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Keeping up with ourselves: Multimodal processes underlying body ownership across the lifespan

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ABSTRACT

The sense of a bodily self is thought to depend on adaptive weighting and integration of bodily afferents and prior beliefs. While the physical body changes in shape, size, and functionality across the lifespan, the sense of body ownership remains relatively stable. Yet, little is known about how multimodal integration underlying such sense of ownership is altered in ontogenetic periods of substantial physical changes. We aimed to study this link for the motor and the tactile domain in a mixed-realty paradigm where participants ranging from 7 to 80 years old saw their own body with temporally mismatching multimodal signals. Participants were either stroked on their hand or moved it, while they saw it in multiple trials with different visual delays. For each trial, they judged the visuo-motor/tactile synchrony and rated the sense of ownership for the seen hand. Visual dependence and proprioceptive acuity were additionally assessed. The results show that across the lifespan body ownership decreases with increasing temporal multisensory mismatch, both in the tactile and the motor domain. We found an increased sense of ownership with increasing age independent of delay and modality. Delay sensitivity during multisensory conflicts was not consistently related to age. No effects of age were found on visual dependence or proprioceptive accuracy. The results are at least partly in line with an enhanced weighting of top-down and a reduced weighting of bottom-up signals for the momentary sense of bodily self with increasing age.
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1. Introduction

An impressive feature of human consciousness is that while our body changes across the lifespan in shape and functionality, our sense of body ownership, the sense that the body and its parts belong to oneself, remains generally remarkably stable. The bodily self is thought to be adaptive based on a constant interplay and adjustment between momentary weighting and integration of sensorimotor signals, and a more stable conceptual body knowledge (Apps & Tsakiris, 2014). Such adaptive capacity has been termed bodily self plasticity, and has increasingly been studied using multisensory stimulation paradigms, like the rubber hand illusion, where matching visuotactile stimulation on the hidden own hand, and a rubber hand induce the feeling that the rubber hand belongs to oneself (Botvinick & Cohen, 1998). Body ownership is thought to be a fundamental aspect of the bodily self (Gallagher, 2000) and plasticity of body ownership might play an essential role in the sense of bodily self across the lifespan. Yet, to date, little is known about how bodily self plasticity and stability, and the underlying multisensory and neural processes develop across the lifespan. The limited number of existing studies using the rubber hand illusion paradigm in different age groups did not cover a broad age range and applied different methods and controls, hampering direct comparisons and the formation of a global picture (e.g., Cowie et al., 2016; Kállai et al., 2017).

The early development of body ownership and self-other distinction is tightly linked to the detection, integration, and meaningful interpretation of contingencies between various signals coming from the own body as well as between those coming from the own body and the external world. Such detection ability has been found in infants, newborns, and might even be present prenatally (Rochat, 2011). Results from preferential looking paradigms in infants implicitly suggest a basic awareness of multisensory contingency between visuoproprioceptive, visuotactile, and visuointeroceptive stimuli (Bahrick & Watson, 1985; Filippetti et al., 2013; Maister et al., 2017; Rochat & Morgan, 1995; Thomas et al., 2018; Zmyj et al., 2011). In these studies, the detection of temporal coherence of visual stimuli and own movements has been argued to reflect an online egocentric body schema, a momentary and action-based sense of body, which precedes the formation of a more explicit self concept (Riva, 2018; Rochat, 2003). The importance of coherent multisensory bodily related information for the emerging self concept is for example illustrated by the adequate removal of a mark on the face in a mirror-self-recognition test by three-year-old toddles when the visual information of the video is temporally coherent, but not when it is delayed by 2 sec (Miyazaki & Hiraki, 2006).

Research using the rubber hand illusion in school-aged children shows that these multisensory processes and their relation to conscious body ownership undergo finetuning throughout childhood. The sense of ownership over a rubber hand, as measured through questionnaires, can be induced in children as young as 4 years old (i.e., the earliest age tested to our knowledge), and there is no evidence for age related differences in subjective responses (Cowie et al., 2013, 2016; Nava et al., 2017). Behavioural proprioceptive drift responses on the other hand, only became adultlike at around 10 years of age (Cowie et al., 2013, 2016; Nava et al., 2017). Children demonstrated more proprioceptive drift than adults in the classical rubber hand illusion (Cowie et al., 2013, 2016, but see Nava et al., 2018), but less in the somatic (non-visual) rubber hand illusion (Nava et al., 2017), which might indicate that visuo-proprioceptive integration is still developing at this age. Additional evidence of an active version of the rubber hand illusion, where participants stroked the rubber hand themselves, suggests that proprioceptive drift is also shaped by action. Children located the position of their unseen hand more towards the rubber hand than the veridical hand position, whereas adults did not show increased drift towards the rubber hand when it is actively stroked (Nava et al., 2018). Overall, integration and weighting of visual, proprioceptive, and sensorimotor signals for a number of body related tasks changes across development, and might depend on structural and functional maturation of cortical areas involved in processing of self relevant and multisensory information (Lewis & Carmody, 2008). Children become more sensitive to visuo-proprioceptive asynchrony with age, and for locating their limbs in space older children relied more on proprioceptive information, whereas younger children mainly use unimodal visual cues (Jaime et al., 2014). This suggests that young children rely more on the most reliable sense for the task in place rather than on the integration of all available multisensory information (King et al., 2010; Nardini et al., 2013). Additional findings suggest that the development of multimodal integration is not linear and might be tightly linked to the ongoing physical, sensory, and perceptual changes of the body (Nardini et al., 2013).

Not only in childhood, but also in late adulthood the physical body and its functional properties undergo many changes, and multisensory weighting mechanisms have been suggested to change significantly (Murray et al., 2016). Yet, again, this age group is underrepresented in the embodiment literature, and it remains largely unknown how these changes are related to bodily self plasticity (Kuehn et al., 2018). Initially, it has been hypothesized that the plasticity of the bodily self decreases with age, explained by plausibly a stronger weighting of the long term body cognition (Tajadura-Jiménez et al., 2012). However, recently, a number of studies reported that older adults were similarly sensitive to synchronous visuotactile stimulation in the rubber hand illusion (Campos et al., 2018; Kállai et al., 2017; Marotta et al., 2018; Palomo et al., 2018; Riemer, Wolbers, et al., 2019). These studies consistently report no difference in proprioceptive drift responses between older and younger adults, even though accuracy of proprioception might be reduced in older people (Riemer, Wolbers, et al., 2019). Findings from subjective measures are less conclusive, and some groups report a stronger illusion in elderly (Marotta et al., 2018), whereas others observe a stronger effect for younger participants (Kállai et al., 2017), or no differences between age groups (Campos et al., 2018; Palomo et al., 2018; Riemer, Wolbers, et al., 2019). In the projected hand illusion, a similar paradigm to the rubber hand illusion, a negative correlation between embodiment and age, and a positive correlation between proprioceptive drift and age was reported (Graham et al., 2015).

The direct comparison between these studies is hindered by the methods used, which are often based on a single measure, do not include appropriate control conditions, and demonstrate variability across studies. We thus propose here to comprehensively study the integration of multisensory and sensorimotor bodily signals and how it relates to bodily self plasticity across the lifespan with a more fine-grained and ecologically valid manipulation of multisensory bodily signals of the real body using mixed reality. It has been shown that breaking the temporal coherence of visual, and tactile or motor cues pertaining to the own body, can reduce the feeling of ownership of one's own hand (Gentile et al., 2013; Kannape et al., 2019; Roel Lesur et al., 2020). In a first-person perspective mixed reality setup where participants observed their own body in a head-mounted display (HMD) from a first-person perspective, we manipulated the synchrony between visual and tactile, and sensorimotor signals of the own body by introducing differing delays in the visual feedback on the HMD with respect to the tactile or motor event. This setup allowed for a psychometric approach, by assessing both sensitivity to delay between visual and sensorimotor signals, as well as ownership over one's own body in a repeated number of short trials. It thus provides an important improvement in comparison to the traditional single measures, such a proprioceptive drift or questionnaire responses, used in the rubber hand illusion. Furthermore, the results contribute to current discussions on how different sensory modalities contribute to the bodily self (Pia et al., 2019) and how this might change across development (Nava et al., 2018).

