Dynamics of sensorimotor plasticity during exoskeletal finger augmentation

Dominika Radziun[1*], Siebe Geurts[1*], Valeria C. Peviani[1#], Luke E. Miller[1#]

[1] Donders Institute for Brain, Cognition and Behaviour, Radboud University, Nijmegen, the Netherlands

[*]Dominika Radziun and Siebe Geurts shared first authorship

[#]Valeria C. Peviani and Luke E. Miller shared senior authorship

E-mails: dominika.radziun@donders.ru.nl (DR); siebe.geurts@ru.nl (SG); valeria.peviani@donders.ru.nl (VCP); luke.miller@donders.ru.nl (LEM)

Keywords: body augmentation, tool use, proprioceptive localization

Abstract

How does the brain integrate artificial body extensions into its somatosensory representation? While prior work has shown that tool use alters body representation, little is known about how artificial augmentations alter body representations as they are worn and used. Here, we investigated the dynamics of somatosensory plasticity using a custom-built exoskeletal device that extended users' fingers by 10 cm. Across four time points, before, during (pre- and post-use), and after exoskeleton wear, participants completed a high-density proprioceptive mapping task. We observed three distinct phases of plasticity. First, simply wearing the exoskeleton led to a contraction of the perceived length of the biological finger. Second, following active use, both biological and artificial finger representations expanded significantly, an effect absent when participants trained with a non-augmenting control device. Third, a lasting aftereffect on biological finger representation was observed even after device removal. Our findings demonstrate that wearable augmentations are rapidly integrated into the body representation, with dynamic adjustments in proprioceptive space shaped by both structural and functional properties of the device. This work advances our understanding of how the sensorimotor system accommodates artificial extensions and highlights the potential for body-augmenting technologies to be intuitively integrated into body representation. These results have direct implications for the design of prosthetics, exoskeletons, and other assistive technologies aimed at extending human physical capacity.

Significance statement

How do wearable augmentations reshape our sense of the body? Using a custom-built exoskeleton that extended the fingers, we tracked changes in body representation across four stages of wear and use. We found that the sensorimotor system rapidly integrates artificial extensions into its somatosensory map: first contracting, then expanding perceived finger length in response to structure and function, with the shifts persisting after device removal. Our findings reveal dynamic, use-dependent plasticity in body representation, which has direct relevance for designing prosthetics, exoskeletons, and assistive devices.

Introduction

The human body is remarkably adaptable, capable of integrating artificial enhancements that extend its physical capabilities (Maravita and Iriki 2004). This includes traditional tools (e.g., rakes) that operate outside the body as well as body augmentations (e.g., robotic limbs) that directly interface with the user. Decades of research has found that these technologies influence the user's body representation and its implementation in the brain (Iriki, Tanaka, and Iwamura 1996; Berti and Frassinetti 2000; Longo and Serino 2012; Gallivan et al. 2013; Miller, Longo, and Saygin 2019; Peviani et al. 2024). In contrast, relatively little is known about how body augmentation devices themselves are represented by the user's somatosensory system. Furthermore, most studies use pre-post experimental designs, offering a limited temporal window into the effects of technology. In our study, we aimed to address these gaps by investigating how body augmentation devices are integrated into the body representation over time.

Both tools and augmentation devices drive changes in the user's body representation (Holmes and Spence 2004; Canzoneri et al. 2013; Martel et al. 2016; Eden et al. 2022). Tools alter their user's spatial tactile perception and motor kinematics in ways consistent with stretching the sensorimotor representation of the user's arm (Cardinali et al. 2009; Sposito et al. 2012; Miller, Longo, and Saygin 2014). Body augmentation devices, such as extra arms and fingers, are designed to further expand the body's functional capabilities (Hussain et al. 2016; Mooney and Herr 2016; Penaloza and Nishio 2018; Prattichizzo et al. 2021; Yang et al. 2021;

Umezawa et al. 2022). Controlling an extra robotic finger, the Third Thumb, can modify body representation in motor cortex (Kieliba et al. 2021). However, the above effects are almost always measured after the device is no longer in use; how the user's body representation changes once they are directly interfaced with the technology is unclear. Identifying the influence of technological augmentation at other distinct stages—from the initial wearing of the technology to its use and subsequent removal—is crucial for understanding the dynamics of plasticity.

The human nervous system can use proprioceptive feedback to extract the spatial extent of hand-held tools. This suggests that the sensorimotor system constructs spatial representations of hand-held tools using similar computations as for the body (Miller et al. 2023). It is unknown whether the same is true of body augmentation technology. Furthermore, it is an open question whether similar spatial plasticity (e.g., stretching) occurs for representations of the technology itself as is it does for body representations.

To characterize the temporal dynamics of plasticity, we developed a novel exoskeletal device that directly interfaced with and extended the user's fingers. Participants completed a proprioceptive localization task over four stages: before and after wearing the exoskeleton, and before and after performing motor training tasks that required functional use of the device. This high-density proprioceptive mapping task measured how accurately participants could localize different parts of their finger and the exoskeleton in space, allowing us to quantify changes in body representation at different time points.

We observed three time-specific heterogenous effects of the exoskeletal fingers: (i) an initial compression of the user's biological finger representations upon wearing the device, (ii) a stretch of proprioceptive representations of both the user's biological and exoskeletal fingers that was driven by training to use the augmentative device—an effect that was absent after using a non-augmenting device, and (iii) a stretch of the user's finger representation that persisted after the device was removed and was likely driven by persistent exposure to wearing the exoskeleton. Together, these findings offer theoretically important insight into how the brain dynamically integrates artificial extensions into the body representation.

Results

Experiment 1A: Introduction to task protocols and exoskeleton familiarization

The goal of our study was to elucidate the temporal dynamics of somatosensory representational plasticity during body augmentation. To this end, we explored the effects of finger-length augmentation on somatosensory finger representations. Participants (n=18) performed a high-density proprioceptive finger mapping task in which they used their left hand to indicate on a touchscreen where they felt specific target locations on their right index finger, which remained hidden under the screen. The task involved repeated localization of seven equally spaced points along the length of the finger (and later, also the exoskeleton), enabling fine-grained assessment of perceived spatial structure. This task was performed at various time points relative to learning to use a finger-extending exoskeleton: before wearing the exoskeleton (stage 1); while wearing the exoskeleton, before using it (stage 2); while wearing the exoskeleton, after using it (stage 3); and after the exoskeleton was removed (stage 4). In all stages, we mapped the participant's representation of their biological index finger. In stages 2 and 3, we also concurrently mapped the participant's exoskeletal finger representation. Statistical comparisons involving pre/post-training conditions were evaluated against a Bonferroni-adjusted significance threshold of $\alpha = 0.01$ to account for multiple planned comparisons. While uncorrected p-values are reported for transparency, they should be interpreted in light of this corrected threshold.

