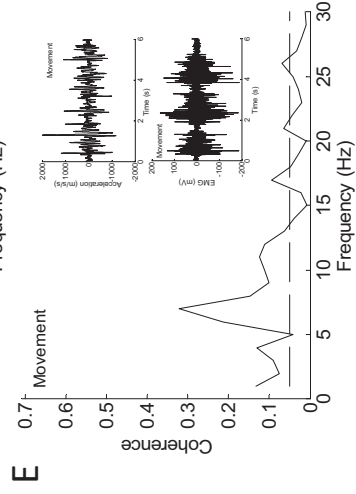
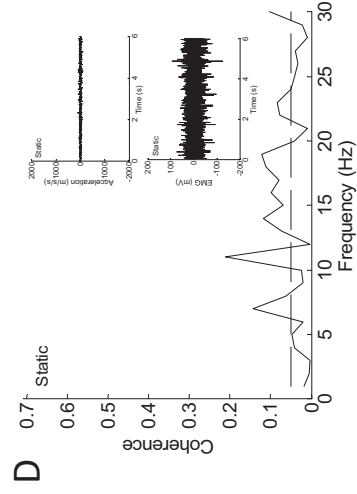
Age Group	Chi ² Diff	Freq (Hz)
4-6 yrs	7.5 ± 6.3*	8.1 ± 2.0
7-9 yrs	9.0 ± 4.9*	8.1 ± 1.8
10-14 yrs	12.6 ± 7.9	8.6 ± 2.2
Adult	32.2 ± 36.0	8.8 ± 1.8

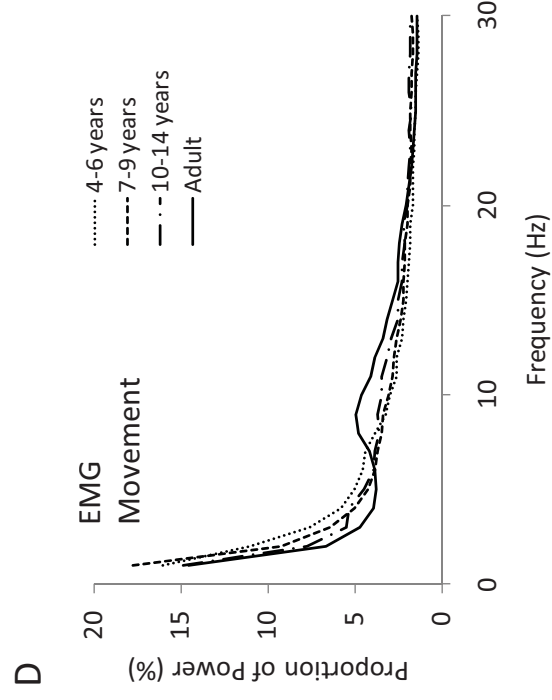