In this study we addressed four hypotheses. Hypothesis 1 is our main hypothesis and concerns that generally, and independently of the type of coherence, we expected the subjective feeling of ownership to be less dependent on the delay or sensorimotor input (either visuotactile or visuomotor) with increasing age (Tajadura-Jiménez et al., 2012), due to a stronger reliance on priors than on online signals, resulting in a decrease of bodily plasticity. Hypothesis 1 thus postulates that age modulates the reduction of ownership over the seen body with increasing incoherence between the visual and tactile/motor signals, so that the modulatory effect of delay is stronger in younger than older participants. Our other three hypotheses concern factors of multisensory integration that have previously been linked to body ownership as measured in our experimental setup and have also shown to be modulated through development but have never been tested in the full age range included in this study. The first factor concerns the sensitivity to delay, which has previously been related to the modulation of body ownership across delay between visual and tactile and motor signals (Roel Lesur et al., 2020) but also has been suggested to be higher in adults than in children and elderly (Murray et al., 2016). In Hypothesis 2, we thus expected the sensitivity to the delays between multimodal signals to be an inverted U-shape across the lifespan. The second factor concerns visual dependence. Weighting style of visual as compared to other bodily cues, as measured by for example the rod-and-frame test (Witkin & Asch, 1948), has been shown to correlate with bodily self plasticity as measured in multisensory stimulation paradigms (David et al., 2014; Rothacher et al., 2018; Thür et al., 2019). Performance in this test has been shown to alter across different age groups, with increased visual dependence in younger children and older adults (Bagust et al., 2013; Eikema et al., 2013; Robert & Tanguay, 1990). We thus expected, in Hypothesis 3, a U-shaped trajectory of visual dependence across the lifespan. Finally, to be able to further disentangle the role of sensory processes that may contribute to the sense of body ownership across the lifespan, we assessed proprioceptive acuity. Previous studies have demonstrated age differences in upper limb proprioception (Adamo et al., 2007; Goble et al., 2005), and it has further been suggested that integration of multisensory bodily information might be differently weighted depending on the sensitivity of each sensory system (King et al., 2010; Nardini et al., 2013). In Hypothesis 4, we expected a U-shaped relationship between age and proprioceptive error, with less acuity in younger and older participants.

To our knowledge, this is the first study that used a lifespan approach to study body ownership and the underlying multimodal processes, by adopting the same experimental paradigm from children to elderly. While covering all ages from the age of seven onwards, we focused on periods in life in which most bodily, neural, and cognitive changes occur, namely childhood and late adulthood. Spacing within age groups was adjusted accordingly, with narrower ranges where faster changes were expected (Craik & Bialystok, 2006; Li & Lindenberger, 2002). While a degree of bodily self plasticity is present in healthy individuals (Apps & Tsakiris, 2014), some authors have suggested that enhanced plasticity is related to pathology (Brugger & Lenggenhager, 2014). In order to further understand the nuances of healthy and unhealthy bodily self plasticity, it is important to consider how it changes throughout human ontogeny. Furthermore, with the growing ubiquity of immersive media in therapeutic settings, education, and entertainment, understanding how people of different ages react to technologically mediated bodily changes has important implications for both developers and consumers of such devices.

2. Methods

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

2.1. *Participants*

In total, 154 healthy, right-handed participants between 7 and 80 years old were included in seven equally sized age groups of 22 participants (7–9, 10–13, 14–17, 18–25, 26–60, 61–70, 71–80 years old; see Supplementary Material section 1.1 for feasibility assessment, and Section 2.5 for a power analysis). The age groups served exclusively for recruitment purposes, to provide sufficient sensitivity across ages where most functional and structural changes in the body occur. A uniform distribution of age within each group was aimed for. Exclusion criteria included current, or a history of psychiatric or neurological disorder, and abnormal vision. Participants, or their caregivers, were asked about these exclusion criteria during recruitment. Recruitment took place via a database of parents who are interested in participating in developmental psychology studies with their children, mailing lists of the University of Zurich, through schools and sports clubs, advertisements on notice boards and online of the University of Zurich, and the database of the University Research Priority Program Dynamics of Healthy Aging at the University of Zurich. Participants received compensation, for children under 16 years old this, was a toy/book worth approximately 5 Swiss Francs; for participants over 16 years old, this was a financial compensation of 20 Swiss Francs per hour. Informed consent was obtained from participants (or their caregivers if the participant was under 16 years old) prior to the experiment. The protocol has been approved by the Ethics Committee of the Faculty of Arts and Social Sciences at the University of Zurich (Approval Number 17.12.15) and was conducted in accordance with the standards of the Declaration of Helsinki. The data for this study were collected between September 2020 and January 2022. The preregistration of the study protocol can be retrieved from https://osf.io/ca5e9/.

2.2. Apparatus

The same apparatus was previously used in Roel Lesur et al. (2020), and is re-described here. An Oculus CV1 head-mounted display (Oculus VR, Irvine, CA, USA) was used for visual stimulation. An ELP 180° webcam (Ailipu Technology Co., Ltd, Guangdong, China) was positioned on the front of the HMD, set to 30 frames per second and a resolution of 1024 × 768 pixels. This webcam filmed the participant from a first-person perspective. A custom-made program in Unity 2018 was used to delay the camera feed, map it onto a 3D model approximately matching the distortion of the camera lens, and project the image on the HMD, thus showing a naturalistic view as if the participant is looking down at themselves from a first-person perspective. Randomization of delays, display of tasks and questions, and recording of responses were accounted for in the Unity program. The experiment was run on an Alienware 15 R3 computer (Nvidia Geforce GTX 1080 8GB; 16GB RAM; Intel Core i7; Windows 10), which added a mean intrinsic delay of 139.1 msec (SD = 18.3 msec). A previous study with the same setup showed that young adults still perceived the intrinsic delay as synchronous (Roel Lesur et al., 2020).

2.3. Procedure

The experimental procedure was kept as constant as possible across age groups (see Fig. 1A for the full procedure and timeline). Special attention was paid to explaining the questions and statements and answering scale to ensure the participant understood these before starting the testing phase. This was achieved by first explaining the questions and visual analogue scale with printed pictures, which has been successfully tested in 32 8-to-12-year-old children (Weijs et al., 2021). First, the rod and frame test was presented to the participants on the HMD (Rothacher et al., 2018) (see section 2.3.1, Fig. 1B). Then, participants saw a black screen on the HMD during the performance of the proprioceptive acuity task (Fig. 1C). Afterwards they proceeded to the real hand illusion to measure bodily plasticity (see section 2.3.2, Fig. 1D and E), and complete a post-test questionnaire.

2.3.1. *Rod and frame test*

We used a previously deployed VR-adapted version of the rod-and-frame test (Rothacher et al., 2018) to assess visual dependence (i.e., the dominance of visual cues over other bodily cues). Participants sat upright on a chair. They saw a virtual, tilted frame surrounding a rod on the HMD, that could be rotated using the left and right key of a mouse. They were asked to set the rod in a perfectly vertical orientation. The virtual rod was composed of a dotted line to prevent giving any cues about its orientation due to the limited resolution of the HMD. Each participant completed 12 trials consisting of a randomized, balanced set of a frame tilted ±20° paired with a rod, initially tilted ±18° (after Takasaki et al., 2012).