The finger-extending exoskeleton (Fig. 1A) is a 3D-printed structure that elongates the fingers of the user's right hand by 10 cm, mounted on the biological fingertips. Their structure was designed to mimic the biological fingers. It consisted of a central rigid component intended to mimic the bone, surrounded by a padded silicon coating intended to mimic the elasticity of the finger pads and surrounding tissue. The latter ensured greater mechanical compliance during object manipulation, improving the user's success. Crucially, the finger-extending exoskeletal device was designed to explicitly allow us to simultaneously measure spatial perception of both the biological and exoskeletal fingers.

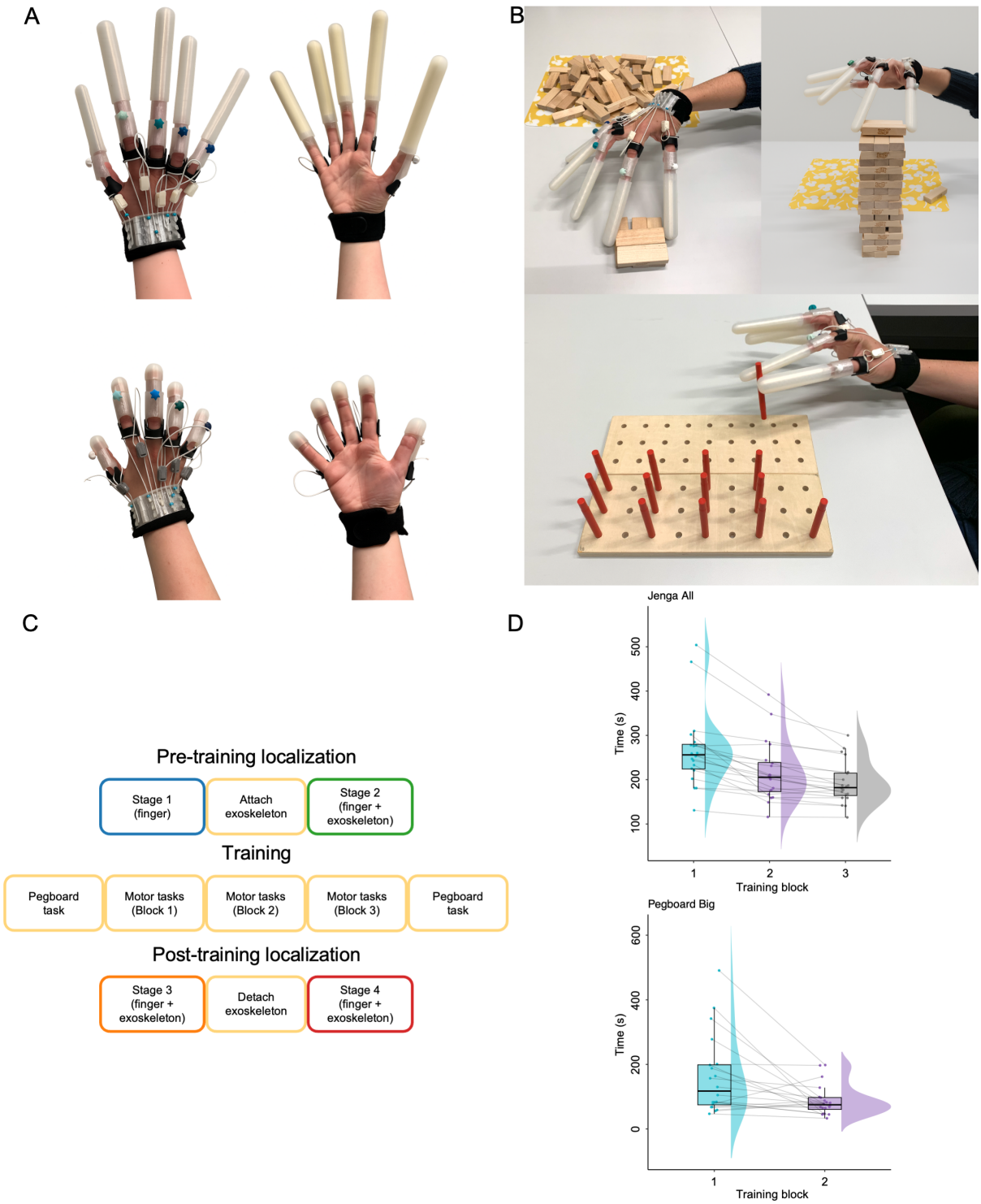

Figure 1. (A) The experimental, finger-extending exoskeleton with 10 cm finger extensions and the control exoskeleton without the extensions. (B) Example of the Jenga stacking training task. Participants wore the exoskeleton and were asked to stack a full Jenga tower; task performance was measured by the time taken to

complete the tower. (C) Outline of the experimental design. (D) Group data showing improvement in performance (reduction in completion time) across training blocks.

Wearing the exoskeleton contracts perceived biological finger length

Participants initially localized seven distinct proprioceptive targets on their index finger (stage 1). We then used linear regression to characterize their biological finger representation, modelling their localization judgments as a function of actual target location. This analysis revealed that participants' representation was geometrically accurate, with regression slopes near one (i.e., full accuracy; mean±sem: 1.06±0.09, 95% CI [0.86, 1.25]).

Participants were then fit with the exoskeletal fingers, providing them a short period of visual and proprioceptive feedback about their mechanics and geometry (around 1-2 minutes). They then performed the proprioceptive mapping task while wearing the exoskeletons (stage 2). Importantly, the task mapped both the biological and exoskeletal fingers simultaneously (bio+exo).

When wearing the exoskeletal fingers, the combined bio-exoskeleton map was geometrically accurate, spanning the true length of the combined surface (true length: 17.40 cm; estimated length: 18.97 cm; paired *t*-test of map versus true length: $t(17) = -1.25$, $p = 0.228$, $BF_{10} = 0.47$). How this space was partitioned up, however, was not proportional across surfaces. Specifically, the biological finger segment was significantly under-represented compared to the exoskeletal

segment (bio slope mean±sem: 0.85±0.06; exo slope mean±sem: 1.17±0.08; two-tailed paired t-test: $t(17) = -4.37$, $p < 0.001$, $BF_{10} = 79.66$). Comparison of the biological finger slopes with the map measured during stage 1 demonstrated that attaching the exoskeletal finger significantly contracted the represented length of the biological finger (19.65% reduction; $t(17) = 2.94$, $p = 0.009$, $BF_{10} = 5.66$).

Active use of the exoskeleton leads to proprioceptive "stretching" of biological and artificial finger segments

After stage 2, participants completed a 30-45 minute training period to familiarize themselves with the exoskeletal fingers. Training performance improved significantly over time, indicating a clear learning effect and increased proficiency with the device. Detailed analyses of individual tasks (such as the Pegboard, Sorting, and Jenga tasks) consistently showed significant improvements across sessions, confirming this effect. Full statistical results and task-specific analyses are provided in the Supplementary Information.