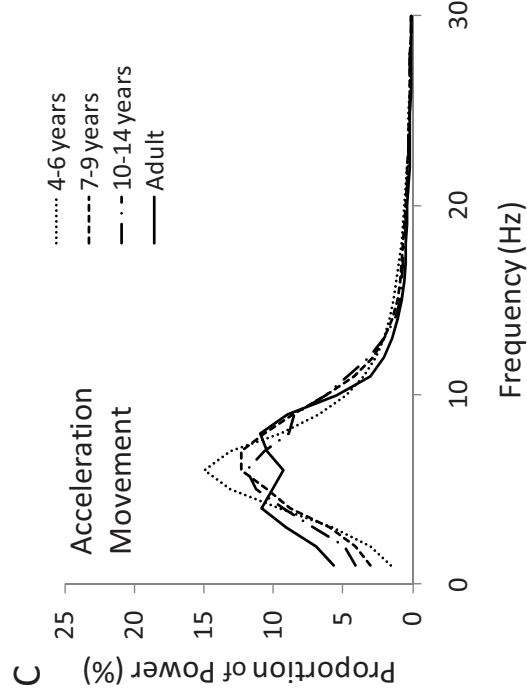
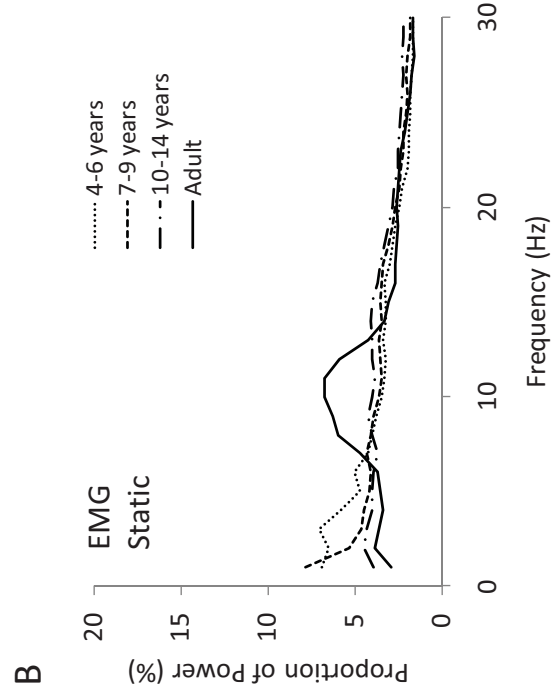
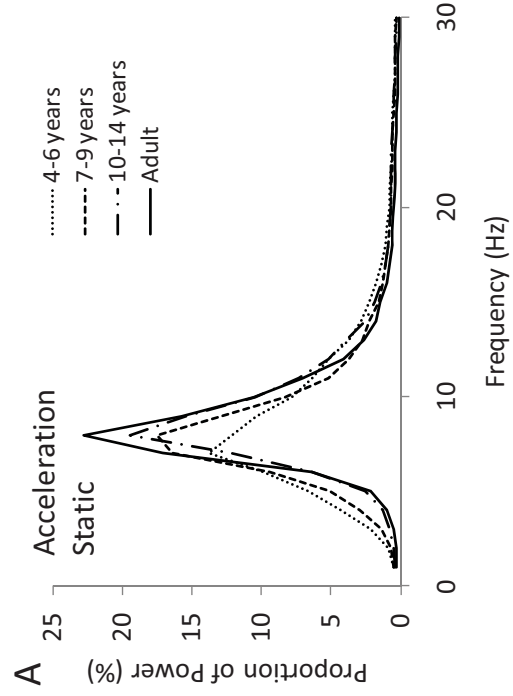
Values are means ± SD. *Significantly smaller than adult group (p <.01). Diff: difference; Freq: Frequency.

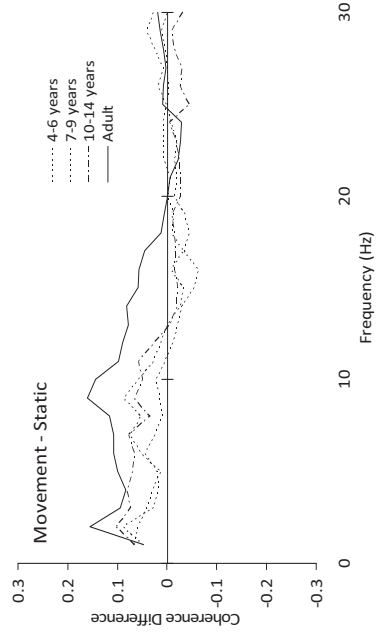