2.3.2. *Proprioceptive acuity task*

To measure proprioceptive acuity closely related to the experimental setup, participants performed an arm position matching task, which was loosely inspired by tasks reported in Adamo et al. (2007) and Goble et al. (2005). Participants saw a black screen on the HMD to block the view of their body and placed their left hand on a marked position on the sliding platform that was also used for the visuomotor condition (see Section 2.3.3). The experimenter instructed the participant to relax the arm. Then, the experimenter moved the platform to a marked position from the starting position, held it for two seconds and then moved the platform back to the starting position. Afterwards, the participant was instructed to match the position, after which the experimenter noted down the distance from the target position. The task consisted of a total of six trials with differing direction (left and right), and distance (5, 10, 15 cm), of which the order was randomized.

2.3.3. *Bodily self plasticity test: the real hand illusion*

To assess the influence of mismatching multimodal cues on the sense of body we used a mixed reality setup. Here, participants saw a video image of their own body in the HMD, as seen from a first-person perspective, fed from a camera mounted on the HMD (see Fig. 1). During this task, participants were seated at a table, with their left hand on a sliding platform mounted on the tabletop, and their right hand next to the platform on the tabletop. They were instructed to look down, as if they were looking at their hands. The height of the chair was adjustable, depending on height of the participant.

The task consisted of 8 blocks, with two conditions: visuotactile and visuomotor stimulation. The order of conditions was counterbalanced to minimize potential order effects. Each block consisted of 10 trials, adding up to a total of 80; 40 per condition. The delay of the visual feedback in the HMD was manipulated, using 5 equidistant delays between 0 and 600 msec (plus the intrinsic system delay of 139.1 msec). These delays were presented in randomized order, where each delay step occurred 8 times in each condition across the full task.

Visuomotor stimulation (Fig. 1D) or visuotactile stimulation (Fig. 1E) in each trial lasted for 7 sec. The visuotactile stimulation was applied from the tip of the index finger to the base of the wrist on the back of the left hand by the experimenter using a paintbrush. Three full strokes were applied

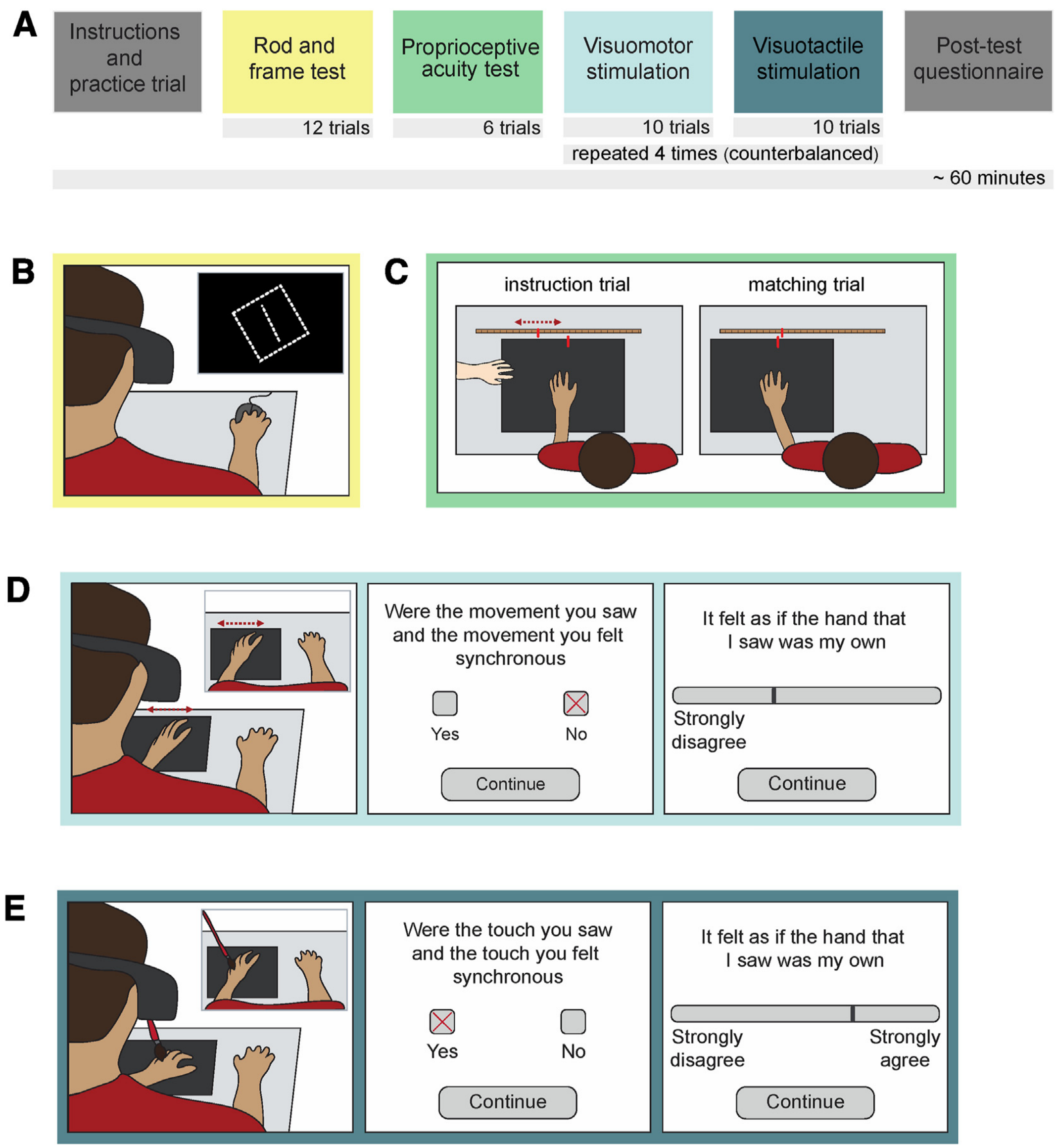

Fig. 1 – Experimental procedure and setup. A) Experimental procedure and timeline. The real hand illusion consisted of visuomotor and visuotactile stimulation. These conditions were altered in blocks of 10 trials, and each occurred 4 times. B) During the rod and frame test, participants were seated at the table and used the mouse to rotate the rod they saw in the HMD to a perfect vertical orientation. C) During the proprioceptive acuity task, participants were blindfolded and had their left hand placed on a sliding platform. In the instruction trial, the experimenter moved the platform to a target position, held it for 2 sec, and moved it back to the starting position. In the matching trial, the participant was instructed to move to the remembered target position. D) Overview of a visuomotor trial, where participants saw the visual display in the HMD (as shown in the frame insert) for 7 sec while they moved their left hand on a sliding platform, then the forced choice question about synchrony detection appeared in the HMD. The final screen shows the body ownership question and VAS scale to answer. E) Overview of a visuotactile trial, which followed the same structure as the visuomotor trial, but here, participants were stroked on their left hand by the experimenter.

within the 7 sec time window. For the visuomotor stimulation, the participant moved their left hand from right to left and vice versa on a sliding platform, again the participant was instructed to move at such a speed that three left to right and back movements can be made in 7 sec. The sliding platform was restrained to keep the range of movement constant and allow for movements exclusively in one axis, and to keep the tactile feedback on the hand palm constant between the visuomotor and visuotactile conditions. Before each block, the experimenter instructed the participant about the condition.

After each 7 sec window, two questions appeared, for which participants could select the answer using their head movements. The first addressed synchrony perception: “Were the movement you saw and the movement you felt synchronous?" in the visuomotor conditions, and "Were the touch you saw and the touch you felt synchronous?" in the visuotactile condition. This was a forced choice question that could be answered with "yes" or "no". The second question concerned body ownership: "It felt as if the hand I saw was my own" and could be answered on a VAS scale from "completely disagree" to "completely agree". The questions were presented in German and have been tested with children (see Supplementary Material section 1.1). The next question was prompted by the participant selecting a "continue" button, ensuring that there was enough time to select a response across the age range.

The task started with a practice trial, in which participants were shown the visuotactile condition, and could practice the timing of the movements in the visuomotor condition. As soon as the participant was able to perform the movement, the scene continued to the questions. Here, we explained how participants could select an answer by using head movements. Once the participant felt comfortable with using the HMD, the experimental procedure started.

