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To cite this article before publication: Elena Amoruso *et al* 2022 *J. Neural Eng.* in press <https://doi.org/10.1088/1741-2552/ac47d9>

Manuscript version: Accepted Manuscript

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Intrinsic somatosensory feedback supports motor control and learning to operate artificial body parts

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ABSTRACT

Objective

Considerable resources are being invested to enhance the control and usability of artificial limbs through the delivery of unnatural forms of somatosensory feedback. Here, we investigated whether intrinsic somatosensory information from the body part(s) remotely controlling an artificial limb can be leveraged by the motor system to support control and skill learning.

Approach

In a placebo-controlled design, we used local anaesthetic to attenuate somatosensory inputs to the big toes while participants learned to operate through pressure sensors a toe-controlled and hand-worn robotic extra finger. Motor learning outcomes were compared against a control group who received sham anaesthetic and quantified in three different task scenarios: while operating in isolation from, in synchronous coordination, and collaboration with, the biological fingers.

Main results

Both groups were able to learn to operate the robotic extra finger, presumably due to abundance of visual feedback and other relevant sensory cues. Importantly, the availability of displaced somatosensory cues from the distal bodily controllers facilitated the acquisition of isolated robotic finger movements, the retention and transfer of synchronous hand-robot coordination skills, and performance under cognitive load. Motor performance was not impaired by toes anaesthesia when tasks involved close collaboration with the biological fingers, indicating that the motor system can close the sensory feedback gap by dynamically integrating task-intrinsic somatosensory signals from multiple, and even distal, body- parts.

Significance

Together, our findings demonstrate that there are multiple natural avenues to provide intrinsic surrogate somatosensory information to support motor control of an artificial body part, beyond artificial stimulation.

INTRODUCTION

The last three decades have seen dramatic advances in the development of interfaces that can extend, substitute, or restore human motor function. Such interfaces allow users to operate assistive or augmentative artificial limbs by decoding intended movements at different levels along the motor system. Current technologies allow the extraction of motor commands from the user's muscle activations and movements (e.g., myoelectric prostheses) or directly from neuronal signals (Brain Machine Interfaces - BMI) (Bensmaia & Miller, 2014).

However, the functionality of these motor interfaces is restricted by the scarce sensory feedback available to the user, whose movements are typically guided mainly through visual monitoring (Bensmaia et al., 2020). In natural conditions, motor control heavily relies on (often subconscious) somatosensory signals for tracking limb state and interactions with objects. Tactile signals from the skin mechanoreceptors are especially important for object manipulation, as they convey information

