RESEARCH ARTICLE



Development of finger force coordination in children

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Abstract Coordination is often observed as body parts moving together. However, when producing force with multiple fingers, the optimal coordination is not to produce similar forces with each finger, but rather for each finger to correct mistakes of other fingers. In this study, we aim to determine whether and how this skill develops in children aged 4-12 years. We measured this sort of coordination using the uncontrolled manifold hypothesis (UCM). We recorded finger forces produced by 60 typically developing children aged between 4 and 12 years in a finger-pressing task. The children controlled the height of an object on a screen by the total amount of force they produced on force sensors. We found that the synergy index, a measure of the relationship between "good" and "bad" variance, increased linearly as a function of age. This improvement was achieved by a selective reduction in "bad" variance rather than an increase in "good" variance. We did not observe differences between males and females, and the synergy index was not able to predict outcomes of upper limb behavioral tests after controlling for age. As children develop between the ages of

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4 and 12 years, their ability to produce negative covariation between their finger forces improves, likely related to their improved ability to perform dexterous tasks.

Keywords Children · Coordination · Finger force · Prehension · Uncontrolled manifold

Introduction

The human hand possesses an amazing range of abilities, and the ability to exquisitely coordinate movements and forces of the hand and fingers is essential for many of our interactions with the world (Johansson and Cole 1992). It is not the strength which is most important, but rather the cooperation between efferent neuronal control of the arm and hand muscles (Lemon 2008) and afferent processing of tactile and visual information (Johansson and Flanagan 2009).

The first finger movements that children demonstrate involve closure of all the fingers together (Forssberg et al. 1991), both as an early reflex as a response to stimulation of the palm, and later as early grasping behavior. With time, more individuated movements are produced (Connolly and Elliott 1972), and different fingers are controlled more individually (Case-Smith 2006). Due to tendons that connect extrinsic muscles to multiple digits, individuated finger movements require more than simply activation of independent muscles. Rather, individuated movements or force production requires the coordination of the muscle action of several muscles (Schieber 1995), such that their combined action results mostly in movement or force production of a single finger. Even in adults, when asked explicitly to produce force with a single finger, the adjoining fingers also produce force, a phenomenon known as enslaving

(Zatsiorsky et al. 2000). This is likely in part due to biomechanical constraints, but also due to neural constraints. In particular, surround inhibition of neighboring muscles is likely to be necessary to achieve individuated movements or force production (Beck and Hallett 2011).

The development of dexterous hand and finger movements proceeds throughout the first decade of life in normally developing children (Forssberg 1999). It is not simply a matter of the ability to produce enough force—levels of force necessary for many actions are reached earlier, around age 4 years (Beenakker et al. 2001). Previous studies have looked at various aspects of the development of dexterous hand finger movements, with multiple studies looking at the development of the precision grip, and the coordination of arm movements and finger aperture in the reach-to-grasp movement (i.e., prehension movements).

The development of the precision grip (i.e., gripping an object using primarily the fingertips) can be characterized by the relationship between the grip force, necessary to prevent the object from slipping out of the hand, and the load force, necessary to lift the object. This develops from a highly variable coordination of grip and load forces, to well-coordinated patterns of load and grip force at approximately age 10 years(Vollmer and Forssberg 2009). In particular, it shifts from being a feedback system, with multiple force peaks observable, to anticipatory force production, with the forces scaled to the physical properties of the system, including the weight of the object (Gordon et al. 1993), and the friction at the digit–object interface (Forssberg et al. 1995; Johansson and Flanagan 2009).

Prehension movements also develop over a similar time span. The prehension movement can be considered as consisting of two components (Jeannerod 1981)—a transport component carrying the hand to the object's location, and a manipulation component, which opens and closes the hand. From approximately 4 months, children make successful reaching movements, but with many submovements, as is evident from the multiple peaks in their velocity profiles (Konczak et al. 1995). As children develop, their hand trajectories straighten, and coordination between the transport and grip formation improves, leading to approximately adult-like kinematic profiles at around age 12 years (Kuhtz-Buschbeck et al. 1998a, b).

