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# Immersive virtual reality alters selection of head-trunk coordination strategies in young children

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# 12 Abstract

13 Developing coordinated motor control is essential for competent interactions with the 14 surrounding world and requires a balanced multisensory integration. This integration can be 15 challenged under altered sensory feedback, as is the case for vision in immersive virtual reality 16 (VR). While recent works suggest that a virtual sensory environment alters visuomotor 17 integration in healthy adults, little is known about the effects on younger individuals. Here, 18 we assessed the development of head-trunk coordination in children aged 6 to 10 years and 19 young adults using an immersive flight simulator and a virtual joint angle reproduction task. 20 Contrarily to previous results, when vision was decoupled from the steering body part, only 21 older children and adults displayed a joint ('en-bloc') head-torso operation mode. Our 22 results reveal that immersive VR affects the coordination strategy in younger children 23 and highlight the immaturity of postural control through the inability to implement a 24 simplified coordination strategy. These findings have implications for pediatric 25 applications of immersive VR, and reveal its usability as an investigation tool for 26 sensorimotor maturation.

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# 28 Introduction

functional hand

Coordinated motor behavior and efficient integration of stimuli from different sensory modalities are necessary for successful interactions with the surrounding environment (1). The development of these abilities follows a long-lasting and elaborate process, starting long before birth and extending into early adulthood. At the motor development level, the skills are usually grouped into two categories. First, gross motor skills comprise postural control and locomotion and require the use of axial and proximal muscles. The maturation of these abilities shows a steep increase until the age of 2 years and continues to refine until later childhood (2–5). Conversely, fine motor skills include precise actions such as 36 movements, but also require multisensory integration such as hand-eye coordination. The 37 time course of fine motor development typically extends over a more extended time period 38 and adult patterns are generally not observed before late childhood (6,7)

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40 The acquisition of a steady posture is a prerequisite for goal-directed behaviors such as 41 reaching from a sitting position or locomotion (1,6). According to the ontogenetic model of 42 postural development during childhood described by Assaiante et al., two main principles 43 guide the selection of a given balance strategy: the choice of a stable reference, which shifts 44 from the pelvis to the head (1,8), and the gradual mastery of the involved degrees of freedom 45 (DOF) (1,9,10). The coordination strategy evolves from an 'en-block' behavior, which minimizes the number of DOF to be controlled (11,12) to a fully articulated strategy, where 46 47 each DOF is controlled individually. Mature, multi-jointed patterns are acquired at different 48 ages, depending on the involved joint and task characteristics. During locomotion, the 'en-49 block' stabilization has been observed from the acquisition of an upright stance until 6 years, 50 while children aged 7 and older started to display a segmental control (10). Similarly, rigid 51 forearm-trunk coupling was observed until 6 years both during voluntary trunk movements 52 and in response to trunk perturbations (13). Instead, in a reaching task, adult head-trunk-arm 53 coordination patterns were observed in children as young as 2-3 years old for movements in 54 the pitch plane and from 4 years onwards in the roll and yaw planes (14). Yet, the activity and 55 temporal recruitment of postural muscles appear to reach mature levels only after the age of 56 11 (8). The ability to decouple head and trunk movements proves to be particularly useful 57 when having to avoid or circumvent an obstacle while walking, where anticipatory head movements were observed from 5.5 years onwards, while younger children displayed a rigid 58 59 head-trunk connection (15). Children thus first build a repertoire of postural strategies, before 60 learning how and when to adequately implement them.

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Nevertheless, successful postural stabilization does not only involve appropriate multi-jointed coordination but also requires the integration of the information provided by different sensory modalities. The Bayesian model of multisensory integration suggests that adults fuse redundant sensory inputs in a statistically optimal way by weighting the sources according to their uncertainty (16,17). The ability to combine different cues to obtain more precise estimates of one's surroundings appears late in childhood development (18,19), that is, after

the individual modalities have matured (20,21), unless additional feedback on the reliability 68 69 of each cue is provided (22). Younger children will thus favor the information provided by the 70 modality with the highest context-dependent reliability (19,23). In the case of postural 71 control, children and adolescents until 15 years standing on an oscillating platform displayed 72 better stabilization with open than with closed eyes, thus indicating a strong reliance on vision 73 (3,24). The display of optic flow patterns to elicit automatic postural movements led to 74 stronger responses in children and adolescents when compared to adults, and the ability to 75 stabilize these movements improved with age until late adolescence (25). This effect was 76 further enhanced when the participants were standing on a sway-referenced platform 77 (26,27). When standing on the unstable platform, which attenuates the proprioceptive 78 feedback, adults use primarily vestibular information to stabilize their posture, and this ability 79 matures only during late adolescence (26).

80 Interestingly, children aged 7–10 years have been shown to display spatiotemporal muscle 81 activation patterns similar to those observed in adults in response to platform oscillations 82 (28), revealing an earlier development of automatic postural responses. Similarly, the 83 predominance of visual cues over self-motion has been observed in children up to 11 years in 84 a navigation task (29,30). The late maturation of visual-vestibular and visual-proprioceptive 85 integration has been correlated with the individual development of these modalities when 86 these are presented in conflict. While adult levels were observed as early as 3 years for proprioception and from 14 years for vision, 15-year-olds still displayed lower levels of 87 88 vestibular function than adults (31).

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90 The reliance on visual cues can be further challenged by the use of immersive VR, where the 91 participants are immersed in a digital environment through a head-mounted display (HMD). 92 This paradigm led to stronger sensory recalibration (32) and recruited different adaptation 93 mechanisms (33) than non-immersive sensory alterations. Thanks to the recent development 94 of lightweight HMDs, the use of VR has expanded to numerous applications designed for 95 children, including neurodevelopmental research (30,34–36), neurorehabilitation (37–40), or 96 distraction from painful medical procedures (41,42). Yet, the majority of these applications 97 offer none or limited interactions with the virtual environment. Therefore, with the exception 98 of two studies showing that children displayed stronger and longer-lasting responses than 99 teenagers to prism adaptation in immersive VR (43), but generally tolerate this kind of bioRxiv preprint doi: https://doi.org/10.1101/2020.10.14.338749; this version posted October 15, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

environment (44), little is known about how children integrate the visual information of thesimulated world.

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103 We previously developed a body-machine interface for the immersive control of a first-person 104 view (FPV) flight simulator and showed that healthy adults reached a higher steering 105 performance with this approach than with a standard joystick (45). Here, we first evaluated 106 the ability of school-aged children to control this flight simulator using either their head or 107 their torso, and we assessed the intersegmental coordination patterns which emerged during 108 the execution of this task. To further investigate the underlying behaviors, we assessed the 109 development of the head and torso proprioception during a virtual joint angle reproduction 110 (JAR) task.

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#### 112 Results

#### 113 <u>Study 1</u>

In the first study, the participants were equipped with a HMD through which they were immersed in a virtual scenario representing a flight on a bird's back along a path represented by a series of coins to catch (Figure 1A). The trajectory of the flight simulator was controlled either by head movements or torso movements. Continuous tracking of the head movements also enabled a dynamic adaptation of the field of view, allowing the users to look around in the virtual environment. Steering with torso movements, therefore, required decoupling of vision and steering commands, whereas these aspects were tied in the head-controlled trials.