Following training, participants again completed the bio+exo finger mapping task (stage 3). This allowed us to examine how proprioception of both the biological finger and the artificial exoskeleton segment changed following this functional exoskeletal augmentation. The perceived length of the biological finger following training (slope mean±sem: 1.00±0.06, 95% CI [0.86, 1.14]) was significantly longer after training (17.89% increase; $t(17) = 3.67$, $p = 0.002$, $BF_{10} = 21.65$), demonstrating that finger augmentation stretched the user's representation.

Interestingly, we identified a similar effect of representational stretch for user's representation of the exoskeletal finger. That is, the perceived length of the exoskeletal finger (slope mean±sem: 1.35±0.08, 95% CI [1.19, 1.52]) was significantly longer after training (15.33% increase; $t(17) = 3.77$, $p = 0.002$, $BF_{10} = 26.01$). Together, these findings indicate that proprioceptive representations of both the biological and artificial segments were stretched following training with the finger-extending exoskeleton.

Removing the exoskeleton increases perceived length of the biological finger

After completing the bio+exo mapping task (stage 3), participants performed the localization task again with the exoskeleton removed (stage 4). This allowed us to examine whether the representational changes to the biological finger persisted after using the exoskeleton.

During stage 3, while wearing the exoskeleton, participants' internal mapping of the combined finger (biological + exoskeleton) was no longer geometrically accurate (true length: 17.40 cm; estimated length: 21.16 cm; paired t-test: $t(17) = -3.09$, $p = 0.007$, $BF_{10} = 7.38$). When analyzing the segments separately, the biological portion was no longer under-represented (slope: 1.00 ± 0.07 SEM; 95% CI [0.86, 1.14]; one-sample t-test vs. 1: $t(17) = 0.01$, $p = 0.99$), while the exoskeleton segment was clearly over-represented (slope: 1.35 ± 0.08 SEM; 95% CI [1.19, 1.52]; $t(17) = 4.36$, $p < 0.001$).

Critically, when comparing the biological segment's representation in stage 3 to its proprioceptive representation after exoskeleton removal in stage 4, we observed a significant stretch—an increase of 32.33% ($t(17) = -4.56$, $p < 0.001$, $BF_{10} = 113.70$).

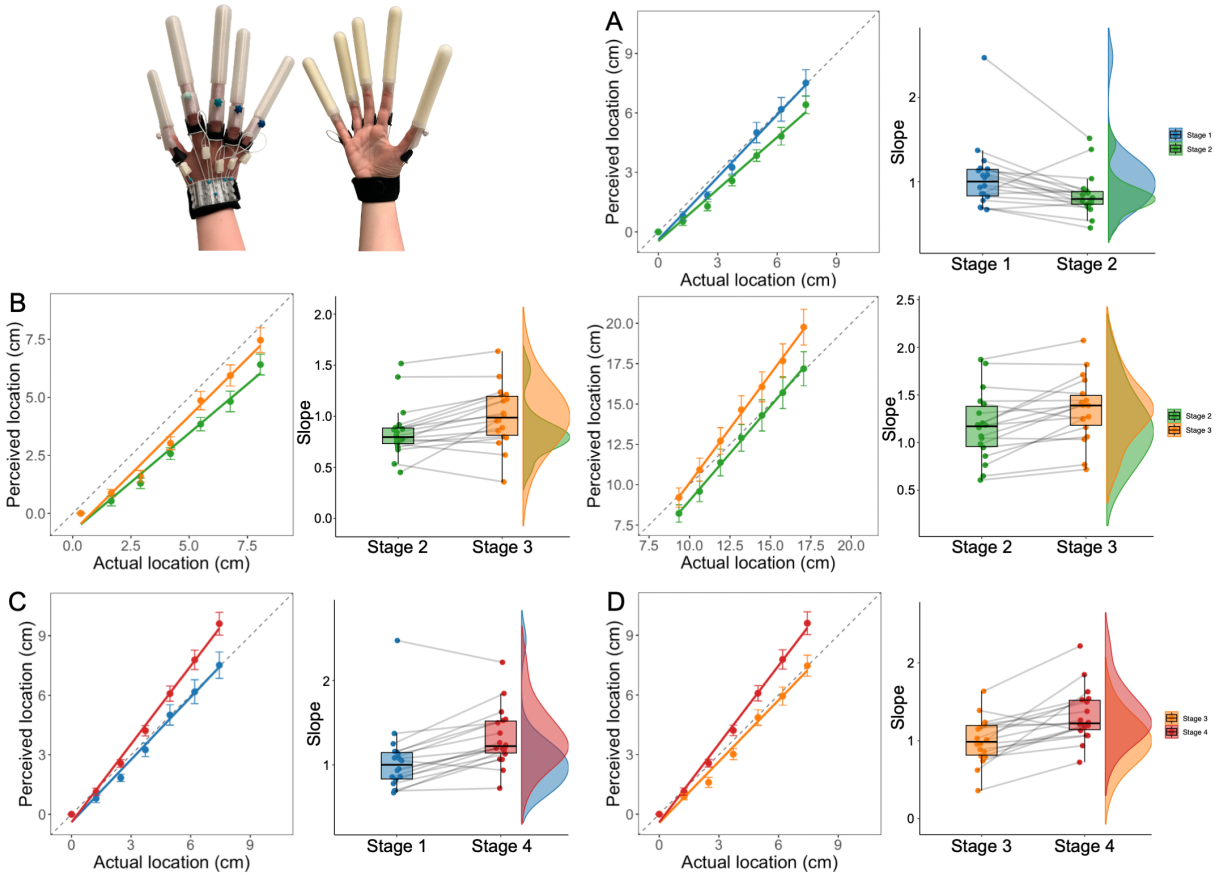

Figure 2. Proprioceptive judgments across stages of augmentation with finger-extending exoskeleton. (A) Comparison of proprioceptive maps from Stage 1 (baseline) and Stage 2 (initial exoskeleton fitting). (B) Left: Comparison of biological finger segment between Stage 2 and Stage 3 (after training). Right: Comparison of artificial finger segment between the same stages. (C) Comparison of biological finger representation from Stage 1 to Stage 4 (post-exoskeleton removal). (D)

Comparison of biological finger representation from Stage 3 (with exoskeleton) to Stage 4 (after removal). In all line plots, perceived location (y-axis) is plotted against actual target location (x-axis). Error bars represent standard error of the mean. The dashed line indicates the identity line (slope = 1). Raincloud plots show individual participant slopes in each stage. The following figure is formatted in the same fashion.