While improved coordination (in terms of moving together) between grip force and load force, and between hand velocity and finger aperture, is a sign of typical development, if we consider how multiple fingers apply force together, for example, when grasping an object, this form of coordination (positive covariation) is not necessarily the optimal strategy. In general, the optimal coordination pattern (positive or negative covariation) is task dependent. In multifinger force production tasks, applying scaled versions of the same forces with all the fingers will cause any errors to be multiplied. Rather, the redundancy inherent in multi-digit grasping can be exploited by using the force of one finger to correct small changes of the force applied by another finger. This task-dependent covariation of forces has been studied extensively in adults and is discussed in the framework of the uncontrolled manifold (UCM) hypothesis (reviewed in Latash 2010).

The UCM hypothesis provides a way of quantifying the amount of "good" variance-changes in performance that do not change the value of an outcome measure (such as the total force produced), as well as the "bad" variancechanges in performance which do cause undesirable variance in the outcome measure. The successful use of more "good" than "bad" variance has been described as a synergy, not to be confused with the more common use of the term (e.g., in muscle synergies, where multiple muscles work together). The UCM method has been used successfully in over 100 studies to quantify these measures of variance in a variety of tasks, including finger-pressing tasks (Friedman et al. 2009), during multi-finger grasping (Gorniak et al. 2009), during postural control (Klous et al. 2010) and reaching tasks (Yang et al. 2007). Older participants showed lower synergy indices (i.e., relatively worse variance) than younger participants (Olafsdottir et al. 2007; Kapur et al. 2010), and in some motor disorders, e.g., Parkinson's disease, lower synergies were also observed (Park et al. 2013).

However, the development of synergies throughout childhood has not been studied in detail. There have been very few studies using the UCM approach in children (Black et al. 2007; Wu et al. 2009), and these studies have not looked at finger tasks. In this study, we aim to track the evolution of force-stabilizing synergies as children develop, in ages 4-12 years, in a finger-pressing task. Based on previous studies of grasping coordination described previously, we predict that 12-year-olds would show similar performance to adults, and chose the lower age bound based on the youngest age at which children could successfully perform the task. We predict that due to improved individuation of the fingers, the synergy index will increase as a function of age, i.e., the relative amount of good variance will increase. Further, we predict that an increase in the synergy index will result in better performance on functional tasks, as quantified using standard tests (Jebsen-Taylor and Box and Blocks).

Methods

Participants

Sixty right-handed children took part in the study, aged between 4 and 12 years. As previous studies were not available to use for sample size estimation, and due to the expected variance, we selected 60 participants to allow us an ample number to determine whether linear correlations occurred over the age groups studied. The participants were recruited using convenience sampling. The children were able to understand the instructions, showed normal mental and motor development, and did not report any neurological impairment. A parent completed a questionnaire in order to exclude children with any pre- or postnatal complications, developmental delay, peripheral or central nervous system disease. In addition, they completed the short form of the revised Conners Parent Rating Scale (CPRS-R) (Conners 1997), excluding children suspected of attention deficit/ hyperactivity disorder (ADHD index T score \geq 65). A parent also identified the handedness of the participant. Information about the participants is detailed in Table 1. The study was approved by the Institutional Review Board at Loewenstein Hospital Rehabilitation Center. Before starting the experiment, the procedure was explained to both the child and the parent. Informed assent was received verbally from the child, and informed consent in writing from one of the parents.

Instrumentation

The finger forces of the four fingers (but not the thumb) were measured using a custom-built apparatus (see Fig. 1a),

Table 1 Summary of the number of participants in each age group and the results from the functional tests