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#### 122 Controlling body part and age affect steering performance

We assessed the steering performance as the average distance to the center of the coins 123 124 (45,46) during three phases: before and after training (Before and After, see Methods), and 125 on the subsequent day (Day After). A repeated measures ANOVA revealed a significant effect of Age (F(4,35) = 7.45, p < 0.001,  $\eta_p^2$  = 0.460), Control (F(1,35) = 29.52, p < 0.001,  $\eta_p^2$  = 0.457) 126 and Phase (F(2,70) = 15.44, p < 0.001,  $\eta_p^2$  = 0.306), as well as significant Age:Phase (F(8,70) = 127 4.41, p = 0.003,  $\eta_p^2$  = 0.335), Age:Control (F(4,35) = 5.97, p < 0.001,  $\eta_p^2$  = 0.405), Phase:Control 128 129  $(F(2,70) = 11.94, p < 0.001, \eta_p^2 = 0.254)$  and Age:Phase:Control  $(F(8,70) = 4.21, p = 0.003, \eta_p^2)$ 130 = 0.325) interactions (Figure 1C).

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Post-hoc Tukey tests revealed that 6-year-olds performed better in the head- than in the torso-controlled trials in all phases (*Before*: p = 0.002, d = 1.17; *After*: p = 0.009, d = 0.83; *Day After*: p < 0.001, d = 1.17). This difference was also significant for 8-year-olds *Before* (p < 0.001, d = 1.45), but not during the other phases, although large effect sizes were observed (*After*: p = 0.83, d = 3.8; *Day After*: p = 0.652, d = 2.15). Similarly, large effect sizes suggested a superiority of the head over the torso in all phases for 9- and 10-year-olds and *After* training for adults (Table S1).

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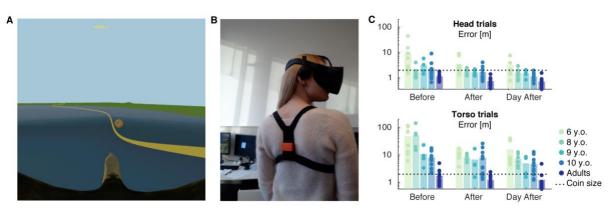


Figure 1: Experimental setup and task performance. A Virtual environment, as seen by the participant, representing the
coins to catch and an underlining ideal trajectory depicted by the yellow line. B Experimental apparatus worn by the
participants, consisting of a HMD and an IMU held in place in the back by a harness. C Performance on the navigation task,
computed as the average distance to the coin centre (error). Dots represent the average error for each individual
participant, bars the average across participants. N = 9 (6 y.o.), 8 (8 y.o.), 4 (9 y.o.), 11 (10 y.o.), 13 (adults). See Tables S3
and S4 for details of the statistical analyses.

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148 When steering with their torso, 6-year-olds performed better After than Before training (p =149 0.013, d = 0.85) and on the Day After than Before (p = 0.014, d = 0.97). The same improvement 150 was observed in 8-year-olds between the evaluations *Before* and *After* training (p = 0.001, d 151 = 1.26) and from Day After compared to Before training (p = 0.002, d = 1.28). While not 152 reaching statistical significance, large effect sizes were observed for 9- and 10-year-olds from Before training to Day After (p = 0.998, d = 0.89; p = 0.998, d = 0.74 respectively). Interestingly, 153 154 large effect sizes suggest that 9-year-olds and adults improved their steering precision in 155 head-controlled trials from *Before* to *After* and *Day After* (Table S1).

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157 In the torso-controlled trials, 6-year-olds showed significantly lower performance than 10-158 year-olds *Before* training (p = 0.023, d = 1.34) and on *Day After* (p = 0.02, d = 1.07) and than

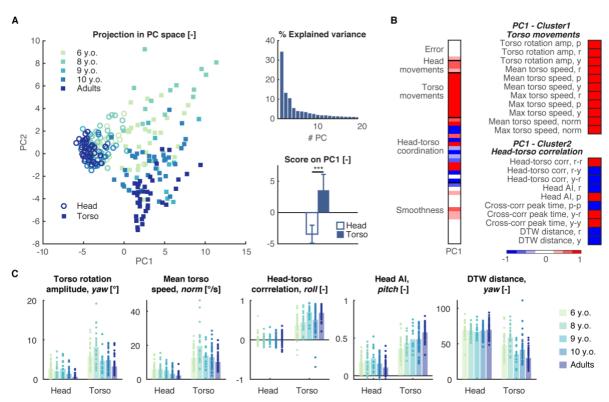
adults in all phases (*Before*: p = 0.006, d = 1.66; *After*: p = 0.042, d = 1.09; *Day After*: p = 0.001, 159 160 d = 1.1.57). Likewise, 8-year-olds performed worse than 10-years-olds and the adults *Before* 161 training (p = 0.015, d = 1.45 and p = 0.005, d = 1.78 respectively). In the head-controlled trials, 162 6-year-olds displayed higher errors than the adults After training (p = 0.001, d = 1.55), and than 10-year-olds and the adults on Day After (p = 0.013, d = 1.07 and p = 0.002, d = 1.52163 164 respectively). Non-significant differences with large effect sizes suggest a gradual 165 development of head-torso motor patterns, particularly between the two older children 166 groups and adults (Table S2).

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# 168 Segmental coordination and torso involvement differ between the torso and head trials

Principal Component Analysis (PCA) applied to all the recorded trials revealed that the first principal component (PC) accounted for 34% of the dataset's variability and separated the head- from the torso-controlled trials (p < 0.001, Figure 2A). The kinematic variables displaying normalized loadings > 0.75 represented torso movements (Cluster 1) and headtorso coordination (Cluster 2, see Figure 2B).

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Figure 2: Segmental coordination and torso involvement differ between torso and head trials. **A** PCA applied to the data collected on all trials. The projection of the data in the space spanned by the first two PCs displays a control-based separation along the first component (left) representing 34% of the overall variance (top right). This division was confirmed by a t-test (bottom left, mean + SEM). **B** Normalized loadings of the descriptive variables on the first PC (left) and variables

with absolute loadings higher than a threshold of 0.75 grouped into functional clusters. C Representative variables selected
 from the functional clusters with significant effect of Control (see also Table S4). B: Before, A: After, DA: Day After

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183 Repeated measures ANOVAs revealed a significant effect of Control on all identified variables 184 (Table S3). In particular, torso movements were executed with larger yaw amplitude (p < p0.001,  $\eta_p^2 = 0.67$ ) and higher average velocity (p < 0.001,  $\eta_p^2 = 0.79$ ) in the torso-controlled 185 186 trials (Figure 2C). Head movements were more similar to trunk movements in torso- than in 187 head-controlled trials, as assessed by the head-torso correlation in the roll plane (p < 0.001, 188  $\eta_p^2$  = 0.89) or the dynamic time warp (DTW) distance between both segments in the yaw plane (p < 0.001,  $\eta_p^2$  = 0.82). Interestingly, the higher pitch head anchoring index (AI) in the 189 torso-controlled trials (p < 0.001,  $\eta_p^2$  = 0.85) reveals that the head is preferentially stabilized 190 191 to the external space than to the trunk in these trials.