Experiment 1B: A non-augmenting exoskeleton does not stretch the user's proprioceptive representations

We next sought to determine whether the observed representational stretch was specific to training with an exoskeleton that spatially augmented the user's fingers. To this end, the same eighteen participants took part in the above experimental procedure with one change: the training was done using short exoskeletal fingers that did not meaningfully elongate the fingers (1.4 cm extension; Fig. 1A). Note that all proprioceptive mapping still included the finger-augmenting exoskeleton as in Experiment 1A.

As in Experiment 1A, the combined bio-exoskeleton map obtained during stage 2 (initial localization with the exoskeleton) was overall geometrically accurate (true length: 17.40 cm; estimated length: 19.31 cm; paired t-test of map versus true length: $t(17) = -1.42$, $p = 0.17$, $BF_{10} = 0.57$). The biological finger segment was significantly under-represented relative to the exoskeletal segment (bio slope mean±sem: 0.93±0.08; exo slope mean±sem: 1.20±0.09; paired t-test: t(17) = -3.87,

p = 0.001, BF_{10} = 31.57). Furthermore, comparing stage 1 (pre-exoskeleton) to stage 2, we observed that attaching the exoskeletal finger significantly contracted the represented length of the biological finger (19.37% reduction; $t(17) = 4.55$, $p < 0.001$, BF_{10} = 112.87).

We next determined the effect of using the control exoskeleton on the biological and exoskeletal finger representations. Participants were immediately fit with the finger-augmenting exoskeleton after their training with the control exoskeleton. In contrast to Experiment 1A, we did not observe changes in proprioceptive localization between stages 2 and 3 (post combined bio+exo map slope: mean±sem: 1.15±0.08, 95% CI [0.98, 1.31], paired t-test between stage 2 judgements and stage 3 judgements: $t(17) = -1.07$, $p = 0.300$, BF_{10} = 0.40). That is, we did not observe a significant change in perceived length of the biological (mean±sem: 0.93±0.07, 95% CI [0.77, 1.09]; $t(17) = -0.69$, $p = 0.50$, BF_{10} = 0.30) or exoskeletal finger representation (mean±sem: 1.27±0.09, 95% CI [1.08, 1.45]; $t(17) = -1.68$, $p = 0.11$, BF_{10} = 0.78). This pattern suggests that proprioceptive stretch of somatosensory representations is specific to the active use of the finger-extending exoskeleton, and not simply due to attachment or observation of such.

Proprioceptive aftereffects emerge following exoskeleton exposure

Lastly, we examined the effect of removing the exoskeletal fingers after training. In the final stage of the experiments (stage 4), participants mapped out their biological finger without wearing the exoskeleton. In both experiments, this stage

followed extensive wearing and engagement with the exoskeletal fingers during the mapping tasks (i.e., stages 2 and 3); however, only in Experiment 1A did participants use the finger-extending exoskeletal fingers.

We observed a modulation in the length of the participant's biological finger representation. Linear regressions revealed a significant increase in scaling factors from pre- to post-training in both the procedure involving the active use of finger-extending exoskeleton (i.e., Experiment 1A; pre slope mean±sem: 1.06±0.09, 95% CI [0.86, 1.25], post slope mean±sem: 1.32±0.08, 95% CI [1.16, 1.49]; paired t-test: $t(17) = -5.15$, $p < 0.001$, $BF_{10} = 345.48$) and in the procedure including training with the control device (Experiment 1B; pre slope mean±sem: 1.12±0.08, 95% CI [0.95, 1.29], post slope mean±sem: 1.35±0.11, 95% CI [1.12, 1.58]; paired t-test: $t(17)= -4.05$, $p < 0.001$, $BF_{10} = 44.19$). There was no significant difference between them in the degree of change ($t(17) = -0.36$, $p = 0.721$, $BF_{10} = 0.26$). These results suggest that this proprioceptive after effect was not due to the training stage, but likely to other factors such as wearing the exoskeleton and using proprioceptive feedback of its geometry to perform the mapping task.

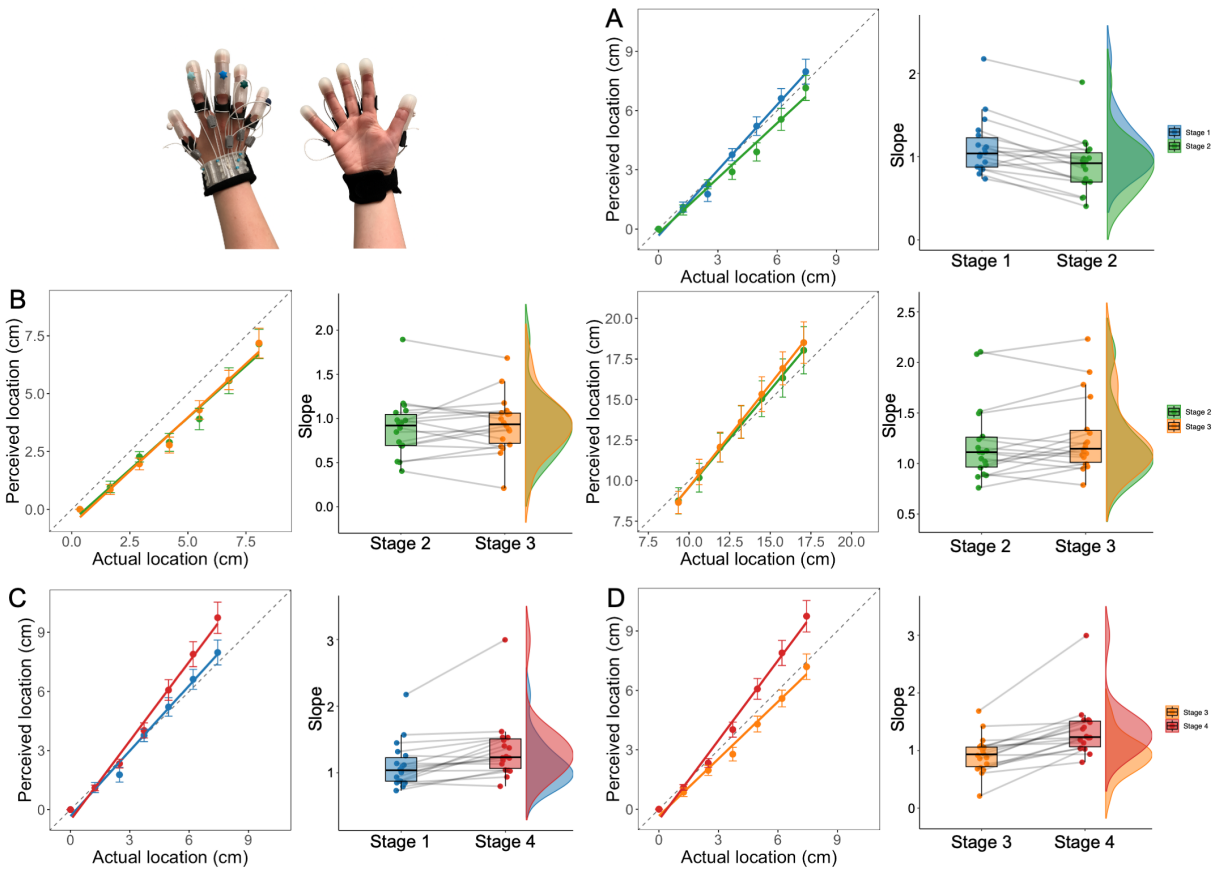

Figure 2. Proprioceptive judgments across stages of augmentation with control, non-extending device.