Age group	4–5	5–6	6–7	7–8	8–9	9–10	10-11	11–12
N	10	6	5	7	8	8	8	7
Female/male	3/7	5/1	2/3	2/5	5/3	5/3	3/5	2/5
Jebsen–Taylor left hand (s)	80.0 ± 24.8	61.0 ± 8.3	45.6 ± 10.5	44.7 ± 11.7	35.2 ± 4.6	36.8 ± 8.3	34.2 ± 8.6	29.9 ± 3.1
Jebsen–Taylor right hand (s)	57.2 ± 11.3	54.3 ± 18.4	39.3 ± 8.8	34.2 ± 5.8	29.7 ± 2.9	33.1 ± 5.1	27.4 ± 4.1	25.1 ± 2.0
Box and Blocks left hand (num)	30.1 ± 6.5	35.7 ± 8.2	41.6 ± 6.7	43.7 ± 7.7	50.9 ± 7.0	51.0 ± 6.2	57.6 ± 8.0	55.6 ± 5.6
Box and Blocks right hand (num)	33.6 ± 5.9	44.3 ± 2.3	49.6 ± 7.3	50.9 ± 5.4	56.0 ± 4.0	55.3 ± 3.8	64.3 ± 5.3	64.4 ± 9.3
MVC (N)	17.9 ± 4.2	24.1 ± 7.3	23.9 ± 5.1	24.6 ± 5.7	30.9 ± 9.1	28.6 ± 6.0	31.1 ± 4.9	35.6 ± 9.3



Fig. 1 Experimental setup. a Schematic of the setup. The subject's forearm was secured to a piece of wood using Velcro straps, adjusted to the size of the subject's arm. The subject rested their palm on the palm rest (a small cushion made of felt) and placed their four fingers on the force sensors. The setup was designed so that the force sensors will only measure finger forces, and not forces produced by the rest of the arm or body. **b**, **c** Examples of the stimuli presented. The black lines indicate the borders of the screen. After appearing at the bottom

of the screen for 1 s, the image on the left moved up at a constant speed for the next 6 s. The participants controlled the height of the object on the right (either the piece of lettuce (10 trials), or the right half of the rainbow (10 trials)) by pressing on the force sensors, with the height of the object proportional to the force presented (bottom of the screen = 0% MVC, top of the screen = 25% MVC). They were instructed to match the height of the two images

similar to that used previously in UCM experiments (Friedman et al. 2009). The apparatus consisted of four unidimensional piezoelectric force sensors (model 208C01; PCB Piezotronics Inc.), connected via a plastic 3D printed piece (available for download from Friedman 2017) to a piece of wood. The sensors were connected to a charge amplifier (model 482C05; PCB Piezotronics Inc.), then to a data acquisition card (USB-1608G; Measurement Computing). The data were recorded on a PC using the Repeated Measures software (Friedman 2014).

The force sensors (12.7 mm diameter) were placed as close as possible to each other (see Fig. 1a)—horizontally, there was 15 mm between the centers of the sensors, and in the forward–back direction there was 7.5 mm spacing between the sensors. The wrist and forearm near the elbow were fastened to a wooden board using Velcro, to prevent movement of the forearm, and the palm of the hand rested on a small cushion. The participants placed each of their four fingers on a single sensor, with the thumb resting on the wooden board. The setup was designed such that the force sensors would only measure forces produced by the fingers and not from the arm or the rest of the body. Visual feedback on the force production was provided on a 15" Lenovo laptop.

Procedure

For all the force production tasks, the participants used only their dominant (right) hand. The participants first performed three trials where they were asked to press as hard as possible with all four fingers for 5 s (between two beep sounds) to calculate the maximum voluntary contraction (MVC). No visual feedback was provided. The highest value of the sum of the forces from the three trials was selected. The participants rested for 30 s between repetitions.

In the following experiments, the sum of the finger force measured by the sensors corresponded to the height of an object on the screen. This was calibrated such that the bottom of the screen corresponded to 0 N force (i.e., no force), while the top of the screen corresponded to 25% MVC for that participant. The participants performed 20 repetitions of the task—10 with each of two different stimuli. Before each trial, the sensors were zeroed (while the participants did not touch the sensors). In the first task, a picture of a guinea pig moved up on the screen while the participant's force controlled a piece of lettuce, which they were instructed to try and keep as close as possible to the mouth of the guinea pig (see Fig. 1b, c). The image appeared statically at the bottom of the screen for 1 s and then moved up at a constant velocity over the next 6 s. In the second task, the left half of a rainbow moved in a similar fashion to the guinea pig, and the participant controlled the right half of the rainbow. We used two different tasks to maintain attention and to test whether generalization would occur between the two tasks. A task requiring a ramp-like increase of force was used (rather than requiring a constant force level) to make the task more challenging and game-like (to help maintain attention), and to measure coordination over a range of force levels in every trial.