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3 about contact timing, size, and location, as well as the optimal amounts of pressure to exert
4 (Johansson & Flanagan, 2009). Proprioceptive signals allow us to plan and guide the dynamics of limbs
5 movements by informing us on current joint position and motion (Proske & Gandevia, 2012). The
6 importance of somatosensory feedback for motor control is well evidenced by the debilitating motor
7 deficits that characterize a total loss of touch and proprioception, as is the case in some acute sensory
8 neuropathies (Gordon et al., 1995). Moreover, increasing evidence shows that the somatosensory
9 system plays a fundamental role not only in the online movement planning and correction processes,
10 but also in motor learning, i.e. the acquisition and consolidation of novel motor skills (Vidoni et al.,
11 2010; see Ostry & Gribble, 2016, for a review).
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14 In light of this, considerable resources are being invested to provide bidirectional sensorimotor control
15 of artificial limbs (Bensmaia et al., 2020). Most of the progress in this work has involved providing
16 information about contact between the device and objects (i.e., touch), either by providing tactile
17 stimulation on a displaced skin surface (Antfolk et al., 2013; see also Hussain et al., 2015 for
18 applications in augmentation), or by directly activating the neural pathways originally supporting the
19 sensory function, e.g. the peripheral nerves (Dhillon and Horch, 2005; Raspopovic et al., 2014; Tan et
20 al., 2014), the spinal cord (Chandrasekaran et al., 2020), or the somatosensory cortex (Romo et al.,
21 1998; Tabot et al., 2013; Flesher et al., 2016; Salas et al., 2018; Flesher et al., 2021; see Bensmaia et
22 al., 2020, for a review). Although the development of such tactile afferent interfaces is at a much
23 earlier stage than their efferent counterparts and critical challenges remain (e.g., the quality of the
24 evoked percepts), the benefits of artificial touch while using bionic limbs are being documented in
25 both lab and home settings (Ortiz-Catalan et al., 2020; Graczyk et al., 2018; Flesher et al., 2021).
26 Conversely, very little progress has been made in reproducing proprioception to provide kinaesthetic
27 feedback, which would allow the user to feel the device's current configuration and state position
28 without the cognitively taxing effort of constant visual monitoring. This omission is mainly due to
29 difficulties in developing reliable systems for artificially providing the multifaceted proprioceptive
30 signals, which in normal conditions are derived from a combination of multiple afferent channels (i.e.,
31 muscles spindle fibers, Golgi tendons, joint angle and cutaneous receptors), and to an incomplete
32 understanding of the representation of this modality at the cortical level (Tomlinson & Miller, 2016).
33 Owing to such technical and scientific considerations, attempts to restore (London et al., 2008;
34 Suminsky et al., 2010; Dadarlat et al., 2015) or substitute (Blank et al., 2008; Schiefer et al., 2018;
35 D'anna et al., 2019) proprioceptive feedback in artificial limbs haven't so far been able to show
36 consistent benefits for motor control.
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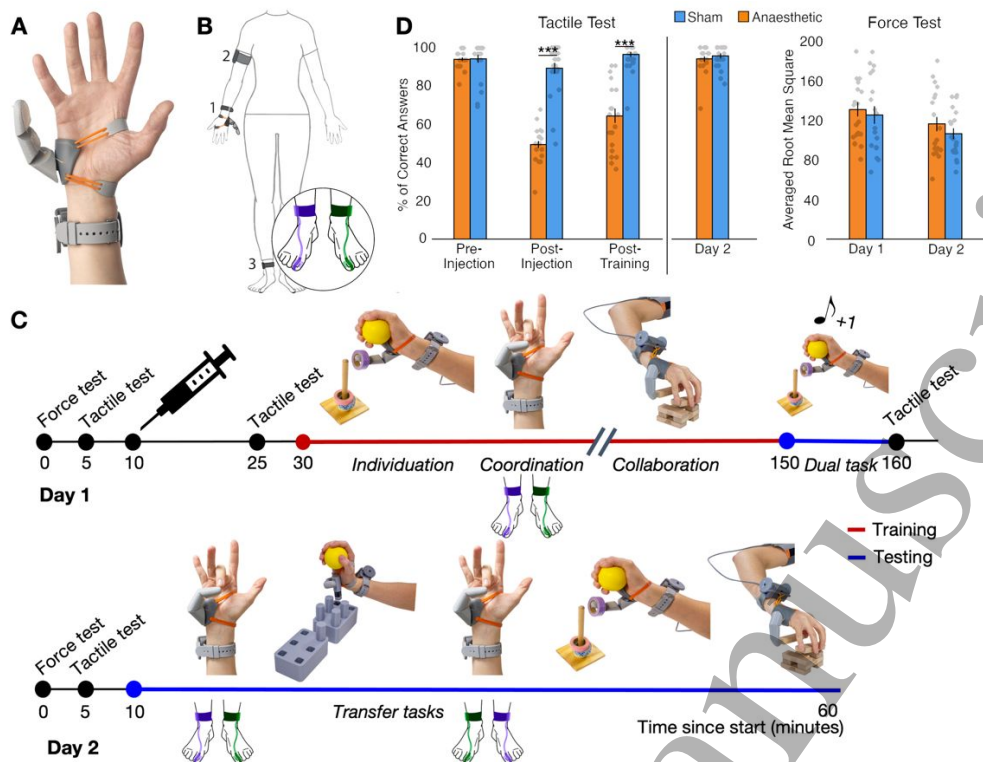
41 The challenges currently posed by reproducing artificial forms of somatosensory, particularly
42 proprioceptive, feedback prompt us to consider simplified approaches that could potentially take
43 advantage of the intrinsic bodily signals emerging from the device control. For example, in the case of
44 traditional myoelectric or body-powered prostheses, when motor commands are sent out by the
45 bodily controller (residual arm and shoulder, respectively), users receive a range of somatosensory
46 inputs. These are not only sensations on the patch of skin interfacing the prosthetic actuator that can
47 inform about contact with objects, but could also include, theoretically, indirect cues about the device
48 state and position. Surrogate position cues could be extracted from the body part which is
49 proportionally controlling the device, through muscle activations or active movements and pressure
50 exertion. Another example relates to patients with spinal cord injuries. While the body itself might
51 only mediate minimal sensory input, intrinsic skeletal vibrations arising from a restorative device (e.g.
52 exoskeleton) might still afford some level of sensory input that could be useful for guiding motor
53 control, even if the patient might not be aware of these implicit inputs. The benefits of such
54 physiologically built-in feedback systems, which may circumvent the need for complex substitutionary
55 or restorative interfaces, have long been highlighted in clinical and rehabilitative settings (Hirsch &
56 Klasson, 1974; Simpson, 1974), yet mostly unexplored. For example, it has been speculated that such
57 intrinsic, although limited, forms of sensory feedback may contribute to amputees' general preference
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3 for body-powered prostheses over more sophisticated ones (e.g. myoelectric), due to the increased
4 sensory information that is received on their body when operating the device (e.g. from extending the
5 cable/harness with the shoulder) (Antfolk et al., 2013). To our knowledge, however, whether and how
6 this naturally available sensory information is actually being harnessed by the motor system for
7 supporting the control of artificial limbs has not been thoroughly investigated or quantified.
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10 To this end, supernumerary (extra) limbs provide an innovative experimental model for isolating the
11 role of intrinsic forms of somatosensory feedback on artificial limbs control (Parietti & Asada, 2017;
12 Guggenheim & Asada, 2020). The Third Thumb (Dani Clode Design, Figure 1A-B) is a 2 degrees of
13 freedom (DOF) robotic sixth digit which is worn on the hand and wirelessly operated by the big toes
14 (controllers). To operate the device, the user needs to vary the pressure applied on a pair of force
15 sensors strapped underneath the big toes (right for flexion/extension and left for
16 abduction/adduction). Here, we investigated whether the somatosensory inputs received by the big
17 toes during the device proportional control can be leveraged to support motor control and learning
18 (Wolpert & Ghahramani, 1995).
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21 Over the course of two days, healthy individuals were first trained to use the Third Thumb and then
22 tested on a series of motor learning outcomes (Figure 1C). To modulate intrinsic somatosensory
23 contributions to the sense of the Thumb's state and position, we used anaesthetic injections to
24 attenuate pressure feedback to the big toes in a test group prior to training. This procedure prevents
25 most tactile signals from the big toes' skin and Golgi tendon receptors, while leaving motor function
26 (enabled by foot/ankle muscles) and proprioception (arising from the ankle's muscle spindles) mostly
27 unaffected. Training performance and learning outcomes were compared against a control group,
28 who received sham injections. We compared participants' ability to acquire, retain and transfer
29 (Kantak & Winstein, 2012) their motor skills to infer the potential benefits of the distal controllers'
30 pressure feedback on motor learning. We hypothesised that, by receiving somatosensory feedback
31 about the amount of pressure exerted with the toes, the Sham group would be able to develop a more
32 accurate internal model of the Third Thumb state and position (i.e., its proprioceptive status), allowing
33 more effective motor learning (Wolpert & Ghahramani, 1995). We also hypothesised that reduced
34 somatosensory information from the device controllers will incur more attention to monitor the
35 Thumb's performance through complementary sensory cues (e.g. visual). As a consequence, the
36 Anaesthetised group would show more deficits in device control when a further cognitive load is
37 added to motor tasks (Poldrack et al., 2005).
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METHODS



Participants

50 right-handed participants were recruited for the study. Exclusion criteria included allergies to local anaesthetics, needle phobia and history of neurological or psychiatric illness. 4 participants dropped out of the study due to a vasovagal response to the injections and 2 participants did not proceed beyond the injections due to an unsuccessful numbing effect (see: Anaesthetic Intervention). The final participant group included 44 participants with 22 participants in the 'Anaesthetised' group (11 female, mean age = 22.91, SD = 3.85, range = 18 to 35 years) and 22 participants in the 'Sham' group