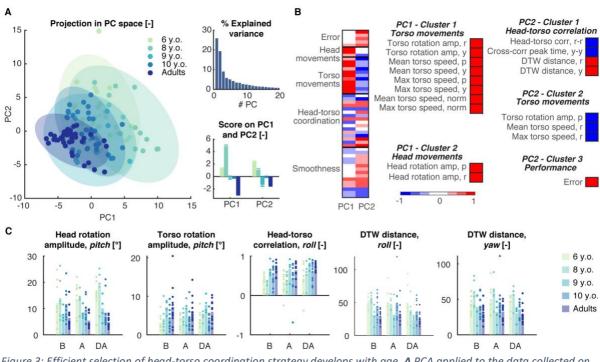
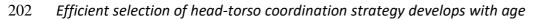


Figure 3: Efficient selection of head-torso coordination strategy develops with age. A PCA applied to the data collected on
 torso-controlled trials. The projection of the data in the space spanned by the first two PCs displays an age-based
 separation along the first two components (left) representing respectively 26% and 19% of the overall variance (top right).
 Group means of the scores on the first two PCs (bottom left, mean + SEM). B Normalized loadings of the descriptive
 variables on the first PC (left) and variables with absolute loadings higher than a threshold of 0.75 grouped into functional
 clusters. C Representative variables selected from the functional clusters with significant effect of Age (see also Table S5). B:
 Before, A: After, DA: Day After

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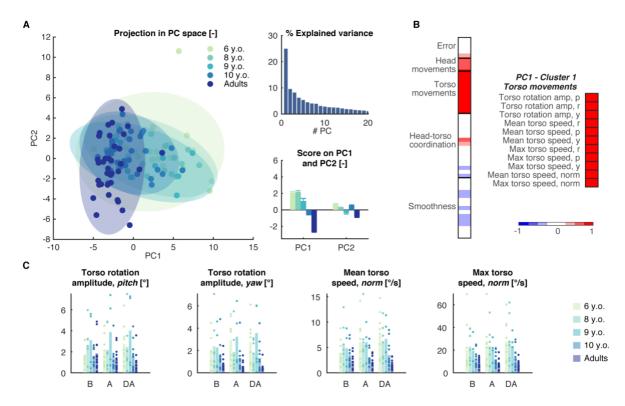


To extract the specific variability inherent to torso steering, we repeated the procedure described above, using only the data from the corresponding trials. On this partial dataset, PCA revealed an age-based separation in the space spanned by the first two PCs, accounting respectively for 25.91% and 19.38% of the total variance (Figure 3A). Individually, both PC1 and PC2 showed a decreasing trend with age (Figure 3A).

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209 The selection of relevant descriptive variables yielded five functional clusters: Cluster 1 (PC1) 210 and Cluster 2 (PC2) holding variables describing the torso movements, Cluster 2 (PC1) 211 corresponding to head movements, Cluster 1 (PC1) characterizing head-torso correlation and 212 finally Cluster 3 (PC2) containing only the error (Figure 3B). All the identified variables showed 213 a significant effect of Age and/or Age:Phase interaction (Table S4). Younger children displayed 214 larger vertical head movements (p = 0.004,  $\eta_p^2$  =0.42, Figure 3C) and smaller torso movements (p = 0.003,  $\eta_p^2$  = 0.44). Remarkably, the similarity between head and torso 215 216 movements augmented with age, as revealed by the increased correlation in the roll plane (p 217 = 0.01,  $\eta_p^2$  = 0.43) or the DTW distance in the roll (p = 0.005,  $\eta_p^2$  = 0.39) and yaw planes (p = 0.003,  $\eta_p^2 = 0.44$ ). 218





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along the first component (left) representing 25% of the overall variance (top right). Group means of the scores on the first
two PCs (bottom left, mean + SEM). B Normalized loadings of the descriptive variables on the first PC (left) and variables
with absolute loadings higher than a threshold of 0.75 grouped into functional clusters. C Representative variables selected
from the functional clusters with significant effect of Age (see also Table S6). B: Before, A: After, DA: Day After

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#### 228 Torso involvement in head-controlled trials decreases with age

For head-controlled trials, PCA revealed a soft age-based separation along with the first principal component, accounting for 25% of the total variance (Figure 4A). Clustering the variables with normalized loadings larger than 0.75 yielded one single cluster describing torso movements (Figure 4B). All the identified variables showed a significant effect of Age and/or Age:Phase interaction (Table S5). The amplitude of the torso movements decreased with age in the pitch (p = 0.016,  $\eta_p^2$  = 0.31, Figure 4C) and yaw planes (p = 0.015,  $\eta_p^2$  = 0.32), as well as the average (p = 0.016,  $\eta_p^2$  = 0.3) and maximal torso velocity (p = 0.015,  $\eta_p^2$  = 0.32).

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#### 237 <u>Study 2</u>

To further elucidate the mechanisms underlying the observed behavior, in particular the importance of mature and reliable proprioceptive inputs when the visual feedback is altered, we designed a second study in which the participants were immersed in a virtual landscape as previously and asked to execute a joint angle reproduction (JAR) test using their head or their torso. The JAR paradigm is an active test for proprioception that reflects the functional use of this sensory pathway and relies on kinesthetic memory (47,48), a necessary competence for the proficient use of the flight simulator tested in study 1.

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#### 246 Error

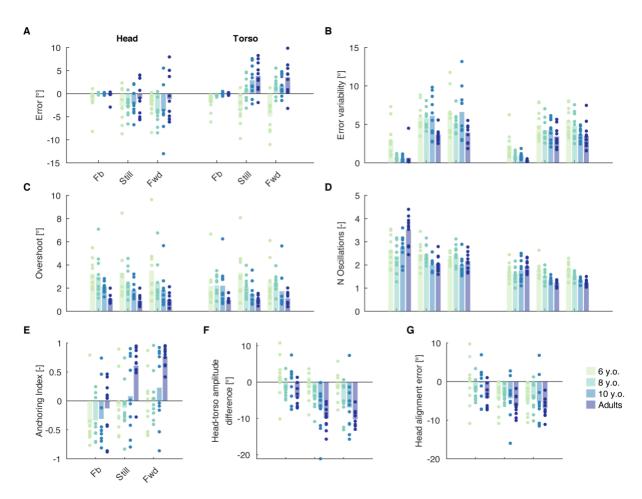
We first evaluated the angle reproduction error under three conditions: *Feedback*, where a 247 248 line indicated the current position of the tested body part, *Still*, where the feedback line was 249 removed, and Forward, where a constant forward speed was simulated. A repeated-250 measures ANOVA revealed a significant effect of Age (F(3,35) =7.99, p < 0.001,  $\eta_p^2$  = 0.406) and Control (F(1,35) = 21.19, p < 0.001,  $\eta_p^2$  = 0.377), and significant Age:Control (F(3,35) = 251 252 5.24, p = 0.004,  $\eta_p^2$  = 0.446) and Age:Control:Condition interactions (F(3,35) = 3.99, p = 0.003) 253  $\eta_p^2$  = 0.255). A posthoc analysis revealed that all age groups except the 6-year-olds increased 254 their error when using their torso compared to the head trials, overestimating their position in the former case and underestimating it in the latter (see tables S6 and S7 for details). This 255

was particularly the case in the *Forward* condition for the 8- and 10-year-olds and the adults,
and in the *Still* condition for the 10-year-olds and the adults (Figure 5A).

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There was a significant effect of Age (F(3,35) = 9.41, p < 0.001,  $\eta_p^2$  = 0.446), Condition (F(2,70) = 152.40, p < 0.001,  $\eta_p^2$  = 0.813) and Control (F(1,35) = 10.98, p = 0.002,  $\eta_p^2$  = 0.0.239) on the variability of the error, but none of the interactions involving Age were significant. Posthoc tests revealed that adults showed significantly less variability than 6- and 10-year-olds (p < 0.001, d = 0.92 and p = 0.028, d= 0.45 respectively, Figure 5B).