After the force measurements, the participants performed two functional tests. First, a timed version of the Jebsen–Taylor hand function test was performed (Jebsen et al. 1969; Taylor et al. 1973), apart from the writing task, with each of the six parts timed individually. Additionally, the Box and Block test (Mathiowetz et al. 1985) was performed. Both tests were performed for both the left and right hands.

Data analysis

The data were collected at 170 Hz and processed using custom Matlab (The Mathworks) code. The forces were filtered using a fourth-order two-way Butterworth low-pass filter, with a cutoff of 4 Hz. Force initiation was identified as the last time the force was below 5% of the peak force before first reaching 50% of the peak force. This was used rather that the more typical measure of the first time the force was greater than 5% of peak force to avoid falsely identifying small force fluctuations preceding the voluntary start of force production. Many of the children released the force sensors at the end of the trial-this was identified by checking if there was a large negative peak in the force rate in the last 20% of the movement. If this was the case, we went backward to find the force-rate zero crossing and used this as the end of the force production. In trials without a force drop-off near the end of the trial, the end of the trial was used as the end of force production. Due to the very large variation at the start of the test as the participants learned to use the apparatus, the first two trials for all participants were not analyzed.

To quantify how well the participants performed the task, we calculated the straight line deviation. To do this, we used regression to find the best-fit line to the sum of the finger forces (as a function of time). The straight line deviation was then defined as the mean distance of the actual force to the regression line (i.e., the residuals).

Usually, the UCM technique is performed on the variance across trials (Latash et al. 2002b). However, this is reliant on the assumption that participants use a similar strategy in each trial, something which is unlikely to be the case with children. Instead, we used single-trial UCM analysis (Scholz et al. 2003). To do this, we first detrended the forces in each trial. This is achieved by performing regression on the force of each of the fingers and then subtracting the best-fit line. This results in forces which fluctuate around zero. An example of detrended data can be found in Fig. 2b. **Fig. 2** Data analysis procedure. **a** The data from a typical subject. **b** The same forces after detrending. **c** The detrended forces projected onto the directions which do not change the total force $(f_{||})$ and the directions which change the total force (f_{\perp}) ; see Eqs. (4) and (5) for the exact definitions of $f_{||}$ and f_{\perp}



In this task, the goal was to control the total force F_{TOT} (the performance variable), which is the sum of the four finger forces. This can be written as:

$$F_{\rm TOT} = \Sigma f_i,\tag{1}$$

where f_i is the force of an individual finger. When this equation is differentiated, we obtain:

$$\mathrm{d}F_{\mathrm{TOT}} = [1111]\mathrm{d}f,\tag{2}$$

where dF_{TOT} is the change in the total force, and *df* is the vector of changes in the individual finger forces. The matrix [1 1 1 1] which transforms changes in finger forces to changes in the total force is known as the Jacobian.

In the uncontrolled manifold (UCM) procedure, we ask what proportion of the variance of the forces leads to a change in the performance variable (i.e., total force) and what proportion does not. For example, if the detrended force in one finger increases, while another finger decreases by the same amount, the net effect on the performance variable will be zero, and this variance will be classified as "good" variance. The combinations of forces that result in no change to the performance variable (i.e., those along the UCM) can be found by looking at the null space of the Jacobian, i.e., the solutions e_i to this equation:

$$0 = [1111]e_i. (3)$$

There are three solutions to this equation, specifically:

$$\begin{bmatrix} 1/2 & 5/6 & -1/6 & -1/6 \end{bmatrix}^{T}$$
, $\begin{bmatrix} -1/2 & -1/6 & 5/6 & -1/6 \end{bmatrix}^{T}$
and $\begin{bmatrix} -1/2 & -1/6 & -1/6 & 5/6 \end{bmatrix}^{T}$.