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3 (10 female, mean age = 23.45, SD = 3.60, range = 18 to 33 years). Participants were pseudo-randomly
4 allocated to either the 'Anaesthetised' or 'Sham' group (see: Sampling Validation Tests). Due to
5 updates to the study design after initial data collection, only 40 participants (20 in each group)
6 completed the Dual Task and only 17 participants in the Sham group and 15 participants in the
7 Anaesthetised group completed the retention test for the Collaboration and Individuation tasks. Due
8 to technical issues during data acquisition, pressure sensors recordings from 2 participants in the
9 Anaesthetised group and 5 in the Sham group could not be analysed. All participants provided their
10 informed consent prior to participation. Ethical approval for the study was granted by the UCL Ethics
11 committee (Project ID: 12921/001).
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14 **Third Thumb**

15 The Third Thumb (Dani Clode Design, London, UK) is a robotic extra finger that attaches to the ulnar
16 side of the right hand (see Figure 1A) and is wirelessly operated through pressure sensors strapped
17 underneath the big toes. The Thumb has two degrees of freedom that allow a corresponding
18 proportional control: applying pressure to left big toe sensor causes an adduction/abduction
19 movement, whilst pressure on the right one causes a flexion/extension movement (Figure 1B). The
20 pressure applied by each big toe when the Thumb was switched on during the experiment was
21 recorded and used for off-line analyses (see section: Toes Pressure Analysis). Both pressure sensors
22 contained an SD-card that logged the position of the Thumb's servomotors (range 10-175 degrees for
23 flexion/extension, range 10-80 degrees for abduction/adduction). The position of the motor was
24 linearly proportional to the pressure applied by the participant. This relationship was fixed for all
25 participants in such a way that the same value of pressure was always associated with the same servo
26 position. When using the Third Thumb, participants placed their big toes on a small platform of a
27 footrest, to minimise somatosensory feedback from the other toes or neighbouring foot surface while
28 controlling the Thumb.
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32 **Anaesthetic intervention**

33 All participants received the same deafferentation protocol (Dempsey-Jones et al., 2019). The
34 intervention varied only in the substance injected, which depended on group assignment. Each
35 anaesthetic intervention required an injection of 2.5ml of 2% Lidocaine Hydrochloride and 2.5ml of
36 0.5% Bupivacaine Hydrochloride. Lidocaine Hydrochloride is a fast-acting anaesthetic ensuring an
37 almost immediate numbing effect, while Bupivacaine Hydrochloride is a long-lasting anaesthetic
38 ensuring the numbness lasted for the length of the Day 1 sessions. The Sham injection consisted of
39 3ml of 0.9% Sodium Chloride. The injections were administered on both big toes by medically trained
40 professionals. A 25-gauge sterile needle was inserted into the base of the dorsolateral aspect of the
41 big toe bilaterally and the solution was injected as the needle was withdrawn, achieving a sensory -
42 deafferentation of the entire toe. This procedure blocks sensory inputs from the big toe, whereas the
43 main muscles for operating the Thumb (abductor/adductor hallucis and extensor/flexor hallucis
44 brevis) are in the foot/ankle and remain largely unaffected. In the absence of an acceptable numbing
45 effect, indicated by a score of ~50% in the tactile acuity check (see section: Sampling Validation Tests),
46 the medical professional made a clinical decision on whether to administer further injections. To
47 create a sham effect, participants in both groups were informed that they were receiving local
48 anaesthetic, but that the effects were variable, and they therefore may not subjectively perceive a
49 complete anaesthetic effect.
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54 **Experimental Design**

55 The study was conducted over the course of 2 days, using the same design across both groups. An
56 overview of the experimental time course is shown in Figure 1C. Motor and tactile validation tests on
57 the big toes (black line in Figure 1C) were performed at several different timepoints (see Figure 1D for
58 outcomes). Prior to the pharmacological intervention, force and tactile tests were performed to
59 establish baseline performance, followed by the anaesthetic/sham injections. A post-injection tactile
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3 acuity test was performed by one experimenter. A second experimenter, in charge of administering
4 the subsequent tests, was blinded to the group assignment. A further tactile acuity test was conducted
5 at the end of Day 1. The same force and tactile acuity tests were administered at the beginning of Day
6 2.
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9 Third Thumb training (red line in Figure 1C) was conducted on Day 1 over 3 consecutive sessions, each
10 comprising of 3 different training tasks (Individuation, Coordination, Collaboration; see section:
11 Training Tasks), with task order randomised across participants. Tasks were performed over 10-minute
12 blocks.
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14 Testing tasks (blue line in Figure 1C) were performed at the end of Day 1 (Dual Task) and on Day 2
15 (retention and transfer tests). Task order was fixed on Day 2. Participants completed one 10-minute
16 block of the Coordination task, followed by one block of an adapted individuation task (Individuation
17 Transfer), and one block of an adapted coordination task (Coordination Transfer). Finally, single blocks
18 of the Collaboration and Individuation tasks were completed.
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21 **Sampling Validation Tests**