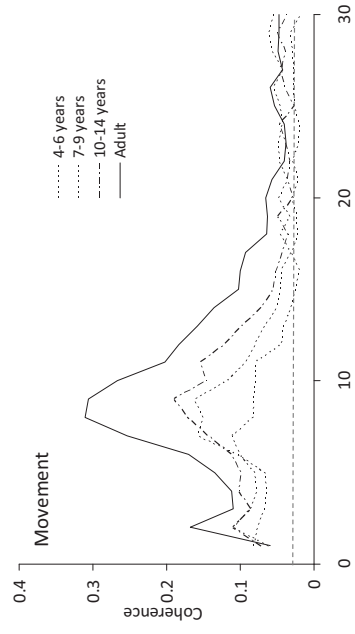
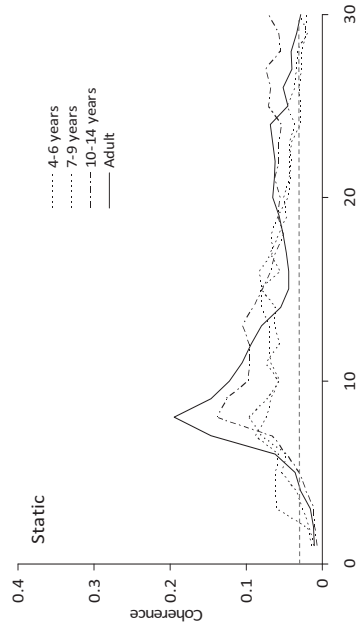
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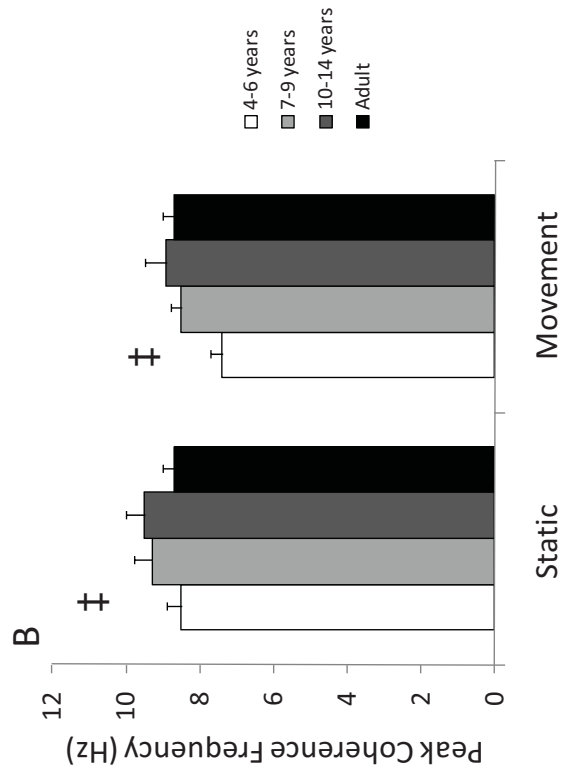
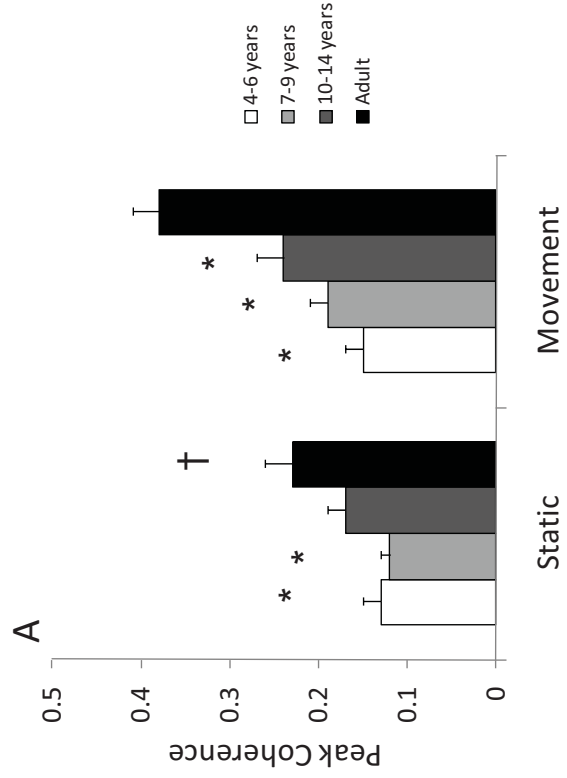


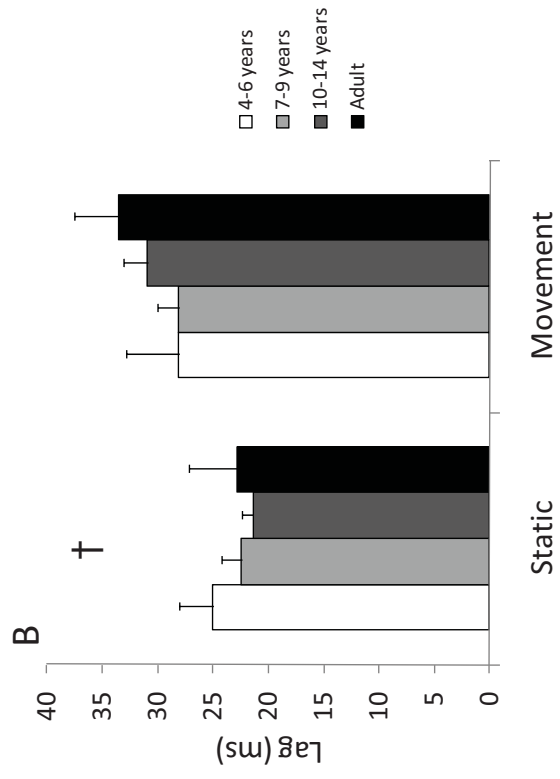
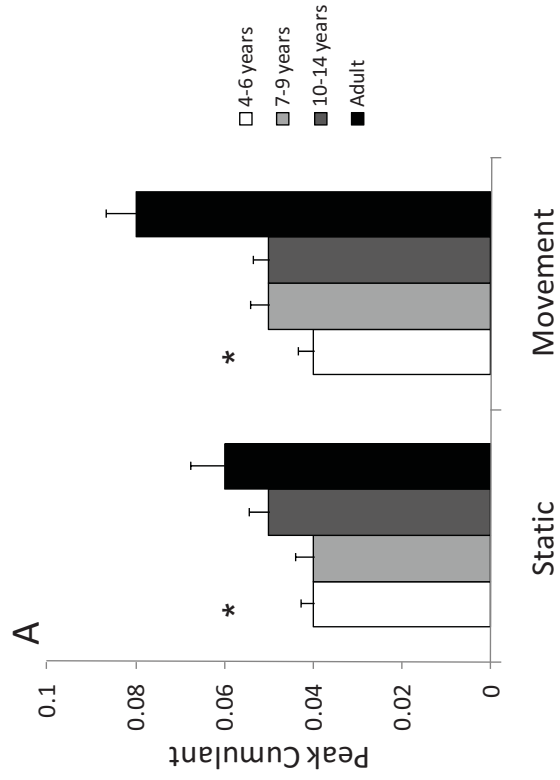