That is, the UCM is a 3D linear space in the 4D space of finger forces, whereas the direction orthogonal to the UCM is one dimensional. We projected the forces produced onto these three null space vectors (i.e., find the component parallel to the null space vectors, using the dot product) for each of the three vectors and took their sum to get f_{11} :

$$f_{||} = \sum_{i=1}^{3} \left(e_i^T \cdot df \right) e_i.$$
(4)

By definition, this is the component of the forces that does not affect the performance variable (total force). Therefore, the remainder of the forces affects the performance variable, i.e.,

$$f_{\perp} = df - f_{||}.\tag{5}$$

Figure 2c shows examples of these quantities.

We then calculated the component of variance which did not affect the performance variable, v_{good} , using the definition of variance, normalized by the dimension of the UCM:

$$v_{\text{good}} = \sum_{i=1}^{N_{\text{samples}}} \frac{\left|f_{\parallel}\right|^2}{3N_{\text{samples}}}$$

And, similarly, for the variance which affects the performance variable, v_{bad} :

$$v_{\text{bad}} = \sum_{i=1}^{N_{\text{samples}}} \frac{\left|f_{\perp}\right|^2}{N_{\text{samples}}}.$$

We were interested in the difference between the amount of good variance and bad variance, which is known as the synergy index or Δv . The difference is divided by the total variance in the finger forces normalized by the dimension of the space in which it is computed:

$$\Delta v = \frac{v_{\text{good}} - v_{\text{bad}}}{\left(3 \times v_{\text{good}} + v_{\text{bad}}\right)/4}$$

Thus, the synergy index Δv can range from -4 (i.e., all variance is bad variance) to +4/3 (i.e., all variance is good variance).

Statistical analysis

We performed linear regression to test whether several measures are linearly related to age: MVC, straight line deviation, finger sharing patterns, Jebsen–Taylor score, Box and Blocks score, the components of variance and the synergy index. In addition, we performed structural equation modeling (SEM) using the R package lavaan (Rosseel 2012) to test the relationships between the different tests. A significance level of 0.05 was used throughout the study.

We quantified learning in terms of the synergy index Δv and straight line deviation, by performing regression on these quantities as a function of trial number. A positive slope (for synergy index) or a negative slope (for straight line deviation) would be considered a sign of learning. This calculation was performed separately for the two tasks (guinea pig and rainbow).

Results

Functional tests

The scores for the functional tests for all 60 children are shown in Fig. 3a, b, together with norms. As expected, there is an approximately linear increase for the Box and Blocks score with age, and a decrease in completion time of the Jebsen–Taylor test with age. These correlations were both significant, and details can be found in Fig. 3a, b. We compared the functional tests to norms published in the literature (Jongbloed-Pereboom et al. 2013; Mathiowetz et al. 1985; Beagley et al. 2016; Taylor et al. 1973) and found comparable values.

Task performance

The maximum voluntary contraction (MVC) was defined as the maximum sum of the force produced by the four fingers. The MVC increased approximately linearly as a function of age, as shown in Fig. 3c. The accuracy in performing the task was quantified by the distance from the best-fit regression line in total force, from force onset to the end of force production. The values were normalized by the MVC, to give normalized force units (NFU). This distance reduced linearly as a function of age, as shown in Fig. 3d, i.e., the accuracy improved with age. The details of the correlation are shown in Fig. 3c, d. We note that for both of these measures, including sex as a factor did not significantly improve the model (using the *F* test), i.e., sex does not significantly predict either MVC or accuracy in the ages studied here.

Specific instructions were not given regarding which fingers to use, and due to the redundant nature of the task the participants could share the applied force between the fingers in a myriad of ways. We quantified the percentage of force produced by each finger, averaged over time and across trials, for each participant. These forces are shown in Fig. 3e. A significant reduction was observed in the percentage of force produced by the index finger as a function of age, while for the middle and little fingers the percentage increased.