Discussion

This study provides a detailed characterization of how the human somatosensory system dynamically adapts to a wearable body-augmenting exoskeleton. Using a high-density proprioceptive mapping task, we show that spatial representations of both the biological body and an artificial extension can be flexibly reshaped across time. Specifically, we identified three distinct phases of somatosensory plasticity: an initial contraction of biological finger representation upon wearing the device, a functional "stretching" of both the biological and artificial finger maps

following training, and a lasting aftereffect that persisted even after the exoskeleton was removed. Importantly, the emergence of these changes following training demonstrates that humans can quickly form a somatosensory representation of the exoskeleton based on sensory feedback. While the initial contraction occurred with both the active and control devices, the functional stretching and its associated aftereffects were specific to augmentation with an actively used, finger-extending exoskeleton. Together, our findings reveal how the somatosensory system integrates novel artificial extensions.

We show that finger-extending exoskeletons are an effective means for investigating the dynamics of plasticity in body representation. Unlike hand-held tools, exoskeletal devices are directly interfaced with the body. Learning to use such a device introduces new demands on proprioceptive processing, requiring the integration of additional structure into the body's representational framework (Raisamo et al. 2019). Here, we observed that training with the finger-extending exoskeleton led to measurable changes in how both biological and artificial finger segments were represented. These learning-driven changes were absent when participants used a control exoskeleton that did not augment finger length, highlighting the specificity of functional engagement in driving plasticity (Umiltà et al. 2008; Biggio et al. 2020).

The initial act of wearing the exoskeleton, even before use, triggered a reallocation of representational space, leading to a reduction the represented length of the biological finger (i.e., an under-representation). This suggests that the

somatosensory system responds immediately to the presence of an artificial augmentation, even in the absence of task-specific learning. This observation aligns with theories of neural resource allocation, in which new sensory inputs initially compete with existing representations for limited perceptual or cortical resources (Dominijanni et al. 2021). The contraction of the biological finger's representation may reflect an adaptive mechanism, reallocating capacity toward processing novel sensorimotor structures.

Following training, we observed that both the biological and artificial finger representations underwent a significant stretch, an effect absent when participants trained with the non-extending control device. This parallel plasticity suggests that the brain may apply shared representational mechanisms to both body parts and tool-like extensions, reinforcing the idea that tools can be integrated into the body representation in a body-like manner. The absence of such effect in the control condition emphasizes that this plasticity is not simply a response to attachment, but a specific outcome of using augmentation to achieve new functional outcomes.

We identified a late-stage aftereffect, i.e., an increase in biological finger length perception following exoskeleton removal. Notably, this effect occurred both when participants had actively used the finger-extending exoskeleton and when they had only trained with a control device, suggesting it did not depend on motor training or functional use of the extension. Instead, we interpret this change as a delayed consequence of the repeated sensory-motor engagement involved

in the proprioceptive mapping task itself. Importantly, this engagement occurred while participants were still wearing the device, but its perceptual consequences became apparent only once the exoskeleton was removed and the mapping returned to the biological finger alone. One possible explanation for this delayed onset is that participants may have anchored their spatial judgments to the full (bio+exo) finger configuration during stages 2 and 3. Only when that anchor was removed in stage 4 did a recalibrated internal model of biological finger length become detectable in behavior. An alternative possibility is that the extended period of exoskeleton wear—regardless of use—led to low-level proprioceptive adaptation or sensory recalibration (de Vignemont 2011). This process could accumulate slowly and manifest only when the artificial structure was taken away, making the baseline biological representation feel relatively elongated. Another possibility is that the contrast between the artificially long exoskeletal configuration and the now shorter biological finger may have triggered a “rebound". Future studies might test this directly by interleaving mapping trials with and without the exoskeleton in shorter succession.

Our results further suggest that users build an internal model of the augmented finger, incorporating its geometry into their broader sensorimotor predictions. This internal model likely underlies the system’s ability to coordinate perception and action during interaction with the exoskeleton (Imamizu et al. 2000). The observed representational stretch after training supports the idea that the sensorimotor system actively updates its estimates of both body structure

during learning. Such internal models are thought to play a critical role in tool embodiment, allowing the brain to simulate and predict the outcomes of actions involving both the body and its extensions (Wolpert, Ghahramani, and Flanagan 2001).

In sum, this work demonstrates that the human sensorimotor system is capable of rapidly and flexibly integrating wearable exoskeletons into its spatial framework. Crucially, this integration is shaped by both the physical characteristics of the augmentation and the nature of the user's interaction with it. By showing that proprioceptive representations can quickly adapt to artificial extensions, we provide empirical support for the development of intuitive, body-integrated assistive technologies. Understanding the neural and perceptual mechanisms by which the brain incorporates such devices has direct implications for neurorehabilitation, prosthetics, and the design of human-machine interfaces that feel like natural extensions of the self.

Methods

Participants

A total of 20 healthy right-handed participants were recruited (mean age = 27.2 years, range = 18–54; 13 women, 7 men), all of whom completed two experimental sessions on separate days. Two participants were excluded due to the use of undesired strategies to perform the task, resulting in a final sample of 18. One used their visible left hand to mirror the position of their unseen right hand, resulting in

atypically high accuracy and low uncertainty. The other switched midway from proprioceptive localization to using a fixed visual reference point, producing a bimodal response distribution. All participants had normal or corrected-to-normal vision and no history of neurological or psychiatric conditions. Participants were asked not to have long nails on the day of the experiment, as this could interfere with the usage of the exoskeleton.

The research was approved by the Ethics Committee of the Faculty of Social Sciences, Radboud University. Every participant gave informed consent to participate in the experiment. Participants received a 30-euro voucher or course credits as compensation.

Participants were fitted with either the standard or a larger version of the exoskeleton, the latter designed specifically to accommodate larger hands. To further account for individual variability in thumb size, an additional medium-width thumb was available, intermediate in size between the standard and large versions. Eight participants using the standard exoskeleton and two using the large version were fitted with the medium thumb.