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Figure 5: Joint angle reproduction test. A-D Head and torso trials, E-G Torso trials only. A Signed error at final orientation, positive values indicate final positions exceeding the target angle. B Variability (standard deviation) of the final error. C
 Overshoot. D Number of oscillations around the final position. E Head anchoring index (AI), with AI = 1 meaning complete
 independence of head and torso. F Difference of head and torso final orientation, negative values indicate that the head
 orientation is smaller than the torso orientation. G Difference between final head orientation and target orientation. Dots
 represent the average error for each individual participant, bars the average across participants. N = 10 for each age group.
 See Tables S6 – S9 for details of the statistical analyses. FB: Feedback, Fwd: Forward, see text for description of the

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# 275 Movement strategy

We next evaluated the selected movement strategy through the overshoot with respect to the final position and the number of oscillations around this angle. We found a significant effect of Age (F(3,35) = 5.53 p =0.003,  $\eta_p^2$  = 0.322) and Control (F(1,35) = 4.55 p =0.04,  $\eta_p^2$  = 0.115) on the overshoot, with 6- and 8-year-olds exceeding their final position by a larger extent than adults (p = 0.03, d = 1.40 and p = 0.031, d = 1.53 respectively, Figure 5C).

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282 Assessing the number of oscillations around the final position, we found a significant effect 283 of Condition (F(2,35) = 36.07 p < 0.001,  $\eta_p^2$  = 0.508), and Control (F(1,35) = 342.80, p < 0.001,  $\eta_p^2 = 0.907$ ), and Age:Condition (F(6,70) = 11.97, p < 0.001,  $\eta_p^2 = 0.506$ ), Age:Control (F(3,35) 284 = 9.41, p = 0.015,  $\eta_p^2$  = 0.0.255), and Age:Condition:Control (F(6,70) = 3.37, p = 0.006,  $\eta_p^2$  = 285 286 0.224) interactions. Specifically, we found that adults oscillate more than all children groups 287 when using their head and *Feedback* is provided while younger children oscillate more than 288 older children and adults when using their torso in the Still and Forward conditions. (Figure 289 5D, see tables S8 and S9 for details)

290

#### 291 Head-torso coordination during torso trials

We observed a significant effect of Age, Condition and Age:Condition interaction on the head anchoring index (AI). The 6- and 8-year-olds' AI was significantly lower than the adult's in the *Still* (p = 0.013, d = -1.67 and p = 0.019, d = -1.85 respectively) and *Forward* conditions (p = 0.003, d = -2.15 and p = 0.012, d = -2.14 respectively, Figure 5E).

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The angular difference between the head and torso orientations at the final position showed a significant effect of Age (F(3,36) = 7.29 p = 0.001,  $\eta_p^2$  = 0.378) and Condition (F(2,72) = 36.07 p < 0.001,  $\eta_p^2$  = 0.508). This difference was significantly smaller for 6-year-olds than adults (p < 0.001, d = 1.78, Figure 5F). Finally, there was only an effect of Condition on the alignment error of the head with the target orientation (F(2,72) = 18.11 p < 0.001,  $\eta_p^2$  = 0.335, Figure 5G).

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305 Effect of optical flow

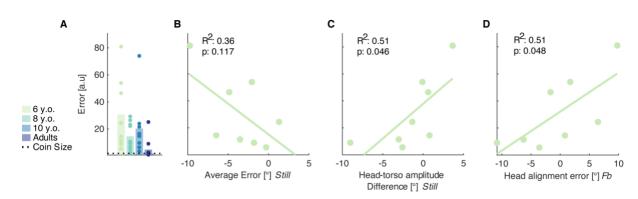
306 Interestingly, the effect of the constant optic flow implemented to generate the *Forward* 307 condition when compared with the *Still* condition was significant only for the head AI, 308 regardless of the age group (p = 0.004, d = -0.26).

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### 310 Prediction of performance in the flight game

311 Eventually, we evaluated the relationship between the metrics computed during the JAR test and the performance during one torso-controlled session on the flight simulator. For the 6-312 313 year-olds, we found a significant relationship of this performance with the head-torso amplitude difference in the absence of visual feedback (*Still*:  $R^2 = 0.51$ , p = 0.046 *Forward*:  $R^2$ 314 315 = 0.60 p = 0.024), as well as with the head alignment error with *Feedback* ( $R^2 = 0.51$ , p = 0.048). 316 None of the regressions were significant for the other age groups. Interestingly, we found no 317 significant relationship between the torso JAR error and the flight performance (Still:  $R^2$  = 0.36, p = 0.117, Forward:  $R^2 = 0.35$ , p = 0.120 for the 6-year-olds). 318

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Figure 6: Prediction of simulator steering performance from JAR test. A Simulator steering performance during a unique
 torso-controlled session. B-D Regression analysis performed using the data of the 6-year-olds, recorded during torso trials
 of the JAR test. B Signed error at final orientation (see Figure 5A). C Difference between final head orientation and target
 orientation (see Figure 5F). D Difference between final head orientation and target orientation (see Figure 5G). Dots
 represent the average error for each individual participant, bars the average across participants. N = 8 (6 y.o.), 10 ((8 y.o.),
 10 (10 y.o.), 10 (adults). FB: Feedback, see text for description of the conditions.

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#### 329 Discussion

In this work, we investigated the development of head-torso coordination when challenged by an alteration of the visual feedback through immersive VR. We first evaluated the ability of children aged 6-10 years and young adults to steer an immersive flight simulator using either their head or their torso (Study 1), followed by a virtual JAR task to decipher the behaviors observed during the steering task (Study 2). 335

336 All the participants were able to steer the simulator using their head in study 1. However, 6-337 year-olds showed lower performances than the oldest children and adults, and while this 338 difference was maintained even after practicing the task, the scores were in a comparable 339 range. When using their torso, 6 and 8-year-olds initially struggled to control the simulator 340 but substantially improved their performance with training. Yet, their average error remained 341 higher than the 10-year-olds' and adults'. Overall, 6-year-olds performed worse with the torso 342 than with the head. Kinematic data revealed a stronger involvement of the torso and a stiffer 343 head-torso link during torso-based steering, particularly for the older age groups. Age-related 344 differences in the torso-controlled trials were attributable to an increase of the torso movements, a decrease of the head movements and an increase in the head-torso 345 346 correlation. Conversely, the age-dependent changes in the head-controlled trials were 347 predominantly caused by a decrease of superfluous torso movements.

348

349 The virtual JAR test carried out in study 2 revealed that in the absence of explicit visual 350 feedback, all participants except the 6-year-olds did not reach the target position with their 351 head while exceeding it when performing the task with their torso. The younger children 352 instead failed to reach the desired orientation with both body parts, overestimating their 353 displacement. During the torso JAR, older children and adults decoupled their heads from 354 their torso, maintaining the head close to the vertical during sideward trials. When explicit 355 feedback was given on the torso position, the 6-year-olds had the tendency to overshoot the 356 target orientation with their head. Lastly, we found that for this age group, the amplitude of 357 unnecessary head movements during the torso JAR correlated with their performance in the 358 torso-controlled flight game.