Portion of trials analyzed

We first segmented each trial into the period of force production, as described in "Methods". On average, 5.35 ± 0.55 s of data were used. We note that the length of data used did not correlate with age ($R^2 = 0.03$, p = 0.19).

Analysis of components of variance

As described in "Methods", we calculated for each participant and trial the good and bad components of variance. The bad components affect the performance of the task, whereas the good components of variance do not. These two components, together with regression lines, are shown in Fig. 4a, b. While the good variance did not change significantly as a function of age, the bad variance decreased. This in turn led to an increase in the synergy index, Δv . Figure 4d, e provides two examples of force production corresponding to (d) low Δv and (e) high Δv . Note that for the low value ($\Delta v = -2.24$), the finger forces are all approximately scaled versions of each other, whereas for the high value ($\Delta v = 0.87$) the finger forces are much more independent.

Relationship between synergy index and functional tests

While a clear relationship was observed between age and synergy index, as shown above, we examined the question

Fig. 3 Performance as a function of age: a Box and Blocks, b Jebsen-Taylor, both performed with the right (dominant) hand. c Maximum voluntary contraction (MVC), d straight line deviation and e finger force sharing. The stars are the values for the children in this experiment; the blue triangles and red squares are norms from the specified papers, with the error bars signifying the standard deviation. The lines are regression lines fit to data from this experiment, with the regression equations shown in the figures



of whether the synergy index Δv is related to the functional tests. To do this, we performed structural equation modeling (SEM), assuming a latent variable we call dexterity, which is a function of age. The SEM model is shown in Fig. 5; only egressions that are significant were included in the final model. We note that we tried including sex as a predictor for dexterity, but it was not significant, neither was the Conner's score. In addition, covariances between the three tests were also not significant, that is, the score on the tests did not predict each other, after the effect of age/dexterity was taken into account. The latent variable dexterity was related to age (standardized coefficient = 0.9). Greater dexterity was then related to better performance on the Box and Blocks test (standardized coefficient = 0.93), the Jebsen–Taylor test (standardized coefficient = -0.84; lower times are better), and the synergy index (standardized coefficient = 0.67).

Learning

As this task is repeated multiple (20) times, the participants may show learning over the course of the experiment. We plotted the average synergy index Δv and straight line deviation as a function of trial, as shown in Fig. 6a, b. To test whether learning did indeed occur, we fit a regression line to the two quantities for each participant, separately for the two tasks (guinea pig and rainbow). For Δv , both tasks showed a significant improvement (i.e., slopes greater than zero), as shown by one-sided *t* tests (guinea pig: slope = 0.068 ± 0.017 , t(59) = 4.06, p < 0.001; rainbow: slope = 0.029 ± 0.015 , t(59) = 1.99, p = 0.03). In addition, we observed transfer from the first task to the second task, as observed by a change in the intercept of the regression line fit to the Δv values

Fig. 4 Components of variance. a The "good" variance does not show a correlation that is significantly different from 0. b The "bad" variance decreases as a function of age. c The Δv increases as a function of age. Note that the values are constrained to be between -3(the finger forces are completely correlated) and 1 (when the finger forces are completely independent). d, e Examples of trials from a subject with a **d** low Δv (-2.24), aged 5 years, and a **e** high Δv (0.87), aged 11 years. The different colors represent the forces produced by the different fingers, with black showing the sum of the forces. d Note that the forces of all fingers are close to being scaled versions of each other. In contrast, in e, the forces produced by the fingers are relatively independent





Fig. 5 SEM model of the relationship between the variables. Only significant regression relationships are shown. The rectangles represent the observed variables; the circle is the latent (unmeasured) variable which we titled dexterity. The numbers are the standardized regression coefficients. The negative sign for the Jebsen–Taylor represents that a better performance in the Jebsen–Taylor test leads to a lower score (time)

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(guinea pig: intercept = -1.25 ± 0.14 ; rainbow: intercept = -1.01 ± 0.12 ; t(59) = -1.9, p = 0.033). To test which component of the synergy index caused this change, i.e., an increase in v_{good} or a decrease in v_{bad} (or both), we performed regression separately on the two components, as shown in Fig. 6c, d. We found that the slopes were significantly greater than zero for v_{good} , but only for the second task (rainbow: slope = 0.0023 ± 0.0010 , t(59) = 2.188, p = 0.02). v_{bad} did not show slopes that were significantly lower than zero. For straight line deviation, no significant improvement was observed, i.e., the slopes were not significantly less than 0 (guinea pig: t(59) = -0.957, p = 0.171; rainbow: t(59) = 1.433, p = 0.921).