Experimental design

Experiments 1A and 1B used a within-subject control design to isolate the effects of training with the exoskeleton on body representation. The same participants completed both sub-experiments (1A and 1B) on separate days (5–30 days apart), with the order of experiments counterbalanced across participants. Each sub-

experiment consisted of four parts: a touchscreen localization task, motor training, and a repetition of the localization task. To further characterize the effects of the training protocol on sensorimotor control, we administered a behavioral test based on the Purdue Pegboard Test before and after the training. A final motor task and questionnaire were also included but are not discussed in this article for brevity.

Experimental setup

The participants were seated comfortably in a cushioned chair with their left arm resting on a padded armrest. They were positioned at a table facing the short end of a 93.2 x 52.6 cm LCD touchscreen (iiyama ProLite TF4237MSC-B3AG, Tokyo, Japan), securely fixed above the table. The right arm was placed under the screen on a board with grooves for each finger to ensure consistent placement, and participants were instructed not to look under the screen. The screen displayed three vertical stripes corresponding to the right index, middle, and ring fingers.

High-density proprioceptive mapping task

Stage 1: The task of participants was to localize different locations on their right index finger using proprioception. Throughout the task, the participants kept their right arm completely still and made localization judgments by touching the touchscreen with their left hand. After the judgment was made, they were asked to move their left hand back to the resting start position, which was 16 cm outside the response field, adjacent to the screen edge.

On a given trial, the procedure was as follows. At the beginning of the trial, an image of a finger was displayed in the lower left corner of the screen. A red dot was placed at the target location within the finger. Participants then pointed on the screen to the corresponding target location on the stripe above their actual index finger. Participants then returned their left hand to the start position. No accuracy feedback was provided. This procedure was repeated for seven equally spaced locations across 20 trials, totaling 140 trials. The order was randomized. This task took about 5 to 10 minutes depending on the participant's speed.

Stage 2: The proprioceptive mapping task was the same as in stage 1 with the exception that participants now also localized targets within the space of the finger-augmenting exoskeleton. There were seven distinct target locations within the biological and exoskeletal finger, for 14 distinct locations in total. There were again 20 trials per location, leading to 280 trials total. This task took around 10 to 15 minutes.

Stage 2 had the distinct procedure that it also required fitting the exoskeletal finger to the participant. After they finished the task in stage 1, they were asked to stay seated and remove their right arm from under the screen. The finger-extending exoskeleton was fitted to their right hand for both experimental and control sessions. After making sure the exoskeleton fit comfortably, the participants' right arm was placed under the screen again in the same position as before.

In Experiment 1A, the participants continued with the finger-extending exoskeleton. In Experiment 1B, after finishing both localization tasks, the finger-extending exoskeleton was removed, and the control exoskeleton was fitted in the same way as the finger-extending exoskeleton.

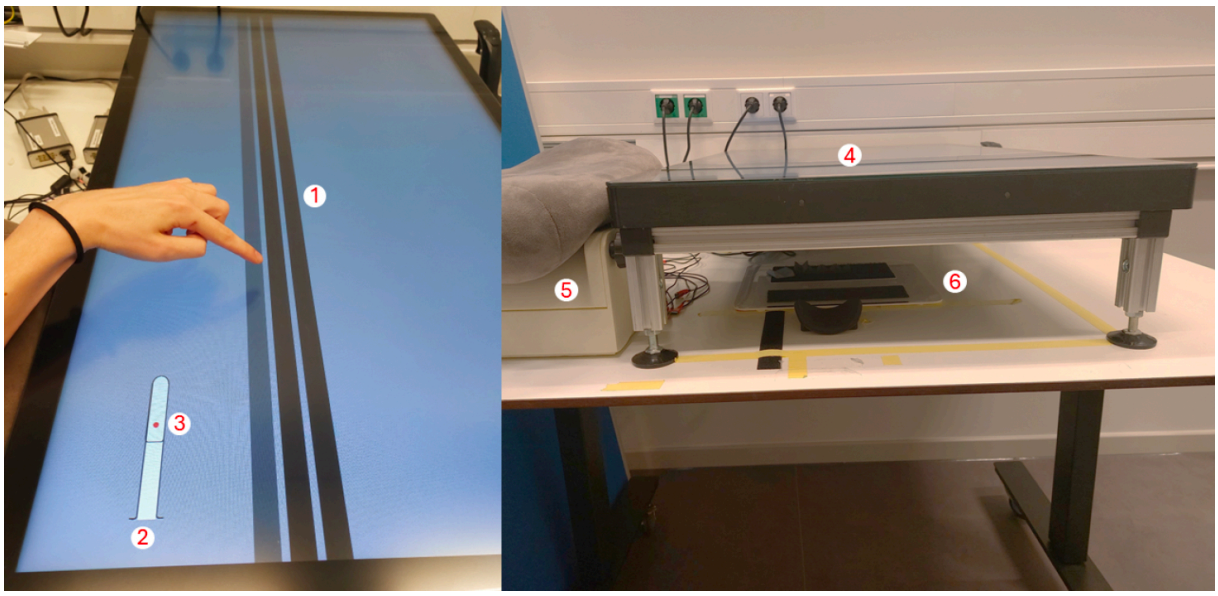

Figure 4. A top-down view of the finger+exoskeleton localization task (left) and a frontal view of the localization task setup (right). (1) The three stripes are aligned with the index, middle, and ring fingers placed under the touchscreen. The left stripe is colored in gray to indicate the finger of interest. (2) The image of a finger with the exoskeleton shown to the participant on which the requested locations are displayed. (3) One of the 14 requested locations displayed on the finger in red. (4) The elevated touchscreen under which the right hand is placed. (5) The elevated armrest on which the right elbow is placed. (6) The board with the finger grooves on which the right hand is placed together with a small armrest for the forearm.

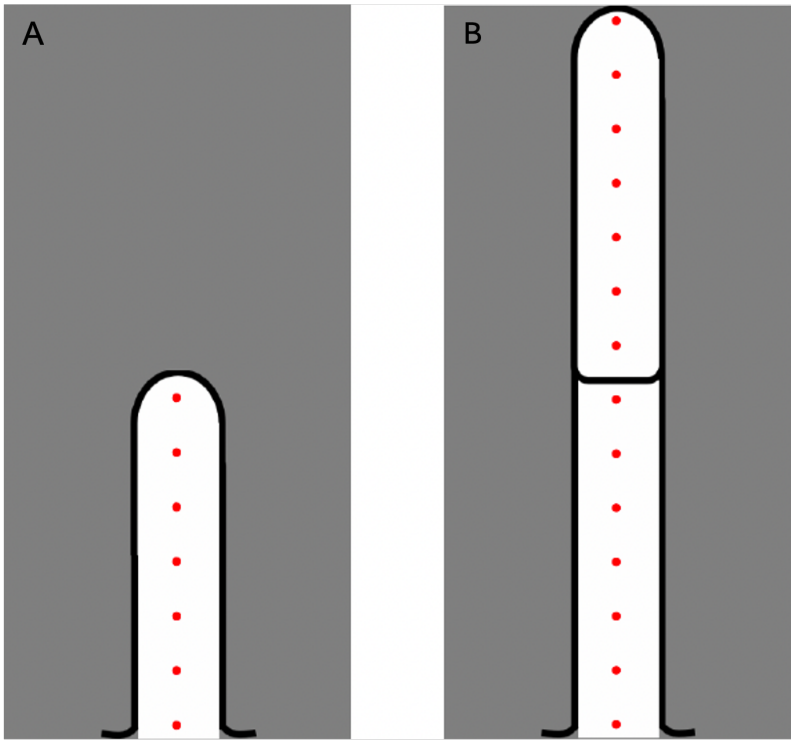

Figure 5. The distribution of 7 locations for the finger (a) and 14 locations for the finger+exoskeleton (b) localization tasks.