359

The comparable performances observed for all age groups in the head-controlled JAR and steering task indicate that children as young as 6 years are able to use and interact with an immersive body-machine interface both for simple and more complex tasks, in line with a recent study (44). The earlier maturation of the head control is not surprising, as this condition does not require the mastery of an articulated control of the head-trunk unit, which develops from 7 years onwards (10). However, even in this simpler experimental condition, younger children still display a higher error variability and a larger overshoot, confirming the

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incomplete development of robust internal models as observed in standard experimentalframeworks (2,49,50)

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370 Kinematic analyses of the head-controlled trials showed that the major age-related difference 371 could be attributed to differences in the torso movements, with rotation amplitudes and 372 mean and maximum rotation velocities are decreasing with age. The ability to decouple head 373 from torso movements thus develops along with childhood, confirming previous results 374 obtained during obstacle avoidance during locomotion (1,15), where adults display 375 anticipatory head movements (15). However, mature coordination patterns appear later with 376 our experimental setup when compared to simple locomotion. This is in line with 377 observations revealing that developing children tend to increase their head-body stiffness 378 with increasing task difficulty (9), and to involve their trunk in situations where such 379 movements are not necessarily required (51,52). In our case, the increased difficulty can be 380 imputed to the use of immersive VR, which provides altered visual information and requires 381 higher cognitive processing abilities to appropriately interpret the displayed environment 382 (53,54). Here, immersive VR appears to increase the contribution of proprioceptive and 383 vestibular inputs to postural control over vision (55).

384

385 When the control of the flight game was based on torso movements; instead, younger 386 children struggled to use the system, even after practicing the task. Assessing the kinematics 387 during this task and the JAR reveals an underlying twofold behavior. First, the age-related 388 increase of the torso amplitude in the steering task and the evolution of the torso JAR error 389 indicate that the immaturity of the torso proprioception leads younger children to 390 overestimate their torso movements. This complements a previous study showing an increase 391 in torso positioning accuracy with age (2). Second, the larger head movements displayed by, 392 the younger participants during the flight game and the amplitude of their head movements 393 during the torso JAR with visual feedback suggest that these children attempt to resolve the 394 visual discrepancy by compensatory head movements. This is likely due to weaker reliability 395 of the neck proprioception, which is not mature yet at this developmental stage (31,56,57). 396 This behavioral pattern also comes in line with recent works showing biases in the perception 397 of visual and haptic verticality to unusual body orientations in younger children (58,59), which is here confirmed by the younger participant's inability to stabilize their head vertically whilealigning their torso to lateral target positions.

400

401 The joint display of these two behaviors led to the unexpected observation that only the older 402 participants favorably selected an 'en-bloc' strategy with a stiff intersegmental link during the 403 steering task. This comes in opposition to previous studies, where such behavior was 404 preferentially observed in younger children (1,13,15). One study found a similar behavior in 405 adults, who displayed a head-to-torso stabilization in dimensions in which independent head 406 movements were not beneficial (14). This is concomitant with our results, as head movements 407 in the torso-controlled trials tended to disturb the participants' spatial orientation. Younger 408 children instead failed to use this simpler coordination pattern, which suggests that the 409 altered visual feedback provided by the VR setup prevented them from selecting an adequate 410 coordination strategy, likely by reweighting the sensory contributions to posture estimation 411 (55). This corroborates the model of postural development as a two-step process in which 412 children first acquire a repertoire of postural strategies and later on learn how and when to 413 select the appropriate strategy (1).

- 414
- 415

#### 416 **Conclusion**

417 This study shows that young children are able to understand and to operate a body-machine 418 interface to interact with immersive VR, but that 6- to 8-year-olds fail to successfully use such 419 a system when decoupling of vision and steering commands is required. In such a sensory 420 environment, these children do not resort to the simpler 'en-block' control strategy usually 421 resorted to at a younger age in challenging conditions, but instead use a less efficient 422 segmental control, overestimating their torso displacement and attempting to correct the 423 visual discrepancy through head movements. This suggests that at these ages, the 424 proprioception at the neck and torso levels is not yet mature enough to be robust to an 425 alteration of the visual feedback, thus preventing an effective visual-vestibularproprioceptive sensory integration, and confirms that the maturation of motor control 426 427 extends beyond childhood.

428 The results of this study indicate the potential of immersive VR to characterize complex 429 aspects of sensorimotor maturation, but that this technology should be used with care for 430 applications such as motor rehabilitation as it alters the selection of postural strategies in a431 developing population.

432

#### 433 Methods

#### 434 Subjects

435 Thirty-six typically developing children participated in the first study, grouped as follows: nine 436 6-year-olds (5 girls), eight 8-year-olds (2 girls), four 9-year-olds (1 girl) and eleven 10-year-437 olds (2 girls). Two children (aged 6 and 8) asked to stop the experiment and two other ones 438 (aged 8 and 10) did not comply with the instructions; their data were excluded from further 439 analyses. In addition, 13 healthy adults participated in the study (3 women, age 28.5±3.4 440 years). Twenty-four typically developing children participated in the second study, grouped 441 as follows: ten 6-year-olds (7 girls), ten 8-year-olds (5 girls), and ten 10-year-olds (5 girls), as 442 well as 10 healthy adults (4 women, age  $27.0\pm3.2$  years). Two 6-year-olds did not complete 443 the session with the flight simulator, their data are reported only for the JAR task. Both studies 444 were approved by the local ethical committees and were carried out in accordance with the 445 Helsinki declaration. All the participants or their legal representative gave their written 446 consent to take part in this study.

447

#### 448 Experimental setup

The participants were equipped with a head-mounted display (HMD, Oculus Rift) through which they were shown the virtual environment, and an inertial measurement unit (IMU, Xsens MTw Awinda) placed in their back between the scapulae and maintained with a custom harness to acquire their trunk's 3-dimensional (3D) rotation (see Figure 1B). The IMU embedded within the HMD was used both to control the view in the virtual environment and to acquire the head rotations. The kinematic data were acquired at a sample period of 68 ms.

#### 456 Virtual environment and navigation task

We created a virtual environment (VE) using the game engine Unity3D, which represented a FPV flight on a bird's back at a constant speed of 12 m/s, (45,46). A succession of coins to catch (distance between consecutive coins: 58m) represented a path to follow, randomly alternating simple forward motion and one of four directional maneuvers (right turn, left turn, ascent, descent). The coins' initial diameter was 1 m, and every time one coin was caught, the next one was enlarged to 2 m. To minimize possible effects of path planning abilities, we additionally displayed a colored line smoothly connecting the coins, computed as a Catmull-Rom spline (60). Similarly, to provide the participants with a visual cue of their own position in space, an eagle was displayed below their visual horizon (see Figure 1A). Finally, to keep the experiment engaging, a tinkling sound was played when the coin was caught at a distance smaller than 10 m, which also added points to a total score for the trial, displayed at the top of the screen.

469

#### 470 Control of the flight simulator

471 The participants were asked to control the flight simulator using either head or trunk 472 movements. Ascent and descent were achieved by flexion and extension of the controlling 473 body part while right and left turns were computed as a linear combination of lateral flexion 474 and axial rotation. The head and torso rotations were reset to zero before each sequence, at 475 the participants' self-selected neutral position corresponding to a straight, forward flight. 476 Continuous tracking of the head movements also enabled a dynamic adaptation of the field 477 of view, allowing the users to look around in the virtual environment. Steering with torso 478 movements, therefore, required decoupling vision and steering commands, whereas these aspects were tied in the head-controlled trials. 479

480

#### 481 Joint angle reproduction (JAR) task

We created a JAR task (47–49) in virtual reality using the game engine Unity 3D. The participants were immersed in a virtual landscape and were asked to align their head or their torso to one of three predefined orientations (0° and +/-15°) indicated by a pink line. We tested three conditions: *Feedback*, where a blue line showed the current orientation of the controlling body part, *Still*: where the additional visual feedback was removed and *Forward*, where a constant forward speed was simulated. The duration of one trial was set to 4 s, and the participants were asked to hold their final position until the next trial.