Fig. 6 Trial-by-trial changes in **a** synergy index Δv , (-) indicates that this quantity is unitless, **b** straight line deviation, **c** v_{good} and **d** v_{bad} . In **a**, **c**, **d**, the error bars indicate standard error, while in **b** they indicate inter-quartile interval (due to the non-normal distribution of straight line deviation). Note that trials 1–10 are the first task (guinea pig), while trials 11–20 are the second task (rainbow)



Discussion

In this study, we tested the developmental trend of interfinger force coordination during a four-finger pressing task. For this task, increased task-dependent coordination manifests itself by negative covariation in the forces produced by the fingers. We found that for 4- to 12-year-old children, inter-finger force coordination increases as a function of age, with an approximately linear relationship between age and a measure of coordination. Thus, our first prediction was confirmed. The second prediction that the synergy index will predict performance in the functional tests (once the effect of age is removed) was not supported by the analysis.

The coordination of grip force and load force in grasping develops gradually in children (Vollmer and Forssberg 2009), as does the coordination of arm transport and aperture (Kuhtz-Buschbeck et al. 1998a, b). In this study, we found that inter-finger force coordination also improves gradually through development. In the younger children, the strategy used can be described as a "fork" strategy (Latash et al. 2002a), that is, it is as if the participant uses a fork to press the force sensors, with each prong on a different sensor. In this case, the forces applied to each of the sensors will necessarily show very high positive covariation. This strategy is suboptimal, because any error in force specification is necessarily multiplied across the four sensors. Indeed, while inter-finger force coordination did improve as a function of age, Δv was negative for most of the participants, suggesting that the younger participants were not able to show negative covariation in their finger force production. This may be partly due to the task demands, which are less precise than the typical ramp tasks used. This additional freedom in performing the task, while it may still be perceived to be performed successfully, may partially explain the relatively low Δv values observed. The older children show a considerable amount of negative covariation in their forces, similar to patterns observed in adults for comparable tasks. This negative covariation can be observed as different patterns of force production in the different fingers.

A related change in finger force sharing patterns was observed as a function of age (see Fig. 3e), with the older children showing a reduced proportion of index finger force, and an increased proportion of ring and little finger force, which led to a more even sharing of force between the fingers in the older children. When two fingers produce most of the force (index and middle fingers, as is the case for many

Dexterity is the ability to manipulate objects with the hands (Aaron 2006). The dexterity of finger movements is known to improve over the age range studied here: for example, as observed in the reduction in time needed to perform a peg moving task (Kilshaw and Annett 1983). To manipulate objects with the hands, individuated but coordinated control of the fingers is needed, for example, to perform in-hand manipulation such as turning over a small object or buttoning a shirt. Whereas dexterity is typically observed through movements of the fingers, in this task we measured an aspect related to dexterity that has not been previously studied in children. We found that as children develop, there is concurrent improvement in the ability to individuate and coordinate forces. This ability is of importance for manipulating objects with demanding force requirements, such as steadily holding a full cup of water. The improvement in the synergy index with age was achieved by a decrease in bad variance, rather than by an increase in good variance (or a combination of the two). In contrast, when we looked at the learning of the task by participants, we observed that, for the second task, the increase in the synergy index within the session was achieved by an increase in good variance, rather than a decrease in bad variance. These findings are similar to those found in prior studies looking at learning using the UCM paradigm, which have also demonstrated an increase in the good variance (Wu et al. 2012, 2013), although in the current study the learning occurred over a very short time frame. The learning effect was not observed for the straight line deviation (i.e., how close the subjects were to increasing the force at a constant rate). This is somewhat surprising, because while the participants could see how smooth their force production was, by seeing how the object on the right moved, no feedback was provided on the variation of the forces produced by the individual fingers. The relative fast learning observed on the task is likely to be due to the task novelty-in other novel tasks, learning has been observed (Kang et al. 2004). We note that there was only a small amount of transfer between tasks-when the participants were faced with the second task (rainbow), their performance in terms of the synergy index returned to approximately baseline level, despite the two tasks being effectively equivalent, requiring the same gradual increase in forces. The only difference was in the feedback providedthe rainbow provided specific accuracy cues (mismatch of the two halves), whereas the relative location of the two images in the guinea pig task was less precisely specified. These differences in accuracy requirements apparently required the participants to relearn the task, although we note that they did not improve in their performance, at least as quantified using straight line deviation.