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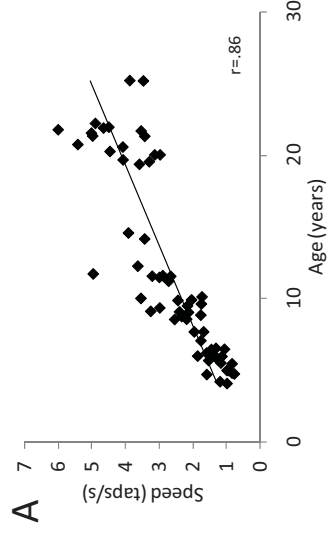




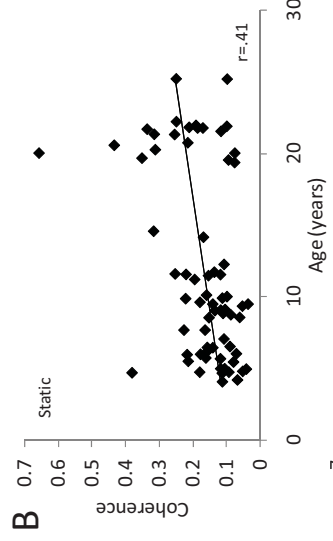




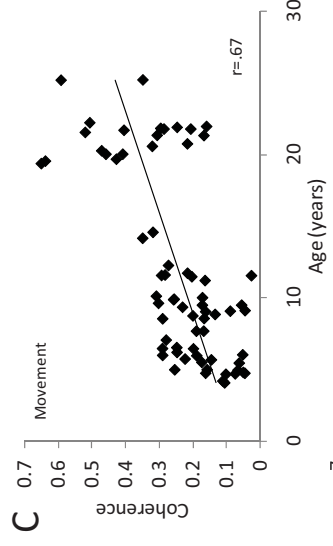




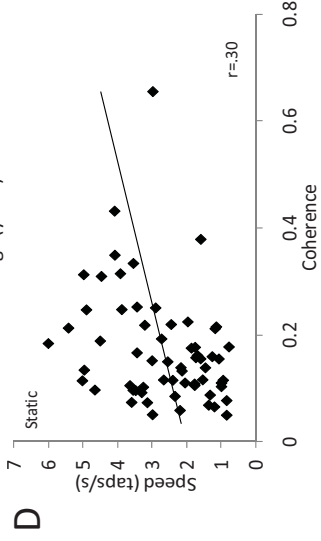
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