2.3.4. *Post-test questionnaire*

Directly after the bodily self plasticity test, the following three questions were presented in the virtual environment, to which participants answered on a VAS scale ranging from (not at all – very much).

- I have experience using virtual reality.
- During the experiment I had an uncanny feeling ("unheimlich" in German).
- How strong would you rate motion sickness during the experiment.

2.4. *Data treatment and analysis*

Data analysis was performed in Rstudio, with R (R Core Team, 2018). A significance level of $\alpha = .02$ (two-sided) was used, and 95% confidence intervals are reported for tested values. Mixed effects analyses were performed with the R packages lme4 (Bates et al., 2015) and lmerTest R (Kuznetsova et al., 2017). Confidence intervals for coefficients in mixed-effects models are based on parametric bootstrapping. The models below are specified in standard lme4 notation. Age was treated as a continuous variable in all models specified below. All data and scripts are available from https://osf.io/2m9an/.

Participants were included in the analyses if they completed at least 6 blocks corresponding to ~75% of the trials in both conditions of the real hand illusion (i.e., visuotactile or visuomotor). Participants who did not complete the minimum number of trials, in either of the two, or both conditions, were replaced by new participants throughout recruitment to ensure group sizes of 22 participants for adequate power. Uncompleted trials for the rod-and-frame task were not replaced, and if the participant completed less than 9 trials in this task, they were excluded from the analysis on visual dependence, and no rod-and-frame mean angle was calculated. Participants who failed to complete the minimum number of trials for the rod-and-frame task were not replaced. The task was the first to occur in the protocol, was very short, and has previously been successfully used in children from age 7 on (Bagust et al., 2013), so we expected the attrition rate to be low. Similarly, participants who failed to complete the proprioceptive acuity tasks were not replaced, because we expected this number to be very low due to the short duration of the task. As a much larger sample size was needed for adequate power to test Hypothesis 1 than Hypotheses 3 (effect of age on visual dependence) or 4 (effect of age on proprioceptive acuity), we did not expect that a low number of potential dropouts would meaningfully compromise the power to test for Hypotheses 3 and 4 (see section 2.5 Power analysis and Supplementary Material). For pre-experimental pilot data and feasibility checks see Supplementary Material.

For each participant who completed at least 9 trials in the rod-and-frame task, a mean angle was calculated as the average of the unsigned angular deviations of the subjective visual vertical from the true vertical in each trial. For each participant who completed all 6 trials in the proprioceptive acuity task, a mean absolute error was calculated as the average of the absolute distance from the target in each trial.

In the visuomotor and visuotactile condition separately, sensitivity to delay was assessed by determining the Point of Subjective Equality (PSE) and Just Noticeable Difference (JND) for each participant. To this end, logistic psychometric functions were fitted to the forced choice synchrony judgements of each participant, using a binomial Generalized Linear Model (glm) with delay as a predictor (synchrony judgement ~ delay). Goodness of fit was assessed with the Hosmer–Lemeshow test, and PSE and JND were calculated if the test did not yield a significant p-value (<.05). In the case of significance, forced choice data were excluded for an individual participant in a specific condition.

2.4.1. *Hypothesis 1*

The main outcome variable of interest is body ownership, which is the extent to which participants identify with the seen body and feel like it is their own, and is expressed as a value between 0 (not all my body) to 1 (completely my body). We hypothesized that generally participants will report reduced ownership over their own body with increasing delay between tactile/motor stimulation and visual stimulation, and that this effect is modulated by age, where younger participants would show more plasticity than older participants. This was tested by fitting two mixed models to the data, for the visuomotor and visuotactile separately. The initial model was specified as (body ownership ~ age*delay + (delay | participant)).

2.4.2. *Hypothesis 2*

For delay sensitivity, we expected an inverted U-shaped relationship between age and sensitivity, with decreased sensitivity in younger and older participants. To test this, we used a linear regression with a quadratic term for age (sensitivity ~ age + age^2). Two separate models were used for sensitivity in the visuotactile and visuomotor condition respectively.

2.4.3. *Hypothesis 3*

Regarding visual dependence, we expected a U-shaped relationship between age and mean angular deviation, with increased deviations in younger and older participants. We tested this with a linear regression (mean angular deviation ~ age + age^2).

2.4.4. Hypothesis 4

We expected a U-shaped relationship between age and proprioceptive error, with increased errors in younger and older participants. A linear regression was used to test this hypothesis (mean error ~ age + age^2).

2.5. Power analysis

2.5.1. Hypothesis 1

To determine the minimum sample size for testing whether age modulates body ownership during the real hand illusion, we conducted a power analysis based on Monte Carlo simulations with the SIMR package (Green & MacLeod, 2016). We focused on the interaction of delay and age for the calculation, because this is the effect of main interest, and we expected that this effect has the smallest effect size. To date, studies looking at bodily self plasticity across the lifespan failed to report conclusive results, which might be due to the rather subtle, but still relevant differences in age that might not be detectable by the currently widely used single-time measures such as questionnaires and/or proprioceptive drift in the classical rubber hand illusion paradigm. When focussing on the effect of age on subjective ownership ratings, recorded on Likert scales, generally no differences were found, despite theoretical reasons for potential effects (Campos et al., 2018; Cowie et al., 2013, 2016; Nava et al., 2017; Palomo et al., 2018; Riemer, Wolbers, et al., 2019). In studies where differences between age groups were found, small to medium effects were reported (Kállai et al., 2017; Marotta et al., 2018; Nava et al., 2018), according to Cohen's interpretation of effect sizes (Cohen, 1992). Based on the inconclusive results of the previous studies, we proposed to use a more fine-grained measure with multiple trials with different visuomotor or visuotactile asynchronies across a wide age range, which allows for potentially more sensitive statistical analyses, thus presumably increasing the power to detect rather subtle effects. Given the previously inconsistent findings, we think that with these improved experimental conditions even a small effect would be worth reporting. We thus performed the power calculation with a relatively small effect for the age*delay interaction. We based the power calculation on an interaction effect size of $b = .01$, which would in practice mean that on average, if participants would have the same baseline level of body ownership, with our maximum manipulation of 600 msec delay, the VAS ownership rating would reduce from .54 to .48 with a 10 year's age difference. Such a difference would not be detected on a 1–7 point Likert scale, which was used in previous studies. The complete lme4 model used for the power calculation was (body ownership ~ delay*age + (delay|participant)). A power curve was calculated based on 1000 simulations per sample size (see Supplementary Material, Fig. S2), and the alpha level was set to .02. This analysis revealed a sample size of 154 participants to detect an interaction effect of delay and age of $b = .01$ with 96.9% power, 95% CI [95.6, 97.9].

2.5.2. Hypothesis 2

Our second hypothesis concerns sensitivity to delays, which we expected to follow an inverted U-shaped trajectory, with reduced sensitivity in childhood and late adulthood. To determine the sample size to test this hypothesis, we conducted a power analysis using the pwr package in R. No previous studies assessed integration of tactile or motor signals, and visual information in a lifespan sample, so we based this power analysis on developmental and lifespan studies investigating both visuotactile and visuomotor integration more generally. Both in studies looking at differences between children and adults (Chen et al., 2018; Jaime et al., 2014), and across adulthood (Poliakoff et al., 2006), the size of the effect of age is relatively large, $\eta^2 \geq .2$, corresponding to $f^2 \geq .25$. This corresponds to an absolute difference in the JND of 50 msec between younger and older adults (Poliakoff et al., 2006), and in perceived simultaneity windows between 7 year old children and adults of 150 msec (Chen et al., 2018). Based on such an effect, the power analysis yielded a recommended sample size of 64 participants to detect an effect of age on sensitivity with 95% power. However, as these studies used different methods, and are based on comparisons of fewer groups with larger age differences, compared to the wide age range we proposed to include, we might detect smaller effects in our study. We thus expected that the effect that can be reliably detected with the required sample size for testing Hypothesis 1, corresponding to $f^2 = .10$, might be more realistic. Such synchrony detection is thought to fundamentally underlie the sense of body ownership, and we think that even small differences in delay detection might be important for both the fundamental understanding of multisensory integration of bodily signals, and potential future embodiment-based applications.