489

#### 490 Experimental protocol study 1

491 Upon arriving, the participants were shown the movements to control the simulator using the
492 head or the torso. They were equipped with the HMD and the IMU, and were seated on a
493 stool or on a chair and asked not to lean against the backrest. The participants were randomly

494 allocated to start the experiment using the head or the torso, using adaptive covariate 495 randomization with the gender as covariate (61). For the torso-controlled trials, the 496 participants were advised to keep their neck rigid as to move their entire upper body as a 497 whole. Similarly, before starting the head-controlled trials, the experimenter made the 498 participants aware that moving their trunk was unnecessary.

499 The recording sessions took place on two consecutive days. On day 1, the participants had to 500 steer the simulator along four paths with each body part. The first sequence contained 26 501 coins and was an initial evaluation of the performance (hereafter: *Before*). The second and 502 third sequences each contained 50 coins; these sequences were considered as training. The 503 fourth sequence contained 18 coins (hereafter: After). All the sequences controlled with a 504 given body part were executed successively. On day 2, one sequence containing 26 coins had 505 to be performed with each body part (hereafter: Day After). Breaks were allowed between 506 the sequences, at the participants' demand.

507

#### 508 Experimental protocol study 2

509 The participants were equipped and seated as previously and were shown the JAR 510 movements by the experimenter. The conditions were tested in the following order: 511 *Feedback, Still, Forward*, while the participants were randomly allocated to start either with 512 the head or the torso, using covariate adaptive randomization with the gender as covariate 513 (61). The orientations were presented in a randomized order, totalling 5 repetitions for each 514 orientation in the *Feedback* condition and 10 repetitions for the *Still* and *Forward* conditions. 515 At the end of the session, the participants executed one flight sequence with the simulator 516 (Before session described above).

517

#### 518 Data processing

The kinematic data acquired in study 1 was divided into segments corresponding to the intervals between consecutive coins. Descriptive variables were computed on these segments and averaged over each entire sequence (see Table 1). Principal component analysis (PCA) was applied to the dataset containing the kinematic variables extracted from all trials, or from the head- and torso-controlled trials, respectively. Outliers were detected as data points whose Euclidean distance to the centroid of the z-scored dataset deviated from the average value by more than 4 standard deviations. These points were given a weight of 0.5 in the PCA 526 computation. The variables with normalized loadings > 0.75 on the first (all trials, head-527 controlled trials) or the first two principal components (torso trials) were considered as 528 significant and were regrouped into functional clusters.

529

The data acquired during study 2 was separated into individual trials, and the final position was averaged over the last 1.5 s of each trial. For each trial, we computed the signed error with respect to the target orientation, the overshoot, the number of oscillations around the final angle, and for the trials involving the torso, the head anchoring index (AI, computed over the entire trial), the final angular difference of the head and the torso and the head alignment

- 535 "error" as the difference between the final head angle and the target orientation.
- 536

# 537 Statistical analysis

538 The statistical evaluations were performed using paired t-tests or repeated-measures

539 ANOVA, using the age as a between-subjects factor and the control type and/or experimental

540 phase as within-subject factors using custom Matlab routines (62). The p-values were

541 corrected using the Greenhouse-Geisser correction when Mauchly's test indicated a violation

542 of sphericity. Post hoc analyses were conducted using Tukey's honest significant differences

- 543 test, with a significance level of .05 for all tests.
- 544

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# 549550 References

5511.Assaiante C, Mallau S, Viel S, Jover M, Schmitz C. Development of Postural Control in552Healthy Children: A Functional Approach. Neural Plast. 2005;12(2–3):109–18.

Ashton-Miller JA, McGlashen KM, Schultz AB. Trunk positioning accuracy in children
 7-18 years old. J Orthop Res. 1992 Mar 1;10(2):217–25.

5553.Mallau S, Vaugoyeau M, Assaiante C. Postural Strategies and Sensory Integration: No556Turning Point between Childhood and Adolescence. PLOS ONE. 2010 Sep 29;5(9):e13078.

5574.Onis M de. WHO Motor Development Study: Windows of achievement for six gross558motor development milestones. Acta Paediatr. 2006;95(S450):86–95.

5. Yeo SS, Jang SH, Son SM. The different maturation of the corticospinal tract and
corticoreticular pathway in normal brain development: diffusion tensor imaging study. Front
Hum Neurosci [Internet]. 2014 Aug 4 [cited 2018 Nov 15];8. Available from:

562 https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4163649/

563 6. Adolph KE, Franchak JM. The development of motor behavior. Wiley Interdiscip Rev

564 Cogn Sci [Internet]. 2017 Jan [cited 2018 Dec 27];8(1–2). Available from: 565 https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5182199/ 566 Simon-Martinez C, Santos GL dos, Jaspers E, Vanderschueren R, Mailleux L, Klingels 7. 567 K, et al. Age-related changes in upper limb motion during typical development. PLOS ONE. 568 2018 Jun 6;13(6):e0198524. 569 van der Heide JC, Otten B, van Eykern LA, Hadders-Algra M. Development of postural 8. 570 adjustments during reaching in sitting children. Exp Brain Res. 2003 Jul;151(1):32-45. 571 Assaiante C, Amblard B. Ontogenesis of head stabilization in space during 9. 572 locomotion in children: influence of visual cues. Exp Brain Res. 1993;93(3):499–515. 573 10. Assaiante C, Amblard B. An ontogenetic model for the sensorimotor organization of 574 balance control in humans. Hum Mov Sci. 1995 Jun 1;14(1):13-43. 575 Bernstein NA. The co-ordination and regulation of movements. Oxford: Pergamon 11. 576 Press; 1967. 226 p. 577 12. Sporns O, Edelman GM. Solving Bernstein's Problem: A Proposal for the 578 Development of Coordinated Movement by Selection. Child Dev. 1993;64(4):960-81. 579 13. Roncesvalles MN, Schmitz C, Zedka M, Assaiante C, Woollacott M. From egocentric 580 to exocentric spatial orientation: development of posture control in bimanual and trunk 581 inclination tasks. J Mot Behav. 2005 Sep;37(5):404–16. 582 14. Sveistrup H, Schneiberg S, McKinley PA, McFadyen BJ, Levin MF. Head, arm and 583 trunk coordination during reaching in children. Exp Brain Res. 2008 Jun 1;188(2):237-47. 584 Grasso R, Assaiante C, Prévost P, Berthoz A. Development of Anticipatory Orienting 15. 585 Strategies During Locomotor Tasks in Children. Neurosci Biobehav Rev. 1998 Mar 586 4;22(4):533-9. 587 Chambers C, Sokhey T, Gaebler-Spira D, Kording KP. The integration of probabilistic 16. 588 information during sensorimotor estimation is unimpaired in children with Cerebral Palsy. 589 PLoS ONE [Internet]. 2017 Nov 29 [cited 2019 Jan 10];12(11). Available from: 590 https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5706703/ 591 17. Ernst MO, Banks MS. Humans integrate visual and haptic information in a statistically 592 optimal fashion. Nature. 2002 Jan 24;415(6870):429-33. 593 Chambers C, Sokhey T, Gaebler-Spira D, Kording KP. The development of Bayesian 18. 594 integration in sensorimotor estimation. J Vis [Internet]. 2018 Nov 15 [cited 2019 Jan 595 10];18(12). Available from: https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6241171/ 596 Gori M, Del Viva M, Sandini G, Burr DC. Young Children Do Not Integrate Visual and 19. 597 Haptic Form Information. Curr Biol. 2008 May 6;18(9):694-8. 598 Burr D, Gori M. Multisensory Integration Develops Late in Humans. In: Murray MM, 20. 599 Wallace MT, editors. The Neural Bases of Multisensory Processes. Boca Raton (FL): CRC 600 Press/Taylor & Francis; 2012. (Frontiers in Neuroscience). 601 Contreras-Vidal JL. Development of forward models for hand localization and 21. 602 movement control in 6- to 10-year-old children. Hum Mov Sci. 2006 Oct 1;25(4):634–45. 603 Negen J, Chere B, Bird L, Taylor E, Roome HE, Keenaghan S, et al. Sensory Cue 22. 604 Combination in Children Under 10 Years of Age. bioRxiv. 2018 Dec 20;501585. 605 Nardini M, Dekker T, Petrini K. Crossmodal integration: a glimpse into the 23. 606 development of sensory remapping. Curr Biol CB. 2014 Jun 2;24(11):R532-534. 607 Viel S, Vaugoyeau M, Assaiante C. Adolescence: a transient period of proprioceptive 24. 608 neglect in sensory integration of postural control. Motor Control. 2009 Jan;13(1):25–42. 609 25. Greffou S, Bertone A, Hanssens J-M, Faubert J. Development of visually driven 610 postural reactivity: A fully immersive virtual reality study. J Vis. 2008 Aug 5;8(11):15–15.