Stage 3: After completing the motor tasks (see "Training protocol" below), participants were guided back to the touchscreen to repeat the localization tasks. In Experiment 1B, the control exoskeleton was replaced with the finger-extending exoskeleton while the participant was blindfolded. The blindfold ensured that participants did not see their hand without the exoskeleton, preventing visual input from recalibrating their hand representation and potentially diminishing the effects of the training. Participants then performed the same proprioceptive mapping task as in stage 2.

Stage 4: For the finger-only localization task, the exoskeleton was removed while participants were blindfolded, and their hand was guided back under the screen before the blindfold was removed. Participants then performed the same proprioceptive mapping task as in stage 1.

Training protocol

During the training, participants were asked to complete a set of tasks to familiarize them with the use of the exoskeletal fingers and train their motor control. They were instructed that the tasks should be completed predominantly with their right, exoskeleton-wearing hand, with grasping and manipulation being performed solely with the right hand, and only supportive role of their left hand. This approach was chosen to make the training more ecologically relevant, as in daily life, both hands would typically be used to complete such tasks. Each task was repeated three times, forming three blocks of trials. The order of tasks in each block was the same for each participant, and it was randomized across participants.

The tasks included in the training were based on a previously introduced protocol (Kieliba et al. 2021): building a tower with wooden blocks, sorting plastic bricks according to their color, and sorting shapes by inserting them into a wooden box.

The tower building task was divided into two subtasks. In the first one, the participants were asked to build as many floors of the tower as possible (one floor consisting of three rectangular wooden blocks) within three minutes. Therefore,

the outcome measure was the number of floors built by the participant. In the second task, the participants were asked to build an entire tower, consisting of 18 floors. Here, the outcome measure was the time it took the participant to complete the task. In both tasks, the participants were only allowed to use their right, exoskeleton-wearing hand to complete them.

In the sorting colors task, the participants were asked to sort plastic bricks into separate plastic trays according to their color. The participants were only allowed to use their right, exoskeleton-wearing hand to complete it. The outcome measure was the time it took the participant to complete the task.

In the sorting shapes task, the participants were asked to insert wooden shapes into a corresponding hole in a wooden box. The participants were instructed that the tasks should be completed predominantly with their right, exoskeleton-wearing hand, with grasping and manipulation being performed solely with the right hand, and only supportive role of their left hand by means of turning the box in such a way that it was possible to place the block inside it. The outcome measure was the time it took the participant to complete the task.

Before and after the training, the participants completed a task based on the Purdue Pegboard task, in which they were asked to move plastic pegs from a wooden pegboard to the other. First, they started with larger pegs, and then they progressed to smaller pegs. The participants were instructed that the tasks should be completed predominantly with their right, exoskeleton-wearing hand, with grasping and manipulation being performed solely with the right hand, and only

supportive role of their left hand by means of keeping the wooden board in a stable position on the table. The outcome measure was the time it took the participant to complete the task.

Data analysis

Linear regression was used to examine the perception of finger and exoskeleton length. In the localization tasks, the perceived location of each target was calculated as the mean of participants' response distributions. The true position of the targets was determined from participants' finger measurements and the known exoskeleton length. By performing regressions of perceived versus true locations, we obtained an offset (β_0) and a slope (β_1). The offset was discarded, as it only reflected where participants perceived their finger to start, without providing information on length perception. The slope, however, indicates the scaling factor and represents participants' length perception.

For the finger-only localization task, one regression was performed per condition (pre- and post-training), resulting in four slopes per participant. For the finger+exoskeleton localization task, two regressions were performed per condition (pre- and post-training): one for the biological finger segment and one for the exoskeleton segment, yielding eight slopes per participant. These slopes quantified perceived spatial scaling along each segment and served as a measure of perceived length. The comparison of length perception involved analyzing the segments separately, leading to two comparisons of condition and pre/post-

training. Changes in slope across experimental stages (e.g., before and after training) were evaluated using paired t-tests. We conducted planned comparisons between stage 1 vs. 2 (finger), 2 vs. 3 (finger and exoskeleton), 1 vs. 4 (finger), 3 vs. 4 (finger) within each of Experiment 1A and 1B, resulting in five paired t-tests per experiment. To control for multiple comparisons, we applied a Bonferroni correction within each experiment, setting the adjusted significance threshold at $\alpha = 0.01$. Additionally, we compared measured representations against true physical lengths using paired t-tests, and tested for deviations from veridical perception (slope = 1) using one-sample t-tests. To assess whether the magnitude of representational stretch predicted increases in localization variability, we used correlational analyses between the predicted and observed uncertainty. All reported p-values are from two-tailed tests and are accompanied by 95% confidence intervals and Bayes Factors.

References

Berti, A., and F. Frassinetti. 2000. "When Far Becomes near: Remapping of Space by Tool Use." *Journal of Cognitive Neuroscience* 12 (3): 415–20.

Biggio, M., A. Bisio, L. Avanzino, P. Ruggeri, and M. Bove. 2020. "Familiarity with a Tool Influences Peripersonal Space and Primary Motor Cortex Excitability of Muscles Involved in Haptic Contact." *Cerebral Cortex Communications* 1 (1): tgaa065.

Canzoneri, Elisa, Silvia Ubaldi, Valentina Rastelli, Alessandra Finisguerra, Michela Bassolino, and Andrea Serino. 2013. "Tool-Use Reshapes the Boundaries of Body and Peripersonal Space Representations." *Experimental Brain Research* 228 (1): 25–42.

Cardinali, Lucilla, Francesca Frassinetti, Claudio Brozzoli, Christian Urquizar, Alice C. Roy, and Alessandro Farnè. 2009. "Tool-Use Induces Morphological Updating of the Body Schema." *Current Biology: CB* 19 (12): R478-9.