2.5.3. Hypothesis 3

To determine the sample size for the third hypothesis, that visual dependence follows a U-shaped trajectory across the age range, we considered that effect sizes for age differences in performance on the rod and frame task between younger and older adults are approximately $f^2 = .75$, when estimated from reported means and standard deviations, corresponding to an absolute difference between 3 and 5° between young and old adults (Eikema et al., 2013; Robert & Tanguay, 1990). We aimed to replicate this effect in our sample across the full lifespan, but to avoid overestimation of the effect size for age differences in visual dependence, we based the power calculation on a large effect size of $f^2 = .35$. This yielded a recommended sample size of 46 participants to detect an effect of age with 95% power. Along a similar line of reasoning as for Hypothesis 2, we expected the effect of age on visual dependence to be smaller due to the differences in design between the current and previous studies, which only compared different groups across adulthood. Again, the recommended sample size for testing Hypothesis 1 was much larger, thus allowing us to detect also smaller effects that might be due to the inclusion of participants across a wider age range, which might nevertheless be meaningful to better understand the mechanisms fundamentally underlying the sense of body ownership. In addition, on a more practical side, as virtual reality applications are heavily based on the mechanism of visual capture, even a small effect might lead to the need to adapt current therapeutic VR settings to age.

2.5.4. Hypothesis 4

The power calculation for the fourth hypothesis is based on the expectation that proprioceptive acuity and age follow a U-shaped trajectory across the lifespan, with lower acuity in children and the elderly. Previous studies that investigated upper limb proprioception across different ages either compared young and old adults (Adamo et al., 2007) or between children and adolescents (Goble et al., 2005) reported large effects of age on proprioceptive acuity for the upper limbs, corresponding of differences of 1–3° between age groups (η^2 = .28–.59, corresponding to f^2 = .39–1.44). In line with this literature, a large effect of age on proprioceptive acuity in a complex proprioceptive acuity task ($\eta_p{}^2$ = .52) has been reported for a lifespan sample (Yang et al., 2019). The power calculation was based on an effect size of f^2 = .20, to avoid overestimation due to the differences between the tasks used to measure proprioceptive acuity. This yielded a recommended sample size of 80 participants to detect an effect of age with 95% power. Again, with the recommended sample size for Hypothesis 1, we would be able to detect smaller effects which might still be relevant to better understand the underlying proprioceptive mechanisms that could play a role in body ownership.

Based on these analyses, we planned to include 154 participants, which would allow sufficient power for testing all four hypotheses.

2.6. *Deviations from preregistration*

Upon inspection of the forced choice responses for delay detection, we noticed that there were many cases of complete or quasi-complete separation in our data (there was often only a single point on the rising edge of the function; other levels of delay yielded 100% ‘yes’ or ‘no’ responses). Therefore, we applied bias reduction in fitting the binomial generalized linear models on the delay detection data. This approach statistically accounts for complete separation of the data to obtain more reliable estimates of PSE and JND (Firth, 1993; Kosmidis, 2021).

3. Results

3.1. *Participants*

We included 154 participants in the final sample, as preregistered (see Table 1). Another ten participants were recruited but had to be excluded because they did not tolerate the HMD (n = 2), did not complete the required minimum number of trials (n = 7), or because of technical issues (n = 1). Following the criteria set for the individual tasks (see Section 2.4 Data treatment and analysis), we had to exclude four participants from the proprioceptive acuity task analyses, because they did not provide sufficient data.

Table 1 – Number of participants, and number of females within each age group that were included in the final sample.

Age group	N total	N female
7–9	22	13
10–13	22	10
14–17	22	13
18–25	22	10
26–60	22	11
61–70	22	9
71–80	22	10

3.2. *Hypothesis 1: Body ownership*

Two linear mixed models, one for the visuotactile condition and one for the visuomotor condition, were used to test Hypothesis 1. In the visuotactile condition, the model showed a significant effect of age [F(1, 152.45) = 23.37, p < .001], and of delay [F(1, 155.72) = 104.41, p < .001]. The interaction of age and delay was not significant [F(1, 154.52) = .01, p = .91; see Table 2 for coefficients of the full model]. Taken together, the model shows that with older age, ratings of body ownership were overall higher, and additionally that body ownership strongly reduced with increasing delay (Fig. 2A).

A linear mixed model with the same parameters described above was fitted on the ownership ratings in the visuomotor condition. A similar pattern of results emerged, and there were significant main effects of age [F(1, 152.03) = 11.91, p < .001], and of delay [F(1, 155.70) = 126.85, p < .001], but the interaction of age and delay was not significant [F(1, 154.21) = .46, p = .50; see Table 3 for coefficients of the full model]. Again, ownership ratings were lower with younger age, and body ownership was strongly reduced with increasing delay (Fig. 2B).

3.3. *Hypothesis 2: Delay sensitivity as measured by the PSE and JND*

Polynomial regressions were used to separately predict delay sensitivity in the visuotactile and visuomotor conditions. To this end, we extracted both the PSE and JND. The PSE reflects the delay at which participants were equally likely to judge the visuotactile or visuomotor stimulation as synchronous or asynchronous, such that a lower PSE can be interpreted as a higher sensitivity to delay. The JND corresponds to the amount of delay required to detect a difference in 50% of cases, again with a lower value reflecting higher sensitivity. Age and the quadratic term of age to account for the hypothesized U-shaped relationship were included as predictors. After testing for goodness of fit of the logistic glm for individuals, 12 participants were excluded in the visuotactile condition, and 17 participants in the visuomotor condition.

In the visuotactile condition, neither the linear (b = .005, t = 1.86, p = .065, f^2_p = .02), nor the quadratic effect of age (b = −.00004, t = −1.37, p = .17, f^2_p = .01) on the PSE were significant [F(2, 139) = 5.67, p = .004, $R^2_{adjusted}$ = .06; Fig. 3A]. In line, neither the linear (b = −.004, t = −1.63, p = .11, f^2_p = .02) nor quadratic effect of age (b = .00005, t = 1.51, p = .13, f^2_p = .02) showed a significant effect on the JND [F(2, 139) = 1.49, p = .006, $R^2_{adjusted}$ = .007; Fig. 3B].

In the visuomotor condition, the PSE was significantly predicted by both the linear (b = .006, t = 2.46, p = .015, f^2_p = .05) and quadratic trend of age [b = −.00007, t = −2.44, p = .016, f^2_p = .04; F(2, 134) = 3.03, p = .052, $R^2_{adjusted}$ = .029; Fig. 3C]. Contrastingly, neither the linear (b = −.0007, t = −.97, p = .33, f^2_p = .007), nor quadratic effect of age (b = .000009, t = 1.06, p = .29, f^2_p = .008) on the JND were significant [F(2, 134) = .64, p = .53, $R^2_{adjusted}$ = −.005; Fig. 3D].

Table 2 – Summary of the mixed model predicting body ownership in the visuotactile condition, including the predictors age, delay, and the interaction between these.

		95% Confidence interval					
Fixed effects	*b*	Lower	Upper	*SE*	*df*	*t*	*p*
Intercept	.831	.787	.877	.023	154.51	36.18	<.001
Age	.003	.002	.004	.0005	152.45	4.84	<.001
Delay	−.637	−.760	−.514	.062	155.72	−10.22	<.001
Age*delay	−.0002	−.003	.003	.001	154.52	−.12	.906

Note: 5814 observations in 154 participants.