We tested the relationship between the synergy index measure and the two functional tests used. As shown by the SEM model in Fig. 5, the behavior in all three tests was predicted well by a latent variable we called dexterity. We note that sex did not have a significant effect on any of the three measures. As the participants in the age range selected were likely before puberty, this is expected (Thomas and French 1985), although some measures of fine motor ability do show a small advantage in females (Comuk-Balci et al. 2016). We did not find any significant covariance between the tests in the SEM analysis, that is, one test does not significantly predict the outcome of another test, once the effect of the dexterity latent variable has been taken into account. This is somewhat surprising, as better task-dependent covariation of finger forces is a sign of improved dexterity and hence it seems reasonable that the synergy index may predict the scores on the Jebsen-Taylor test, which measures fine motor skills. It may be that the effect was not evident due to the relatively small number of participants, both in total number (as typically a much larger sample size is used with SEM) or at any age level. Additionally, it may be because the Jebsen-Taylor test examines many different elements, which include the possibility of highly compensated proximal upper limb movements. Further support for this notion comes from the finding that the synergy index Δv had the lowest standardized coefficient (0.67), i.e., it is less strongly related to dexterity than the other measures. Studying a large number of participants at the same age may help test whether such a connection actually exists.

This study had several limitations. First, only a small number of children were tested in each age group. For this reason, we do not present the work as providing "norms" for this measure, but rather focus on the trends observed as a function of age. In addition, due to unavoidable enslaving between the fingers (Zatsiorsky et al. 2000), some covariation between fingers is expected. The solution to this problem lies in using force modes rather than the measured forces (Friedman et al. 2009). However, to generate the modes, the usual procedure is to have participants press with a single finger in a force ramp task and record the forces generated by all fingers. As it is not clear whether all the participants would understand how to perform the task, and due to the extra time that it would take (as the current task already stretched the patience of the participants), we decided not to include this analysis. We do note, however, that it was recently shown that for linear systems with enslaving, v_{had} in mode space is equal to v_{bad} in force space (Paclet et al. 2014). As enslaving is by definition positive covariation in the finger forces, v_{good} in mode space is necessarily larger than v_{good} in force space, and hence Δv in mode space will also be larger than Δv in force space. If the amount of enslaving is small, as is typically the case with adults, the two analyses will yield similar results. If, however, enslaving plays a large role in the observed Δv values, then measuring enslaving and performing mode space analysis are important future steps in understanding the development of task-dependent covariation in children. In addition, we used convenience sampling for this study; thus, the results may not necessarily correspond to the values for the larger population.

Conclusions

In conclusion, we found that in a pressing task, the synergy index, which is a measure of negative covariation of finger forces, increased approximately linearly as a function of age in children aged 4–12 years. It would be of interest to determine whether this increase in synergy index continues to evolve during puberty and, through testing larger sample sizes, which aspects of motor performance can be predicted by the synergy index. Understanding the development of the synergy index in typically developing children may influence, in the future, our ability to understand force deviations in children with congenital or acquired motor disabilities.

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Compliance with ethical standards

Ethical approval All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki Declaration and its later amendments or comparable ethical standards. Informed assent was obtained from the child participants, and informed consent was obtained from their parents for all participants included in the study.

Conflict of interest The authors declare that they have no conflict of interest.

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