Dominijanni, Giulia, Solaiman Shokur, Gionata Salvietti, Sarah Buehler, Erica Palmerini, Simone Rossi, Frederique De Vignemont, et al. 2021. "The Neural Resource Allocation Problem When Enhancing Human Bodies with Extra Robotic Limbs." *Nature Machine Intelligence* 3 (10): 850–60.

Eden, Jonathan, Mario Bräcklein, Jaime Ibáñez, Deren Yusuf Barsakcioglu, Giovanni Di Pino, Dario Farina, Etienne Burdet, and Carsten Mehring. 2022. "Principles of Human Movement Augmentation and the Challenges in Making It a Reality." *Nature Communications* 13 (1): 1345.

Gallivan, Jason P., D. Adam McLean, Kenneth F. Valyear, and Jody C. Culham. 2013. "Decoding the Neural Mechanisms of Human Tool Use." *ELife* 2 (May): e00425.

Holmes, Nicholas P., and Charles Spence. 2004. "The Body Schema and the Multisensory Representation(s) of Peripersonal Space." *Cognitive Processing* 5 (2): 94–105.

Hussain, I., G. Salvietti, Giovanni Spagnoletti, and D. Prattichizzo. 2016. "The Soft-SixthFinger: A Wearable EMG Controlled Robotic Extra-Finger for Grasp Compensation in Chronic Stroke Patients." *IEEE Robotics and Automation Letters* 1 (February): 1000–1006.

Imamizu, H., S. Miyauchi, T. Tamada, Y. Sasaki, R. Takino, B. Pütz, T. Yoshioka, and M. Kawato. 2000. "Human Cerebellar Activity Reflecting an Acquired Internal Model of a New Tool." *Nature* 403 (6766): 192–95.

Iriki, A., M. Tanaka, and Y. Iwamura. 1996. "Coding of Modified Body Schema during Tool Use by Macaque Postcentral Neurones." *Neuroreport* 7 (14): 2325–30.

Kieliba, Paulina, Danielle Clode, Roni O. Maimon-Mor, and Tamar R. Makin. 2021. "Robotic Hand Augmentation Drives Changes in Neural Body Representation." *Science Robotics* 6 (54).

Krakauer, John W., Alkis M. Hadjiosif, Jing Xu, Aaron L. Wong, and Adrian M. Haith. 2019. "Motor Learning." *Comprehensive Physiology* 9 (2): 613–63.

Longo, Matthew R., and Andrea Serino. 2012. "Tool Use Induces Complex and Flexible Plasticity of Human Body Representations." *The Behavioral and Brain Sciences*. Cambridge University Press (CUP).

Maravita, Angelo, and Atsushi Iriki. 2004. "Tools for the Body (Schema)." *Trends in Cognitive Sciences* 8 (2): 79–86.

Martel, Marie, Lucilla Cardinali, Alice C. Roy, and Alessandro Farnè. 2016. "Tool-Use: An Open Window into Body Representation and Its Plasticity." *Cognitive Neuropsychology* 33 (1–2): 82–101.

Miller, Luke E., Cécile Fabio, Frédérique de Vignemont, Alice Roy, W. Pieter Medendorp, and Alessandro Farnè. 2023. "A Somatosensory Computation That Unifies Limbs and Tools." *ENeuro* 10 (11): ENEURO.0095-23.2023.

Miller, Luke E., Matthew R. Longo, and Ayse P. Saygin. 2014. "Tool Morphology Constrains the Effects of Tool Use on Body Representations." *Journal of Experimental Psychology. Human Perception and Performance* 40 (6): 2143–53.

Miller, Luke E., Matthew R. Longo, and Ayse P. Saygin. 2019. "Tool Use Modulates Somatosensory Cortical Processing in Humans." *Journal of Cognitive Neuroscience* 31 (12): 1782–95.

Mooney, Luke M., and Hugh M. Herr. 2016. "Biomechanical Walking Mechanisms Underlying the Metabolic Reduction Caused by an Autonomous Exoskeleton." *Journal of Neuroengineering and Rehabilitation* 13 (1): 4.

Penaloza, Christian I., and Shuichi Nishio. 2018. "BMI Control of a Third Arm for Multitasking." *Science Robotics* 3 (20): eaat1228.

Peviani, V. C., L. N. Pfeifer, G. Risso, M. Bassolino, and L. E. Miller. 2024. "Tool Use Fine-Tunes Arm and Tool Maps." *BioRxiv*. https://doi.org/10.1101/2024.06.06.597694.

Prattichizzo, Domenico, Maria Pozzi, Tommaso Lisini Baldi, Monica Malvezzi, Irfan Hussain, Simone Rossi, and Gionata Salvietti. 2021. "Human Augmentation by Wearable Supernumerary Robotic Limbs: Review and Perspectives." *Progress in Biomedical Engineering (Bristol, England)* 3 (4): 042005.

Raisamo, Roope, Ismo Rakkolainen, Päivi Majaranta, Katri Salminen, Jussi Rantala, and Ahmed Farooq. 2019. "Human Augmentation: Past, Present and Future." *International Journal of Human-Computer Studies* 131 (November): 131–43.

Sposito, Ambra, Nadia Bolognini, Giuseppe Vallar, and Angelo Maravita. 2012. "Extension of Perceived Arm Length Following Tool-Use: Clues to Plasticity of Body Metrics." *Neuropsychologia* 50 (9): 2187–94.

Umezawa, Kohei, Yuta Suzuki, Gowrishankar Ganesh, and Yoichi Miyawaki. 2022. "Bodily Ownership of an Independent Supernumerary Limb: An Exploratory Study." *Scientific Reports* 12 (1): 2339.

Umiltà, M. A., L. Escola, I. Intskirveli, F. Grammont, M. Rochat, F. Caruana, A. Jezzini, V. Gallese, and G. Rizzolatti. 2008. "When Pliers Become Fingers in the Monkey Motor System." *Proceedings of the National Academy of Sciences of the United States of America* 105 (6): 2209–13.

Vignemont, Frédérique de. 2011. "Embodiment, Ownership and Disownership." *Consciousness and Cognition* 20 (1): 82–93.

Wolpert, Daniel M., Zoubin Ghahramani, and J. Randall Flanagan. 2001. "Perspectives and Problems in Motor Learning." *Trends in Cognitive Sciences* 5 (11): 487–94.

Yang, Bo, Jian Huang, Xinxing Chen, Caihua Xiong, and Yasuhisa Hasegawa. 2021. "Supernumerary Robotic Limbs: A Review and Future Outlook." *IEEE Transactions on Medical Robotics and Bionics* 3 (3): 623–39.

Acknowledgements and funding

We would like to thank Sibrecht Bouwstra for the development of the exoskeletons.

D.R., V.C.P, and L.E.M are supported by an ERC 101076991 SOMATOGPS grant.

Declaration of interests

The authors declare no competing interests.