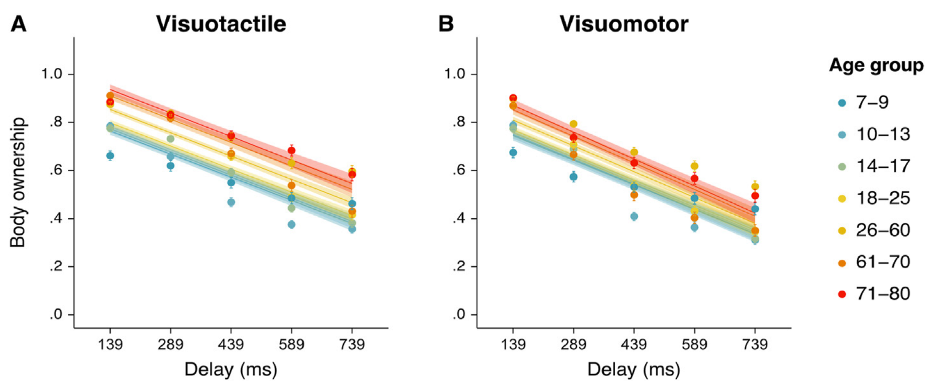

Fig. 2 – Body ownership ratings were significantly predicted by age and delay in both the A) visuotactile and B) visuomotor condition. Age was entered as a continuous variable in the models, and the grouping by age here is only for illustrative purposes. Points and error bars represent the mean observed values and standard errors for each age group. The lines and shaded areas represent the predicted values yielded by the models.

3.4. *Hypothesis 3: Visual dependence*

A polynomial regression demonstrated that there was no significant linear ($b = -.08$, $t = -.84$, $p = .40$, $f^2_p = .005$) or quadratic effect [$b = .001$, $t = 1.21$, $p = .23$, $f^2_p = .01$; $F(2, 151) = 2.97$, $p = .054$, $R^2_{adjusted} = .03$; Fig. 4A] of age on visual dependence as tested by the rod-and-frame test.

3.5. *Hypothesis 4: Proprioceptive acuity*

A polynomial regression showed neither a significant linear ($b = -.048$, $t = -2.07$, $p = .041$, $f^2_p = .03$) nor quadratic [$b = .0005$, $t = 1.79$, $p = .076$, $f^2_p = .02$; $F(2, 147) = 3.30$, $p = .04$, $R^2_{adjusted} = .03$; Fig. 4B] effect of age on proprioceptive error.

3.6. *Exploratory analyses*

3.6.1. *Additional predictors of body ownership across delays*

In exploratory analyses, we added additional predictor variables to the models used to test Hypothesis 1, to assess whether these explain ownership beyond age and delay. BIC values were assessed to compare model fit, while penalizing for added complexity. To this end, participants with missing data in any of the explanatory variables (PSE, visual dependence, and proprioceptive acuity) had to be removed to compare model fit on datasets of equal size. This led to the exclusion of 16 participants in the visuotactile condition, and 19 participants in the visuomotor condition. Neither in the visuotactile, nor visuomotor condition did the addition of

Table 3 – Summary of the mixed model predicting body ownership in the visuomotor condition, including the predictors age, delay, and the interaction between these.

		95% Confidence interval					
Fixed effects	*b*	Lower	Upper	*SE*	*df*	*t*	*p*
Intercept	.821	.771	.871	.025	153.97	32.43	<.001
Age	.002	.001	.003	.0006	152.02	3.45	<.001
Delay	−.673	−.791	−.556	.060	155.70	−11.26	<.001
Age*delay	−.0009	−.004	.002	.001	154.21	−.68	.497

Note: 5802 observations in 154 participants.

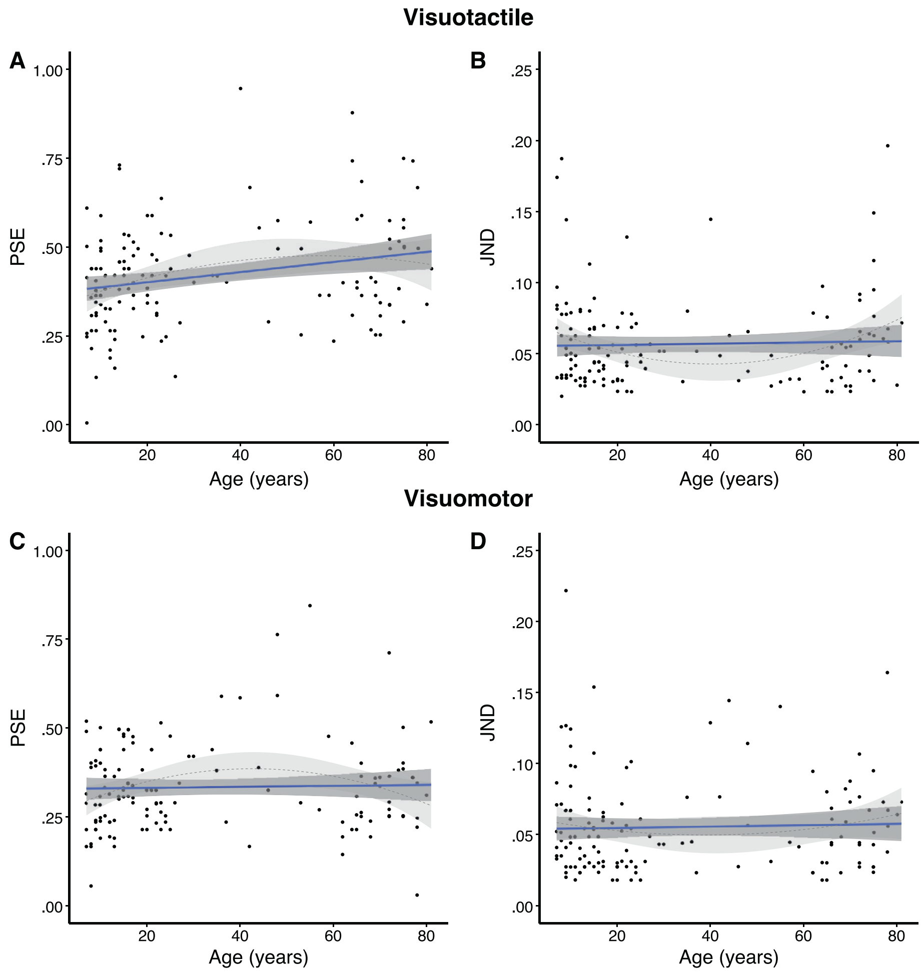

Fig. 3 – Linear (continuous blue line) and quadratic (grey dashed line) trends of PSE and JND by experimental condition. In the visuotactile condition, there were no significant linear or quadratic effects of age on either the PSE (A) or JND (B), In the visuomotor condition, both the linear, and quadratic effect of age on PSE (C), were significant, but not on the JND (D). Shaded areas represent standard errors and dots represent the individual data points.

sensitivity to delay, proprioceptive error, or visual dependence significantly improve the fit of the model and/or meaningfully reduce the BIC. Statistics of these analyses are reported in the Supplementary Material.

3.6.2. *Nonlinear effects of age on ownership*

After visual inspection of the results of Hypothesis 1, we observed non-linear effects of age on ownership responses across delays, especially in the younger age groups (see Fig. 5). In line with previous studies, we used age group as a categorical variable in the linear mixed models for ownership in Cowie et al. (2013, 2016). To further explore these dynamics within the three younger age groups (7–9, 10–13, and 14–17-year-olds), we fitted two separate linear mixed models on ownership responses in the visuomotor and visuotactile condition respectively (see Fig. 5).