22 **Tactile acuity.** Orientation discrimination tests (adapted from Tong et al., 2013) were conducted at
23 four different timepoints (before the injections, immediately after the injections, at the end of Day 1,
24 at the beginning of Day 2; Figure 1D) to assess baseline acuity and the effectiveness of the anaesthetic
25 intervention. A Touch Test® two-point discriminator with a 13mm spacing was presented to the
26 glabrous surface of the distal pad of each big toe for ~2-3 seconds in one of two randomly assigned
27 orientations, with a total of 16 trials per test and inter-trial intervals of ~5 seconds. Participants
28 verbally reported the perceived orientation using a two-alternative forced choice ('down' or 'across').
29 The outcome measure was the percentage of correct answers.
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32 This data was used to confirm similar group performance during baseline and that the anaesthetic
33 intervention was successful at attenuating somatosensory inputs throughout Day 1. Due to violations
34 of the normality assumption, as well as the presence of several tied values and the lack of true
35 continuity in the data, group differences in tactile acuity were analysed using percentile bootstrap
36 independent-samples tests (see: Statistical Analyses). Before receiving the injections, both groups
37 showed equal tactile acuity on the big toes (mean accuracy Anaesthetised = 93% ± 4.6%, Sham = 94.0%
38 ± 9.6%; bootstrapped 95% CI [-4.12%, 4.47%], $p=.935$). On Day 2, the Sham and Anaesthetised groups
39 performed similarly and close to ceiling (mean accuracy Anaesthetised = 94% ± 6.6%, Sham = 95.6% ±
40 5.7%; bootstrapped 95% CI [-5.40%, 1.82%]; $p=.370$), suggesting that the numbing effects had
41 effectively washed out by the following day.
42
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44 Next, we confirmed that the injections of local anaesthetic affected tactile acuity relative to the sham
45 injections. Following the injections, tactile perception in the Anaesthetised group dropped to chance
46 level (mean accuracy = 49.3% ± 8.8%), whereas performance of the Sham group was relatively high
47 (mean accuracy = 89.2% ± 13.3%), resulting in a significant group difference immediately after the
48 injections (bootstrapped 95% CI [-46.05%, -33.21%], $p<.001$). A similar effect was also recorded at the
49 end of Day 1 (mean accuracy Anaesthetised = 64.3% ± 17%, Sham = 96.3% ± 5.9.6%; bootstrapped
50 95% CI [-39.43%, -24.44%], $p<.001$).
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53 **Force.** A force test was administered at the very beginning of each day and repeated on each big toe
54 in order to assess baseline motor abilities and determine the pseudo-random group allocation of the
55 participants. Participants pressed down on a force sensor, taped to their big toe, to control the vertical
56 direction of a horizontally-moving dot displayed on the laptop screen. Their aim was to maintain the
57 appropriate force to hit a series of bars, whose height was determined using 20%, 50% and 80% of the
58 maximum force the participant could apply. The force test consisted of four trials. Each trial contained
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6 bars displayed simultaneously on the screen (each bar 20%, 50% or 80% of the participant's maximum applied force). The bars of each trial were arranged in a way that either formed an up/down staircase (20% - 50% - 80% - 80% - 50% - 20%) or in a random order. Participants completed two identical up/down trials and two non-identical randomised trials. The outcome measure was the root mean square error from the ideal force required to maintain the moving dot at the top of each bar, averaged across all four trials. This data was used to confirm that baseline motor abilities were matched across groups and determine group allocation. The first 20 participants were randomly allocated to the Sham or Anaesthetised groups. The group means of the outcome measure were then calculated and participants thereafter assigned to groups based on their performance on the force test, to ensure that baseline motor abilities remained matched. Independent samples t-tests indicated that both Anaesthetised and Sham groups performed similarly in the force test at baseline on Day 1 ($t(38)=0.36$, $p=.720$) and on Day 2 ($t(38)=0.22$, $p=.824$).

Training Tasks

Training tasks were selected to probe the range of motor skills characterizing unimpaired Third Thumb motor control: using the Thumb in isolation from the hand for dexterous activities, coordinating hand and Thumb movements in a synchronous fashion, continuously collaborating with the hand for objects manipulation (Kieliba et al., 2021; Figure 1C). Retention of the trained tasks was additionally measured on Day 2.

Individuation. In the individuation task participants had to work on the fine motor control of the Third Thumb, while not relying on any support from the hand. Using only the Third Thumb, participants were required to pick up 6 tape rolls one-by-one and stack them on to a pole, while holding a foam ball to occupy their biological fingers (Figure 1C). Each block lasted for either 10 minutes or 10 trials, whichever came first. A trial lasted for however long it took the participant to stack all 6 rolls. If a given trial was still ongoing when 10 minutes had passed, the participant was allowed to complete it for up to an additional 5 minutes. The dependent variable was the time taken to stack all 6 tape rolls averaged across each block.

Coordination. To monitor the ability to coordinate the Thumb in synchrony with the hand, we used a finger opposition task (Meraz et al., 2018; Kieliba et al., 2021; Figure 1C). Participants were seated in front of a computer screen that displayed task stimuli. They were instructed to move the Thumb to touch the tip of a randomly specified finger of the augmented hand. A MATLAB script was used to randomly select a target finger (thumb, index, middle, ring or little) and to display the finger name on the computer screen. The experimenter manually advanced the program to the next stimulus when the participant successfully touched the tip of the target finger with the Third Thumb (hit), or when a wrong finger had been touched (miss). Participants were instructed to attempt to make as many successful hits as possible within a 1-minute trial, and completed a total of 10 trials per block. The outcome measure was the average number of hits completed in each block.

Collaboration. To measure continuous collaboration of the Third Thumb with the other fingers, participants were asked to build a 2x2 wooden bar tower with the augmented hand (Figure 1C). To do this they had to pick up 2 bars at a time from the table, using the Third Thumb in collaboration with a finger to hold or support one of the bars and two fingers to hold the other. Each block consisted of 10, 1-minute trials, with the dependent variable being the number of 2-bar floors built in 1 minute averaged across each block.

Testing tasks

The testing tasks were variations of the training tasks, designed to examine the automaticity and flexibility of motor learning under different task requirements.

Dual task. In order to evaluate if pressure feedback from the Third Thumb controllers is associated with a reduced need for cognitive control over performance (i.e. with increased automaticity), participants were asked to complete a dual (motor and numerical) task at the end of Day 1. The task was adapted from previous studies, showing that numerical cognition impacts motor performance

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3 while controlling a virtual prosthetic arm (Witteveen et al., 2012) or a brain-computer interface
4 (Guthrie et al., 2019), but does not impact Third Thumb control (Kieliba et al., 2021). The task involved
5 completing an extra 10-minute block of the Individuation task, with a simultaneous counting task.
6 Participants were instructed to complete the Individuation task as described above, but they now had
7 to also complete a simultaneous counting out loud task, as their primary task. At the beginning of each
8 trial a random number would be presented, then a series of high (550 Hz) and low (250 Hz) pitch tones
9 would be sounded at random intervals (between 2 and 6 seconds) in a randomised order. Participants
10 were instructed to add 1 to the current number after hearing a high tone, and subtract 1 from the
11 current number after hearing a low tone. After each mathematical operation, participants were
12 instructed to verbally respond with the resulting number. The outcome measure was the time taken
13 to complete the secondary Individuation task, under the interference effects of the primary numerical
14 task.

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17 **Coordination Transfer task.** This task was aimed at probing transfer of learning by modulating task
18 demands from training. The transfer version of the Coordination task was conducted using the same
19 procedures as described above, but with the force sensors controlling the Third Thumb swapped onto
20 the opposite feet. This resulted in having to adapt to a new mapping between the controlling
21 movements of the toes and the Third Thumb responses, i.e. pressing with the left toe for a
22 flexion/extension movement and with the right toe for adduction/abduction.