611 26. Gouleme N, Ezane MD, Wiener-Vacher S, Bucci MP. Spatial and temporal postural 612 analysis: a developmental study in healthy children. Int J Dev Neurosci. 2014 Nov 1;38:169-613 77. 614 27. Sparto PJ, Redfern MS, Jasko JG, Casselbrant ML, Mandel EM, Furman JM. The 615 influence of dynamic visual cues for postural control in children aged 7-12 years. Exp Brain 616 Res. 2006 Jan; 168(4): 505-16. 617 Shumway-Cook A, Woollacott MH. The Growth of Stability. J Mot Behav. 1985 Jun 28. 618 1;17(2):131-47. 29. 619 Nardini M, Jones P, Bedford R, Braddick O. Development of Cue Integration in 620 Human Navigation. Curr Biol. 2008 May 6;18(9):689–93. 621 Petrini K, Caradonna A, Foster C, Burgess N, Nardini M. How vision and self-motion 30. 622 combine or compete during path reproduction changes with age. Sci Rep. 2016 Jul 623 6;6:29163. 624 31. Hirabayashi S, Iwasaki Y. Developmental perspective of sensory organization on 625 postural control. Brain Dev. 1995 Mar 1;17(2):111-3. 626 32. Ramos AA, Hørning EC, Wilms IL. Simulated prism exposure in immersed virtual 627 reality produces larger prismatic after-effects than standard prism exposure in healthy 628 subjects. PLOS ONE. 2019 May 24;14(5):e0217074. 629 33. Anglin JM, Sugiyama T, Liew S-L. Visuomotor adaptation in head-mounted virtual 630 reality versus conventional training. Sci Rep. 2017 Apr 4;7:45469. 631 Cowie D, McKenna A, Bremner AJ, Aspell JE. The development of bodily self-34. 632 consciousness: changing responses to the Full Body Illusion in childhood. Dev Sci. 633 2018;21(3):e12557. 634 Morrongiello BA, Corbett M, Milanovic M, Beer J. Using a Virtual Environment to 35. 635 Examine How Children Cross Streets: Advancing Our Understanding of How Injury Risk 636 Arises. J Pediatr Psychol. 2016 Mar 1;41(2):265–75. 637 36. Segovia KY, Bailenson JN. Virtually True: Children's Acquisition of False Memories in 638 Virtual Reality. Media Psychol. 2009 Nov 23;12(4):371–93. 639 37. Biffi E, Beretta E, Cesareo A, Maghini C, Turconi AC, Reni G, et al. An Immersive Virtual Reality Platform to Enhance Walking Ability of Children with Acquired Brain Injuries. 640 641 Methods Inf Med. 2017 Mar 23;56(2):119-26. 642 Bortone I, Leonardis D, Mastronicola N, Crecchi A, Bonfiglio L, Procopio C, et al. 38. 643 Wearable Haptics and Immersive Virtual Reality Rehabilitation Training in Children With 644 Neuromotor Impairments. IEEE Trans Neural Syst Rehabil Eng. 2018 Jul;26(7):1469–78. 645 de Mello Monteiro CB, Massetti T, da Silva TD, van der Kamp J, de Abreu LC, Leone C, 39. 646 et al. Transfer of motor learning from virtual to natural environments in individuals with 647 cerebral palsy. Res Dev Disabil. 2014 Oct 1;35(10):2430-7. 648 Gagliardi C, Turconi AC, Biffi E, Maghini C, Marelli A, Cesareo A, et al. Immersive 40. 649 Virtual Reality to Improve Walking Abilities in Cerebral Palsy: A Pilot Study. Ann Biomed Eng. 650 2018 Sep;46(9):1376-84. 651 Sharar SR, Carrougher GJ, Nakamura D, Hoffman HG, Blough DK, Patterson DR. 41. 652 Factors Influencing the Efficacy of Virtual Reality Distraction Analgesia During Postburn 653 Physical Therapy: Preliminary Results from 3 Ongoing Studies. Arch Phys Med Rehabil. 2007 Dec 1;88(12, Supplement 2):S43-9. 654 Won AS, Bailey J, Bailenson J, Tataru C, Yoon IA, Golianu B. Immersive Virtual Reality 655 42. 656 for Pediatric Pain. Children [Internet]. 2017 Jun 23 [cited 2019 Jan 1];4(7). Available from: 657 https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5532544/