The model on the ownership responses in the visuomotor condition showed significant main effects of age group [$F(2, 65.29) = 5.16$, $p = .008$], and of delay [$F(1, 66.14) = 215.65$, $p < .001$; see Table S1 for a full summary of the model]. There was also a significant interaction of age group and delay [$F(2, 66.12) = 9.61$, $p < .001$]. We followed up on this analysis by post hoc comparisons of the linear trends for each age group. This analysis revealed that the reduction in ownership across delays was lowest in the youngest group ($b = -.372$, $SE = .08$), and significantly different between the 7–9-year-olds, and 10–13-year-olds ($b = -.774$, $SE = .08$, $t = 3.62$, $p = .002$), and between the 7–9-year-olds, and 14–17-year-olds ($b = -.793$, $SE = .08$, $t = 3.81$, $p = .001$). There was no significant difference between the 10–13-year-olds and 14–17-year-olds ($t = .17$, $p = .98$). A similar pattern of results was revealed for the visuotactile condition, again the main effect of age group [$F(2, 65.51) = 6.51$, $p = .003$], delay [$F(1, 66.52) = 186.28$, $p < .001$], and their interaction [$F(2, 66.50) = 8.03$, $p < .001$] were all significant (see Table S2 for a full summary of the model). Again, ownership decreased less strong in the youngest group ($b = -.356$,

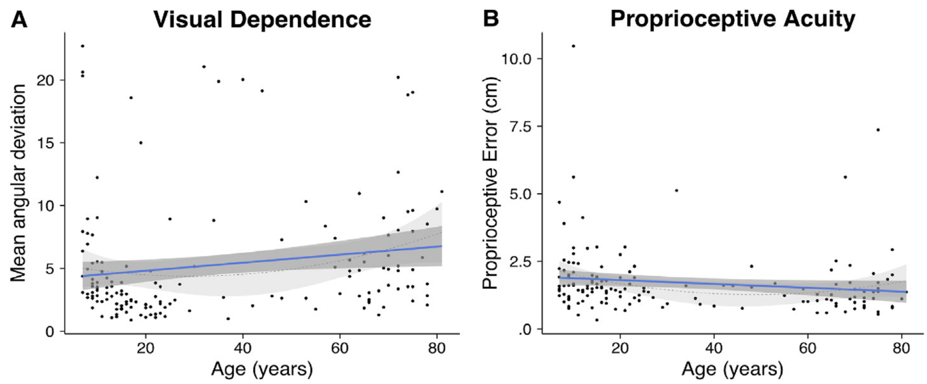

Fig. 4 – Linear (continuous blue line) and quadratic (grey dashed line) trends of A) visual dependence, and B) proprioceptive acuity. None of the plotted effects were significant. Shaded areas represent the standard error and dots the individual observations.

SE = .08), than in both the 10–13-year-old group ($b = -.760$, $SE = .08$, $t = 3.59$, $p = .002$), and the 14–17-year-old group ($b = -.711$, $SE = .08$, $t = 3.179$, $p = .006$), but there was no significant difference between the two older groups ($t = -.44$, $p = .90$).

3.6.3. *Nonlinear effects of age on visual dependence in the rod-and-frame test*

To further elucidate the difference in ownership ratings, which in children have been suggested to be linked to changes in visual dependence (Cowie et al., 2013, 2016), we also included age as a categorical variable in the analysis of the of the rod and frame test. In a linear model with visual dependence predicted by age group, we found that the difference between the 7–9-year-olds and 10–13-year-olds was not significant ($b = -3.08$, $SE = 1.31$, $t = -2.35$, $p = .06$), but with the 14–17-year-old group it was significant ($b = -3.95$, $SE = 1.31$, $t = -3.01$, $p = .01$). The 7–9-year-old children showed higher visual dependence than the two other groups (see Fig. 5C).

3.6.4. *Nonlinear effects of age on proprioceptive acuity*

To assess difference between the three youngest age groups in proprioceptive error, we fitted a linear model with proprioceptive error predicted by age group. We did not observe any significant differences in proprioceptive error between the 7–9 year-olds and 10–13 year-olds ($b = .65$, $SE = .42$, $t = 1.53$, $p = .28$), or 14–17 year-olds ($b = -.27$, $SE = .42$, $t = -.64$, $p = .80$).

3.6.5. *Post-test questionnaire*

Final exploratory analyses concern the three items of the post-test questionnaire, asking about an uncanny feeling, nausea, and experience with VR. Agreement with the "uncanny" statement was rather low ($M = .21$, $SD = .25$), and it did not significantly correlate with age ($r = -.05$, $p = .52$). Agreement with the "nausea" statement was also quite low ($M = .28$, $SD = .30$), and did also not show a significant correlation with age ($r = -.06$, $p = .48$). VR experience ($M = .40$, $SD = .38$) showed a significant negative correlation with age ($r = -.28$, $p < .001$), with youngest participants reporting most use of VR before the experiment.

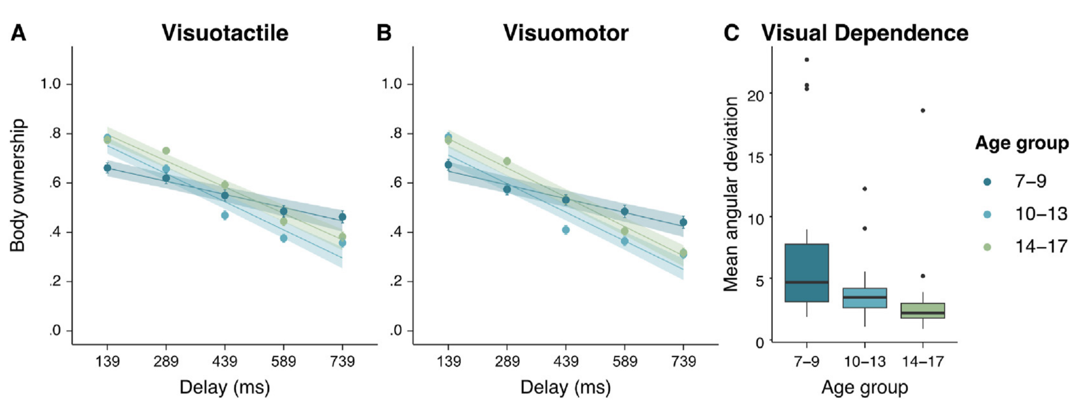

Fig. 5 – Body ownership predicted by delay in the younger age groups in the A) visuotactile and B) visuomotor conditions. In both conditions ownership reduced less strongly across delays in the 7–9-year-olds as compared to the other two groups. C) Visual dependence was higher in the youngest age group, compared to the older groups. Boxes represent the interquartile range, whiskers the minimum and maximum, outliers are represented by dots.

4. Discussion

In this study, we assessed bodily self plasticity and underlying multisensory processes in a lifespan sample. In line with our expectations, we found that feelings of body ownership decreased with increasing delays between multisensory (visuotactile and visuomotor) input consistently across the lifespan. Contrary to the hypothesized interaction of delay and age, we found that younger, as compared to older participants, reported lower feelings of ownership across all multisensory mismatches and delays. There was thus a main effect of age but no interaction with delay. Furthermore, age predicted sensitivity to delay between visual and motor stimuli of the own hand, as hypothesized. This effect was, however, not present for visuotactile stimuli. Contrary to our hypotheses, we further did not find evidence for an effect of age on visual dependence, or on proprioceptive accuracy. Finally, in exploratory analyses on the participants below 18 years-old, we observed that 7–9-years-olds demonstrated a weaker reduction of body ownership across delays than the older two age groups in both the visuomotor and visuotactile condition.

4.1. *Hypothesis 1: Body ownership*

In this study, we replicated previous findings that increasing delay between visual and tactile or motor feedback from one's own body reduces the feeling of body ownership (Gentile et al., 2013; Kannape et al., 2019; Roel Lesur et al., 2020, 2021; Weijs et al., 2022). Importantly, this finding is extended to a lifespan sample in the present study.

It provides evidence that coherent multisensory signals are not only required for the illusory embodiment of external objects (Botvinick & Cohen, 1998), but also for the maintenance of a stable sense of embodiment of one's own body (Apps & Tsakiris, 2014). Here, we observed a reduction in repeated self-reported body ownership with increasing delay from childhood to old age.