23
24 **Individuation Transfer task.** This task aimed to get participants to transfer the fine motor techniques
25 developed in the Individuation task to a distinct setting. The task was inspired by grooved pegboard
26 tasks widely used to assess motor functioning and dexterity in clinical neuropsychology (Rabin et al.,
27 2005). A brick of 6 3-D printed pegs was placed to the participants' left and a brick of 6 holes for the
28 pegs to fit in was placed to their right. Participants were instructed to pick up each peg using only the
29 Third Thumb and plant it in a designated hole, while holding a foam ball to occupy their biological
30 fingers. They were instructed to move the pegs in a set order, starting from the right back peg, ending
31 on the left front peg. The block was completed when all 6 pegs had been placed, or when 15 minutes
32 had passed, whichever came first. Participants completed one block of this task. The outcome
33 measure was the time taken to complete the block.

34 35 36 **Toes motor control analysis**

37 As a follow-up analysis, we investigated potential differences in how the two groups used the big toe
38 pressure sensors to control the Third Thumb at the very first stages of motor learning. We focused on
39 Block 1 of the Collaboration task, where no group differences on the main outcome measure were
40 observed. The data corresponding to the first block of the Collaboration task was identified using the
41 timestamps and manual logs and was then imported into MATLAB. The average servomotor position
42 (linearly dependent on the force applied) for both the flexion/extension and the abduction/adduction
43 sensors for the duration of the Collaboration task was extracted for each participant. This was then
44 normalised by dividing the average value by the maximum servomotor angle (respectively, 175 and
45 80 degrees). The total time spent making a flexion/extension or abduction/adduction movement was
46 then calculated by first identifying the timestamps at which participants applied force, moving the
47 servomotor out of its baseline position of 10 degrees. This was then used to find the proportion of
48 task time corresponding to each of the movements. Using the same approach, we also calculated the
49 time spent making bilateral movements (moving both servomotors at the same time), as a proportion
50 of the total movement time.

51 52 53 **Statistical analyses**

54 To identify violations of the normality assumption Shapiro-Wilk's values were inspected. Within- and
55 between-participants comparisons in task performance across acquisition, retention and transfer of
56 coordination and collaboration skills were assessed using mixed analysis of variance (ANOVA).
57 Significant interactions were followed up with confirmatory comparisons using independent and
58 paired samples t-tests, where appropriate. For repeated-measurement factors with more than two
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factor levels, if the assumption of sphericity was violated, Huynh–Feldt corrected p-values are reported. Due to violations of normality, data from the individuation tasks, the tactile acuity tests and the toes pressure sensors were analysed using independent-samples percentile bootstrap tests, which do not require any assumption on the underlying distribution of the data. For each variable of interest, we calculated the difference in group means on each iteration (10000) and estimated a 95% confidence interval and p-value of the difference in group means from the resulting distribution. Multivariate Mixed ANOVA was used to compare group differences in performance across the different tasks and blocks. All task scores from the first three blocks of training on Day 1 and the retention test on Day 2 were first normalised by subtracting the lowest score on the task during all four sessions by the range of task scores across the sessions, resulting in scores ranging from 0 to 1 across all tasks. The normalised scores for the Individuation tasks were subtracted from one so that a higher score reflected a better performance, as in the Coordination and Collaboration tasks. On all datasets, data points were removed separately for each task and/or block if they exceeded the outlier threshold of 2 standard deviations above or below the group mean. Less than 2% of data points across all tasks were removed for this reason. All parametric tests were performed on SPSS 25 (IBM, Chicago, Illinois), percentile bootstrap tests on RStudio 1.3 (RStudio PBC, Boston, Massachusetts).

RESULTS

Faster acquisition of robot individuation skills

We first considered the role of pressure feedback while controlling the Third Thumb individually, i.e. independently from the rest of the hand. Here, without any complementary information from the biological fingers about interaction with objects, task success is dependent on the development of dexterous motor control with the Third Thumb alone. We found that under these conditions, the anaesthetic intervention impacted the early stages of motor learning. Due to violations of the assumption of normality, we used bootstrapping approaches. To obtain a measure of the improvement on the task for both groups through Day 1 training, we subtracted the score (time taken to stack all the rolls) of Block 3 from Block 1, akin to the interaction term of a mixed ANOVA (Figure 2A). A bootstrapped independent-samples test performed on the obtained difference score was significant (bootstrapped 95% CI [28.297, 144.501], $p=.003$). Additional bootstrapped tests revealed a significant group difference in performance at Block 1 [Mean Anaesthetised (N=20) = 262s, Mean Sham (N=21) = 175s; bootstrapped 95% CI [13.216, 158.814], $p=.018$], but only marginally at Block 3 [Mean Anaesthetised (N=22) = 78s, Mean Sham (N=21) = 72s; bootstrapped 95% CI [-21.455, 29.160], $p=.064$]. Therefore, the Anaesthetised group showed initial deficits on performance when first approaching this dexterous task, but eventually appeared to reach a similar skill level to the Sham group by the end of the training day (see further results in the next section).

We next examined whether a similar level of retention of learning was obtained across both groups. The Bootstrap test on the subtracted scores of Day 2 from Block 3 of Day 1 revealed no significant group differences (bootstrapped 95% CI [-21.370, 144.501], $p=.919$). An additional Bootstrap test performed on the retention test scores confirmed that both groups retained their acquired skills similarly [Mean Anaesthetised (N=15) = 53s, Mean Sham (N=16) = 46s; bootstrapped 95% CI [-11.283, 24.983], $p=.419$]. We also tested for the transfer of the individuation skills, and found no significant group differences [Mean Anaesthetised (N=20) = 241s, Mean Sham (N=21) = 196s; bootstrapped 95% CI [-41.971, 135.916], $p=.324$], suggesting that the Anaesthetised group was able to transfer the individuation skills learned on Day 1 to similar tasks' settings as effectively as the Sham group. Together, these findings suggest that, once learned, the individuation skills were retained and transferred similarly by the two groups.