658 43. Adams H, Narasimham G, Rieser J, Creem-Regehr S, Stefanucci J, Bodenheimer B. 659 Locomotive Recalibration and Prism Adaptation of Children and Teens in Immersive Virtual 660 Environments. IEEE Trans Vis Comput Graph. 2018 Apr;24(4):1408–17. 661 44. Tychsen L, Foeller P. Effects of Immersive Virtual Reality Headset Viewing on Young Children: Visuomotor Function, Postural Stability, and Motion Sickness. Am J Ophthalmol. 662 663 2020;209:151-9. 664 45. Miehlbradt J, Cherpillod A, Mintchev S, Coscia M, Artoni F, Floreano D, et al. Data-665 driven body-machine interface for the accurate control of drones. Proc Natl Acad Sci. 2018 666 Jul 31;115(31):7913-8. Cherpillod A, Floreano D, Mintchev S. Embodied Flight with a Drone. In: 2019 Third 667 46. IEEE International Conference on Robotic Computing (IRC). 2019. p. 386–90. 668 669 Hillier S, Immink M, Thewlis D. Assessing Proprioception: A Systematic Review of 47. Possibilities. Neurorehabil Neural Repair. 2015 Nov 1;29(10):933-49. 670 671 48. Goble DJ. Proprioceptive Acuity Assessment Via Joint Position Matching: From Basic 672 Science to General Practice. Phys Ther. 2010 Aug 1;90(8):1176-84. 673 49. Goble DJ, Lewis CA, Hurvitz EA, Brown SH. Development of upper limb 674 proprioceptive accuracy in children and adolescents. Hum Mov Sci. 2005 Apr;24(2):155–70. 675 Sigmundsson H, Whiting HTA, Loftesnes JM. Development of proprioceptive 50. 676 sensitivity. Exp Brain Res. 2000 Dec 1;135(3):348–52. 677 51. Schneiberg S, Sveistrup H, McFadyen B, McKinley P, Levin MF. The development of 678 coordination for reach-to-grasp movements in children. Exp Brain Res. 2002 679 Sep;146(2):142-54. 680 Peeters LHC, Kingma I, Faber GS, Dieën JH van, Groot IJM de. Trunk, head and pelvis 52. 681 interactions in healthy children when performing seated daily arm tasks. Exp Brain Res. 682 2018 Jul 1;236(7):2023-36. 683 53. Baumgartner T, Speck D, Wettstein D, Masnari O, Beeli G, Jäncke L. Feeling present 684 in arousing virtual reality worlds: prefrontal brain regions differentially orchestrate presence 685 experience in adults and children. Front Hum Neurosci. 2008;2:8. Jäncke L, Cheetham M, Baumgartner T. Virtual reality and the role of the prefrontal 686 54. 687 cortex in adults and children. Front Neurosci. 2009;3:6. 688 Akizuki H, Uno A, Arai K, Morioka S, Ohyama S, Nishiike S, et al. Effects of immersion 55. 689 in virtual reality on postural control. Neurosci Lett. 2005 Apr 29;379(1):23-6. 690 Mergner T, Siebold C, Schweigart G, Becker W. Human perception of horizontal trunk 56. 691 and head rotation in space during vestibular and neck stimulation. Exp Brain Res. 692 1991;85(2):389-404. 693 57. Pettorossi VE, Schieppati M. Neck Proprioception Shapes Body Orientation and 694 Perception of Motion. Front Hum Neurosci. 2014 Nov 4;8:895. 695 Cuturi LF, Gori M. The Effect of Visual Experience on Perceived Haptic Verticality 58. 696 When Tilted in the Roll Plane. Front Neurosci. 2017 Dec 6;11:687. 697 Cuturi LF, Gori M. Biases in the Visual and Haptic Subjective Vertical Reveal the Role 59. 698 of Proprioceptive/Vestibular Priors in Child Development. Front Neurol [Internet]. 2019 699 [cited 2019 Sep 4];9. Available from: 700 https://www.frontiersin.org/articles/10.3389/fneur.2018.01151/full#h9 701 Catmull E, Rom R. A Class of Local Interpolating Splines. In: Computer Aided 60. 702 Geometric Design. New York: Academic Press; 1974. p. 317–26. 703 61. Frane JW. A Method of Biased Coin Randomization, its Implementation, and its 704 Validation. Drug Inf J. 1998 Apr 1;32(2):423–32.

- Caplette L. Simple RM/Mixed ANOVA for any design [Internet]. MATLAB Central FileExchange. [cited 2020 Aug 6]. Available from:
- 707 https://www.mathworks.com/matlabcentral/fileexchange/64980-simple-rm-mixed-anova-708 for-any-design
- 709 63. Berndt DJ, Clifford J. Using dynamic time warping to find patterns in time series. In 710 Seattle, WA: AAAI; 1994. p. 359–70. Available from:
- 711 https://www.aaai.org/Papers/Workshops/1994/WS-94-03/WS94-03-031.pdf
- ten Holt GA, Reinders MJT, Hendriks EA. Multi-Dimensional Dynamic Time Warping
   for Gesture Recognition. In 2007.
- 714 65. Balasubramanian S, Melendez-Calderon A, Burdet E. A Robust and Sensitive Metric
- for Quantifying Movement Smoothness. IEEE Trans Biomed Eng. 2012 Aug;59(8):2126–36.
- 716 66. Gulde P, Hermsdörfer J. Smoothness Metrics in Complex Movement Tasks. Front
- 717 Neurol [Internet]. 2018 [cited 2018 Dec 27];9. Available from:
- 718 https://www.frontiersin.org/articles/10.3389/fneur.2018.00615/full#B21
- 719 67. Rohrer B, Fasoli S, Krebs HI, Hughes R, Volpe B, Frontera WR, et al. Movement
- 720 Smoothness Changes during Stroke Recovery. J Neurosci. 2002 Sep 15;22(18):8297–304.
- 721 68. Dipietro L, Krebs HI, Volpe BT, Stein J, Bever C, Mernoff ST, et al. Learning, Not
- 722 Adaptation, Characterizes Stroke Motor Recovery: Evidence From Kinematic Changes
- 723 Induced by Robot-Assisted Therapy in Trained and Untrained Task in the Same Workspace.
- 724 IEEE Trans Neural Syst Rehabil Eng. 2012 Jan;20(1):48–57.
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726

#	Variable	Details
Steering p	erformance	
1-3	Error [m]	Unsigned distance to the coin center, computed when the participant crossed the vertical plane perpendicular to the trajectory supporting the coin.
4	Path ratio [-]	Quotient of the travelled path and an ideal path computed as a Catmull-Rom interpolation between the coins. Computed for the entire sequence.
5	Time [s]	Duration of the interval between two consecutive coins.
Head mov	ements	
6-8	Head rotation amplitude [°]	Interquartile range. Pitch, roll, yaw
Torso mov	vements	
9-11	Torso rotation amplitude [°]	Interquartile range. Pitch, roll, yaw
12-14,18	Mean torso speed [°]	Angular velocity. Pitch, roll, yaw, norm
15-17, 19	Maximum torso speed [°]	Angular velocity. Pitch, roll, yaw, norm
	o coordination	
20-24	Head-torso correlation	Absolute correlation. Pitch-pitch, roll-roll, yaw-yaw, roll-yaw, yaw-roll
25-27	Head anchoring index (AI)	Computed as $\Delta \sigma = \frac{\sigma_r - \sigma_a}{\sigma_r + \sigma_a}$ , where $\sigma_a$ is the standard deviation of the absolute head angles and $\sigma_r$ the standard deviation of the head angles relative to the torso. Positive $\Delta \sigma$ values indicate a preferred head stabilization to the external space and negative values a better head stabilization to the torso (9,14). <i>Pitch, roll, yaw</i>
28-32	Peak time of head-torso cross-correlation	Occurrence of the peak in cross-correlation. Negative delays indicate that the head is moving ahead of the body. <i>Pitch-pitch, roll-roll, yaw-yaw, roll-yaw, yaw-roll</i>
33-35	DTW distance	Dynamic time warping (DTW) distance between the head and torso sequences. Both segments were linearly interpolated to keep the number of data points constant across sequences (63,64). Pitch, roll, yaw
Movemen	t smoothness	
36-38	Torso SAL	3-dimensional smoothness metric based on the arc length of the movement speed profile's normalized Fourier magnitude spectrum; higher absolute values relate to jerkier movements(65)
39-41	Number of peaks head	Time-normalized number of peaks (66). <i>Pitch, roll, yaw</i>
42-44	Number of peaks torso	Time-normalized number of peaks (66). <i>Pitch, roll, yaw</i>
45-47	Number of peaks bird	Time-normalized number of peaks (66). <i>Pitch, roll, yaw</i>
48-50	Torso speed ratio [-]	Ratio of the mean to the maximum velocities; a ratio close to 1 stands for smooth movements, while lower values indicate jerkier movements (67,68). <i>Pitch, roll, yaw</i>