Extending previous findings, we showed that overall body ownership increased with age after visuotactile and visuomotor stimulation. Unexpectedly, however, body ownership was similarly modulated by delay across all ages. Thus, while the increasing sense of body ownership with increasing age might suggest a stronger effect of the top-down contributions to the maintenance of body ownership, and a reduced sensitivity to sensory stimulation, the lacking interaction with delay suggests a more complex picture. Studies using embodiment illusions found increased plasticity in children compared to adults (i.e., children showed higher ownership for of an external body (part), which was less dependent on multisensory synchrony; Cowie et al., 2013; Nava et al., 2017; Weijs et al., 2021). This suggests that younger children have a less established, and thus more flexible sense of body and aligns with our current findings of a generally reduced sense of ownership over the own arm, corresponding to a stronger disembodiment illusion. This finding extended to the full lifespan, revealing highest levels of ownership in older participants, which could in line with previous findings (Kuehn et al., 2018; Tajadura-Jiménez et al., 2012) be explained by an increased weighting of top-down information for the sense of bodily self with increasing age. As people gain increasing experience with their own body, and the top-down body knowledge crystallizes, multisensory mismatches might be decreasingly important, even if not negligible, in determining the momentary sense of embodiment (Riva, 2018). This could potentially lead to an overall higher sense of body ownership over time.

In exploratory post-hoc analyses, which zoomed in on the younger end of the sample and used age categories in line with previous studies (Cowie et al., 2013, 2016; Nava et al., 2017), we saw that the youngest participants (7–9-year-olds) showed a flatter slope than the older two age groups (10–13 and 14–17-year-olds; Fig. 5). Younger participants thus demonstrated a reduced dependence on synchrony body ownership in both visuotactile and visuomotor conflicts. This is in line with previous studies using the rubber hand (Cowie et al., 2013, 2016) or full body illusion paradigm (Weijs et al., 2021), which showed that visual dependence in such conflicts is stronger in younger age and becomes adult-like around the age of 10 (Cowie et al., 2016).

Thus here, the sight of their own body might have driven the sense of ownership in younger participants, as previously shown in the rubber hand illusion (Cowie et al., 2016). The results of the exploratory analysis on visual dependence in the rod-and-frame test confirm this interpretation. While there was no effect of age in the full sample, we found such effect in the younger end of the sample, suggesting higher visual dependence for the youngest group (see also below).

4.2. *Hypothesis 2: Sensitivity to delay*

We observed an effect of age on sensitivity to delay as measured by the PSE specifically for the visuomotor condition (i.e., not for the visuotactile condition). Contrary to our hypothesis, we found the highest sensitivity to delay (lowest PSE) at the younger and older extremes of the sample. However, age did not significantly predict the JND in this condition. In addition to the quadratic trend, we also observed a significant linear trend, which suggests that especially children were more likely to detect delays. As we had more data points at the extremes and more variance in early and middle adulthood (see Fig. 3), we encountered heteroscedasticity and decided to avoid overinterpreting these effects. The current delay detection task was designed to be feasible to conduct across the full age of this study, and in the context of the body ownership task. The limited levels of delays used resulted in complete separation of the data. Even though we statistically corrected for this, we cannot exclude that more fine-grained measures would have led to more accurate estimates of the PSE and JND.

While it was not a main hypothesis of the current work, it might be noteworthy that according to our exploratory analyses, the PSE did not predict the ownership ratings in either the visuotactile or the visuomotor condition, pointing rather towards independent processes. While the relationship been mismatch-detection and body ownership in situations of visuo-tactile conflict has been debated (Costantini et al., 2016; Roel Lesur et al., 2020, 2021), it has recently been suggested that both ownership and multisensory (a)synchrony perception are based on similar computational principles (Chancel et al., 2022). Future studies might consider using adaptive methods for threshold detection (cp. e.g., Chancel et al., 2022) and two-alternative forced choice tasks (Chancel & Ehrsson, 2020; Roel Lesur et al., 2021) to improve the measures of delay sensitivity. This might also overcome issues of complete separation when fitting psychometric curves, leading to more reliable estimates of PSE and JND. Further improvements in sensitivity could be achieved by using newer VR systems with higher visual and temporal resolution than the Oculus CV1, and integrated high-resolution 3D cameras instead of the webcam used in this study.

4.3. *Hypotheses 3 and 4: Proprioceptive acuity and visual dependence*

Unlike previous studies (Adamo et al., 2007; Chancel et al., 2018; Greenfield et al., 2017; Jaime et al., 2014) we did not find an effect of age on proprioceptive acuity. Similarly, and again unlike previous studies (Bagust et al., 2013; Eikema et al., 2013; Robert & Tanguay, 1990), we did not find an effect of age on visual dependence as tested with the rod and frame test. While the reason for such lack of significant results is unclear, we assume it might be linked to the precision of our measures. For the proprioceptive acuity task, we used a matching task loosely inspired by tasks reported in Adamo et al. (2007), and Goble et al. (2005). We adapted the tasks in a way that it seemed feasible and short enough to work for the full age range tested here, alongside the other tasks in the procedure. However, the task has not been validated or used before. Future studies would have to compare the results of our task with other proprioceptive acuity tasks for validation. Concerning the rod-and-frame task, even though this test has previously been used in virtual reality (Rothacher et al., 2018), this could have introduced variations which might have reduced the precision necessary to detect effects of age. When focussing on the young participants in explorative analyses however, the results are in line with our hypothesis that children below 10 years old are more dependent on visual than proprioceptive cues (Cowie et al., 2013; Nava et al., 2017; Weijs et al., 2021). This is also in line with findings that young children show a stronger sense of ownership over a foreign body (part) by just looking at it without synchronous visuotactile or visuomotor stimulation than older children or adults (Cowie et al., 2016; Filippetti & Crucianelli, 2019).

4.4. *Limitations and outlook*

In the current analyses, age is considered as a continuous variable, and linear models were used to assess effects on body ownership. While this has the unique advantage that processes underlying the sense of bodily self can be assessed and compared across the lifespan, such a broad perspective might also hamper investigations of dynamics within specific narrower age ranges. Previous research showed that the development of aspects underlying embodiment might not follow a linear trajectory within childhood (Nardini et al., 2013), and these non-linear dynamics might have been overlooked by the current preregistered analyses. Exploratory analyses partially addressed this issue, where we focused on effects within the younger end of the sample, indeed revealing age effects that were not found in the preregistered analyses. Future studies should use similar comparable methods, ensuring comparability and generalizability, but zoom in on specific age ranges, potentially even in longitudinal designs, to be able fully probe the dynamic changes underlying the sense of bodily self.

Furthermore, it is important to consider the limitations of the experimental setup. As we found that younger participants were most sensitive to visuotactile mismatches, it may have been that the intrinsic delay of the system was already enough to introduce a detectable visuotactile mismatch in the synchronous condition, and thus reduce body ownership. In a similar setup, children detected a visuotactile delay at chance level with 100 msec delay, but clearly above chance with 200 msec delay (Greenfield et al., 2017), the 139 msec of our system lies in between these levels. In previous studies from our lab using the same setup as here, young adults did not detect the visuotactile delay at the baseline of 139 msec (Roel Lesur et al., 2020, 2021).

In addition, as already mentioned, the adapted versions of the proprioceptive acuity and the visual dependence tasks used in this study, should be validated, and might have to be improved for more precise measures. Despite these limitations, this study might be a first step in bridging the gap between literature on early development of the sense of bodily self, and the expansive adult literature characterized by different methods and diverging results (Lee et al., 2021; Riemer, Trojan, et al., 2019) by applying the same experimental method across a wide age range.

Open practices

The study in this article has earned Open Data, Open Materials and Preregistered badges for transparent practices. The data, materials and preregistered studies are available at: https://osf.io/ca5e9/.

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Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cortex.2024.05.013.

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