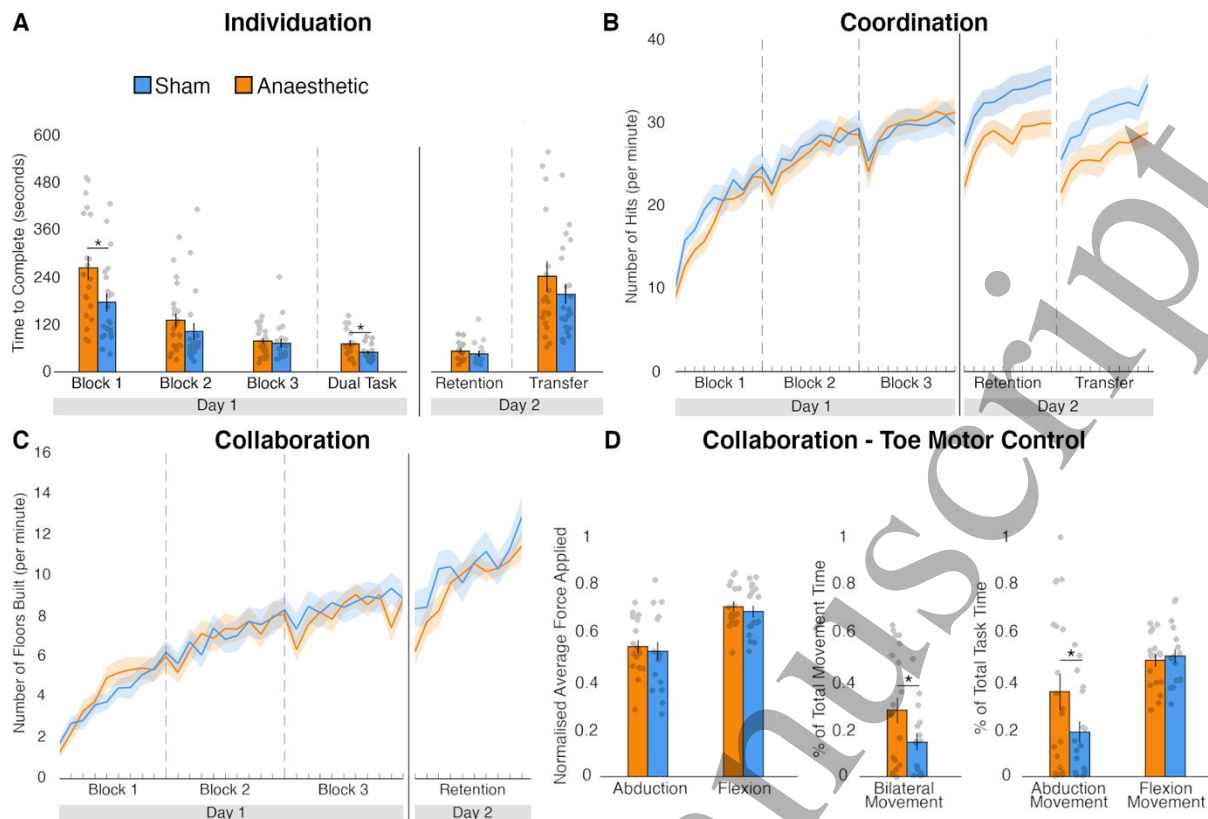


Figure 2. Task outcomes. **A)** In the Individuation task, the Anaesthetised group had significant deficits at the beginning of training and when a further cognitive load was added (Dual Task), but groups performed similarly in the retention and transfer tests of Day 2. **B)** In the Coordination task, despite similar Day 1 training performance, the Anaesthetised group showed significant deficits in the Day 2 retention and transfer tests. **C)** Both groups showed similar performance throughout the Collaboration task. **D)** Toe motor control analysis for Block 1 of the Collaboration task: no group differences in the amount of force applied; the Anaesthetised group used significantly more bilateral movements than the Sham group; the Anaesthetised group used significantly more adduction/abduction movements throughout the task, whereas there was no difference for flexion/extension movements. The bars depict group means; error bars represent standard error of the mean. Individual dots correspond to individual participants' scores. Asterisks denote significant effects at $* p < 0.05$.

Lower cognitive demands during robot control

We also examined differences in skill learning by increasing cognitive task demands, using a simultaneous counting task (Figure 2A). Whilst there was no difference in the proportion of incorrect answers given by each group on the counting task (bootstrapped 95% CI [-0.16688, 0.23674], $p = .783$), we found that the increased cognitive load uncovered a deficit in motor performance induced by the anaesthetic intervention. A direct comparison of performance on the Dual Task was significant [Mean Anaesthetised ($N = 19$) = 71s, Mean Sham ($N = 19$) = 41s; bootstrapped 95% CI [5.579, 39.263], $p = .008$], indicating an increased interference effect of the primary task. In other words, with attenuated sensory feedback, motor performance may reach less automaticity and require higher-order resources. It is important to note that no group differences were observed when comparing the difference scores between the Dual Task and Block 3 (bootstrapped 95% CI [-7.473, 32.211], $p = .277$), indicating that this observed deterioration of performance in the Anaesthetised group might have already been present, though latent, regardless of the cognitive load task.

More effective retention and transfer of hand-robot coordination skills

A unique challenge for artificial limbs control is the need to coordinate the movements of the robotic body part synchronously with our biological body. Overall, the anaesthetic intervention did not significantly affect the acquisition of hand-Thumb coordination skills throughout the training day (Figure 2B). To assess the acquisition of coordination skills across groups, we first ran a mixed ANOVA

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3 with Training Time (all training blocks of Day 1: Blocks 1, 2 and 3) and Group (Anaesthetised and Sham)
4 as predictors of performance. Here, we found a statistically significant main effect of the Training
5 Time, $F(2,82)=186.242$, $p<.001$, confirming improvements in performance over the training day, as
6 expected. However, we did not observe a significant main effect of Group ($F(1,41)=.231$, $p=.634$), or
7 interaction ($F(2,82)=.934$, $p=.380$), suggesting that, despite a qualitative (non-significant)
8 disadvantage observable in the Anaesthetise group at Block 1 (Figure 2B), the two groups showed
9 overall a similar performance during the first stages of motor learning, independently of the
10 anaesthetic intervention.
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13 We did find, however, that the anaesthetic intervention impacted the retention of the acquired
14 coordination skills. For this purpose, we ran a mixed ANOVA with Day (the final training block of Day
15 1 and the testing block on Day 2) and Group (Anaesthetised and Sham) as the independent variables.
16 The ANOVA revealed a significant interaction ($F(1,42)=15.429$, $p<.001$), and no significant main effects
17 of Day ($F(1,42)=2.269$, $p=.139$), or Group ($F(1,42)=1.210$, $p=.278$). Confirmatory paired samples t-tests
18 indicated that the Sham group improved from Day 1 to Day 2 ($t(21)=4.090$, $p=.001$), whereas the
19 Anaesthetised group did not ($t(21)=1.620$, $p=.120$). This resulted in a significant group difference on
20 Day 2 ($t(42)=2.285$, $p=.027$), which indicates that the Sham group retained the hand-robot
21 coordination skills more effectively than the Anaesthetised group over the ~24 hours interval.
22 Furthermore, the anaesthetic intervention impaired the transfer of coordination skills, resulting in a
23 worse performance in the Anaesthetised group on the Transfer Coordination task relative to the Sham
24 group ($t(41)=-2.10$, $p=.042$). Collectively, these findings indicate that, despite similar acquisition,
25 pressure feedback from the toes may afford a stronger and more flexible learning to coordinate
26 movements between the Third Thumb and the fingers of the hand. However, given that retention and
27 transfer on Day 2 were assessed without anaesthetics, it is possible that these findings may be
28 influenced by the changed context relative to training. Note, though, that, as seen below, similar
29 retention and transfer were observed in the Individuation and Collaboration task even while the
30 context in Day 2 (no anaesthetics) was varied relative to training, making this interpretation less likely.
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34 **No benefits to acquisition and learning of hand-robot collaboration skills**

35 Finally, to complete the picture of hand-robot motor interactions, we examined the impact of the
36 anaesthetic intervention on the ability to use the Third Thumb in close collaboration with the
37 biological fingers to grip, lift and transport objects, while maintaining constant pressure. This task
38 contains elements of coordination, but in addition also allows for increased reliance on sensorimotor
39 control of the biological fingers, that maintain constant pressure on the object to afford the joint grip
40 with the Thumb. Under such cooperating conditions, we did not find any significant impact of the
41 anaesthetic intervention on task performance and learning (Figure 2C).
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44 To assess the acquisition of collaboration skills, we first ran a mixed ANOVA with Training Time (all
45 training blocks of Day 1: Blocks 1, 2 and 3) and Group (Anaesthetised and Sham groups) as predictors
46 of performance. Here, we found a significant main effect of Training Time ($F(2,78)=114.749$, $p<.001$),
47 but no significant main effect for Group ($F(1,39)=.044$, $p=.834$), or an interaction ($F(2,78)=.116$,
48 $p=.884$), suggesting the groups did not improve differently across the training day. To test for group
49 differences in retention, we ran a mixed ANOVA with Day (the final training block of Day 1 and the
50 testing block on Day 2) and Group (Anaesthetised and Sham) as the independent variables. We found
51 a significant main effect of Day ($F(1,29) = 6.717$, $p=.015$), but no significant effects for Group
52 ($F(1,29)=.003$, $p=.960$) or for the interaction ($F(1,29)=.320$, $p=.576$). Overall, these results suggest that
53 the skills needed to perform the Collaboration task were acquired and retained similarly by the two
54 groups.
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Different somatosensory demands across tasks and learning stages

The results presented so far suggest that pressure feedback was not equally important across the three tasks and stages of motor learning. This was statistically assessed by running a Multivariate Mixed ANOVA on normalised performance scores, which revealed a significant three-way interaction between the factors Task (Individuation, Coordination, Collaboration), Time (the three training blocks of Day 1 and the testing block of Day 2) and Group (Anaesthetised and Sham): $F(6,16) = 2.806$, $p = .046$, Pillai's Trace = .513. This result further confirms that various sources of somatosensory feedback might differentially support the device's proprioceptive status, resulting in different learning profiles.

Different toe motor control despite similar task performance during hand-robot Collaboration

It is possible that while overall performance appears similar between the two groups, the underlying strategies for achieving the same skill level are divergent. We therefore investigated differences in how the two groups used the pressure sensors to control the Third Thumb at the very first stages of motor learning. We focused on performance during Block 1 of the Collaboration task, where, as seen in Figure 2C, no performance differences were apparent. We found that the motor action patterns shown by the Anaesthetised group to achieve the same scores as the Sham group were less lateralised.

Due to violations of the assumptions of normality, group differences were analysed with bootstrap tests. Both groups did not differ in the amount of average force applied during flexion/extension and abduction/adduction movements (Flexion: Mean Sham (N=17) = 0.691 ± 0.10 , Mean Anaesthetised = 0.710 ± 0.09 , bootstrapped 95% CI: [-0.045, 0.081], $p = .555$; Abduction: Mean Sham (N=17) = 0.525 ± 0.16 , Mean Anaesthetised (N=17) = 0.544 ± 0.12 , bootstrapped 95% CI: [-0.074, 0.111], $p = .685$). However, the Anaesthetised group spent a significantly longer proportion of time making bilateral movements (movements including the simultaneous flexion and abduction of the Third Thumb) – Mean Sham (N=16) = $14.5\% \pm 14.3\%$, Mean Anaesthetised (N=20) = $27.8\% \pm 24\%$, bootstrapped 95% CI: [0.011, 0.258], $p=.033$. Further analyses show that this can be attributed to the Anaesthetised group spending a larger proportion of the task time making adduction movements (Mean (N=20) = $35.5\% \pm 33.9\%$), when compared to the Sham group (Mean (N=17) = $18.7\% \pm 18.6\%$, bootstrapped 95% CI: [0.006, 0.342], $p=.043$). The proportion of the task time spent making flexion movements did not differ between the Anaesthetised (Mean (N=19) = $48.6\% \pm 11.1\%$; and Sham (Mean (N=17) = $50.4\% \pm 12.6\%$) groups - bootstrapped 95% CI: [-0.096, 0.055], $p=.636$). These findings indicate that even when a task can be equally performed with attenuated sensory feedback from the Thumb controllers, this is achieved through arguably more complex and energy-consuming control patterns.

DISCUSSION

We tested if pressure feedback from the body part proportionally controlling an extra robotic finger (Third Thumb) can support control and learning, presumably as a proxy for inferring the device state and position (device proprioceptive status). Using local anaesthesia in a placebo-controlled design, we show that attenuating intrinsic somatosensory inputs from the robotic finger's controllers results in impoverished motor control and learning. Given that in our model the bodily controller (i.e. the big toes) is a body part physically distant from the effector (i.e. the extra thumb worn on the hand), our findings also demonstrate that a common infrastructure between distal body parts can be successfully shaped for closing the sensorimotor loop. Deficits in motor control were found both during skill acquisition (for the Individuation task), and at the delayed retention and transfer tests (for the Coordination task). Importantly, our findings also demonstrate that despite these deficits, participants were able to learn to control the Thumb even when these intrinsic pressure signals were not available. Most strikingly, performance was not impaired by anaesthesia when tasks involved close collaboration with the biological fingers, indicating that the brain could 'close the gap' of the missing state and position cues by complementary means, including through continuous task-relevant somatosensory feedback from other body parts involved in the task. Nevertheless, the impairments in multitasking and the somewhat less economical control patterns underlying the performance of the Anaesthetised

group highlight the unique advantages that the displaced and intrinsic pressure feedback from the device controllers can provide for more automatic and efficient control. Together, our findings indicate that there are multiple available avenues – involving somatosensory signals from both distal controllers and collaborating body-parts – that could be harnessed to increase the bidirectionality of artificial limbs control.

Initial deficits in skill acquisition were seen in the Individuation task, which required dexterous control of the Third Thumb in isolation from the biological fingers, highlighting the benefits of supplementary sensory feedback when first approaching a task where extra precision is needed (Blank et al., 2008). Such early deficits, however, seemed to resolve by the end of the training sessions. Moreover, this effect was not observed in the Collaboration task and did not reach statistical significance for the Coordination task, which both required using the Thumb in conjunction with the other fingers, likely allowing for an increased reliance on sensorimotor control of the biological hand for task success (Zhu et al., 2019). These findings suggest that, during the initial stages of motor learning, other sensory cues can probably sufficiently compensate for the lack of pressure feedback from the controllers of the device. Such complementary cues include visual and auditory inputs from the Thumb, but also, perhaps most notably, somatosensory inputs from the collaborating hand.

Nevertheless, such increased reliance on complementary feedback modalities appears to result in more pronounced cognitive demands for motor control, at least during the early stages of learning. This is well evidenced by the impairments shown by the Anaesthetised group on a Dual Task, requiring participants to multi-task by simultaneously carrying out the Individuation task and numerical operations (Witteveen et al., 2012; Guthrie et al., 2019). When fewer executive resources were available due to the need to prioritise the numerical task, the poorer motor performance in the Anaesthetised group appeared to resurface. This finding suggests that automaticity in device control can more readily be achieved when users can rely on task-intrinsic pressure feedback. A related finding on the distinct control patterns characterising the performance of the two groups was revealed in the Collaboration task. Here, we uncovered a potentially redundant, and thus less efficient, use of the pressure sensors to operate the Third Thumb by the Anaesthetised users in the early stages of learning. Specifically, to achieve equal task performance as the Sham group, Anaesthetised participants used more complex and energy-consuming bilateral movements. These findings show that even when the advantages afforded by the controllers' pressure feedback are not reflected in task performance, they provide opportunities for optimisation that are not as readily available to users relying only on other complementary sensory cues.

Further clues for the potential advantages of surrogate state and position cues for motor learning were revealed during retention and transfer. Performance on the retention tests, which involved the repetition of the practiced tasks on the following day, reflects the relative strength of the motor memory representation over time, whereas performance on the transfer tests reflects its flexibility. Here, the impact of practice with reduced pressure feedback was evident for the Coordination task, where the Sham group continued to show improvements whereas the Anaesthetised group did not, even if toes sensitivity was by then restored for both groups. It is possible that the pressure feedback from the Thumb controllers during task training may have enabled a more accurate internal model of the motor plan, thereby resulting in a more effective error-based learning (Wolpert & Ghahramani, 1995), and, in turn, a more robust and flexible motor memory representation. Consistent with that, we have previously shown that, once trained, participants can complete the coordination task even with no visual feedback (Kieliba et al., 2021), suggesting that users can develop a sense of position of the Thumb relative to the fingers relying mostly on somatosensory information. No group differences in retention or transfer were observed in the Collaboration task and, perhaps most surprisingly, in the Individuation task, where users could not rely on complementary information from the biological fingers. Given the importance of somatosensory feedback for motor learning, as highlighted in

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3 previous literature (Ostry & Gribble, 2016), and the noticeable initial deficit in skill acquisition we
4 documented here (Figure 2A), this finding calls for a more detailed understanding of the circumstances
5 (e.g., task demands or learning stages) where users can in fact benefit from added somatosensory
6 information about the proprioceptive state of the device. It is important to consider that both groups
7 were receiving normal pressure feedback during the retention and transfer tests of Day 2. Therefore,
8 it is possible that although participants learnt effectively to perform the Coordination task without
9 pressure feedback, the incoming somatosensory inputs on Day 2 may have required them to re-learn
10 how to integrate this information into their internal model. It was impossible for us to empirically test
11 the theory that under anaesthesia retention would have been more complete, due to unsafe toxicity
12 build-up that could result from consecutive-day anaesthetic blocks. Nevertheless, considering that
13 performance during Day 2 did not vary across groups for the other tasks, as further demonstrated in
14 the significant interaction across tasks and days, we believe this interpretation is less likely.
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18 Our findings bear important implications for the development of assistive and augmentative motor
19 interfaces. For example, it is well recognised that some of the remaining functional inadequacy of
20 BMIs derives from the lack of somatosensory feedback, including both touch and proprioception. Akin
21 to deafferented patients and the anaesthetised participants in our study, BMI-controlled movements
22 require considerable attention and do not typically achieve near-natural levels of dexterity and fluidity
23 (Tomlinson & Miller, 2016). Here, we show that leveraging task-intrinsic somatosensory inputs can
24 substantially enhance motor performance and learning with wearable robotic limbs, even when such
25 inputs arise from displaced locations. By reading motor commands from the cortex and bypassing
26 completely the body, current BMIs may be missing important opportunities for harnessing such task-
27 intrinsic somatosensory signals for optimising control. Moreover, engaging the body in some form of
28 device control may not only optimise motor control through increasing task-relevant sensory
29 feedback, but also serve rehabilitation by providing physical activity, with the potential to prevent
30 muscle atrophy and maintain any residual mobility (Pierella et al., 2015). In light of the advantages
31 documented here, we suggest that BMI systems would probably benefit from exploring a hybrid
32 approach, where neuronal recordings are coupled with some form of bodily engagement. BMI systems
33 that restore movement through neuromuscular stimulation of the patient's own limb (Bouton et al.,
34 2016, Ajiboye et al., 2017; Bockbrader et al., 2019; Ganzer et al., 2020) may already be benefiting from
35 such opportunities.
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39 **ACKNOWLEDGEMENTS**

40 This work was supported by an ERC Starting Grant (715022 EmbodiedTech) and by Sir Halley Stewart
41 Charitable Trust (580), awarded to TRM, who was further funded by a Wellcome Trust Senior
42 Research Fellowship (215575/Z/19/Z). A CC BY or equivalent licence is applied to the AAM arising
43 from this submission, in accordance with the grants' open access conditions.
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