Transcutaneous Spinal Cord Stimulation Provides Sensations to the Missing Hand of Individuals With Upper Limb Amputation

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***Abstract*— Restoring sensory function post amputation remains a major challenge. Peripheral nerve stimulation and targeted reinnervation may partially restore somatotopic feedback, but their need for surgery hinders widespread adoption. Here, we investigate the feasibility of transcutaneous spinal cord stimulation (tSCS) as a non-invasive approach for sensory restoration in upper-limb amputees. In a study involving seventeen able-bodied participants and five individuals with upper-limb amputation, we show that tSCS can evoke a range of sensations, including touch, tapping, vibration, and movement, perceived as originating from the missing limb. Notably, these perceptions were primarily isolated to the missing limb and absent in the residual limb in 98% of trials. Participants with amputations found tSCS tolerable, with some reporting increased comfort during stimulation. tSCS evoked sensations in the fingertips of 93% of able-bodied participants, though these were mainly paraesthetic. We further characterised how stimulation parameters, including electrode placement, carrier frequency, and burst frequency, modulated the quality and type of perceived sensations. Additionally, we show that tSCS maintained force proprioception necessary for effective prosthesis control. These findings support the potential of tSCS as a non-invasive sensory feedback approach for upper-limb prosthesis users.**

***Index Terms*— Transcutaneous spinal cord stimulation. electrophysiology, spinal cord, sensorimotor control, limb loss, prosthetics.**

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I. Introduction

RESTORING natural sensory perception in prosthesis users remains a significant challenge. Despite advancements in prosthetic technology, the lack of sensory feedback in these devices is a critical gap in their design and application. Here, we explore the potential of transcutaneous spinal cord stimulation (tSCS) as a non-invasive method to restore sensory feedback in individuals with upper-limb amputation, particularly focusing on eliciting natural sensations in missing limbs.

The human upper limb, densely innervated by approximately 350,000 nerve fibres, predominantly comprises sensory nerves (90%), and a minority (10%) of axons dedicated to motor function [1]. This unbalanced distribution underscores the importance of sensory input in regulating and refining motor actions, particularly in the dexterous movements of the hand. The absence of sensory feedback resulting from amputation, especially when proximal, severely impairs functional outcomes and the overall quality of life of prosthesis users. These sensory deficits often lead to the abandonment of prosthetic devices due to their limited functionality and the unnatural, cognitively demanding control required in their operation [2], [3], [4].

The landscape of sensory feedback in prosthetic technology shows a stark preference for body-powered systems over sophisticated myoelectric prosthetics, often due to the natural feedback inherent in mechanical systems [5]. However, the desire for enhanced prosthetic functionality has driven research

towards developing sensory feedback methods that directly stimulate neural pathways, either through the central nervous system (CNS) [6], [7], [8], [9] or the peripheral nervous system (PNS) [10], [11], [12], [13]. While each method has its merits, PNS-interfaces are not suitable for individuals with proximal amputations or impaired peripheral nerves, and the invasiveness of existing CNS-interfaces and their inconsistent outcomes have limited their widespread adoption [14], [15], [16], [17].

Spinal cord stimulation (SCS), particularly tSCS, offers a compelling alternative by targeting sensory pathways non-invasively through the spinal cord. This method is based on the activation of natural sensory pathways, potentially allowing for the modulation or restoration of a range of sensations, including touch, pressure, and proprioception, without the risks associated with direct neural implantation [18]. SCS can evoke sensations originating from distal areas of the body [19], [20], possibly by modulating the same afferents targeted by PNS-based sensory feedback methods for prosthetics [21]. Recently, the first attempt at applying SCS for sensory feedback has proven that epidural SCS (eSCS) can modulate cervical spinal circuitry in individuals with different amputation levels and evoke sensations that are perceived to be emerging from their missing upper limb [22]. In all individuals with amputation including those with shoulder disarticulation, the evoked sensations reached as distally as the fingers. These recent results have proven that SCS is a promising sensory feedback interface for people with upper-limb amputation, regardless of their amputation level.

While eSCS has shown efficacy in restoring sensory function, it comes with inherent risks and drawbacks that are challenging to mitigate. These include requiring multiple surgeries, possible use of anaesthesia or deep sedation [23], and the risk of complications derived from the surgery [24], [25], [26], [27]. The invasive nature of eSCS and its associated risks significantly hinder its widespread adoption.

tSCS offers a non-invasive alternative to eSCS, targeting the same neural structures with reduced spatial selectivity [28]. tSCS, combined with training, has proven to facilitate upper- [29] and lower-limb [29], [30], [31] motor function after a spinal cord injury. While tSCS has demonstrated to improve upper-limb sensory function in patients with spinal cord injury [29] and patients with severe paralysis [32], its potential to restore or induce sensations in individuals with upper-limb amputations remains unexplored. tSCS could provide a more accessible, adjustable, and potentially safer method than eSCS, filling a critical gap in current neuromodulation techniques.

In this study, we characterised and mapped the sensations elicited by tSCS in able-bodied (AB) and participants with upper-limb amputations (ULA) when stimuli were delivered at sub-motor thresholds (that is, without the stimuli directly evoking muscle responses). The study was designed to demonstrate the possibility of evoking sensations in the distal upper limb in AB participants and eliciting somatosensations in the missing limb of ULA participants. We also examined how stimulation parameters—such as location, carrier frequency and burst frequency—affected the location and quality of evoked percepts. Finally, we show that sub-motor-threshold tSCS does not impede electromyography (EMG) -based control in ULA participants.

TABLE I
CLINICAL DATA OF PARTICIPANTS WITH AMPUTATIONS

ID	***ULA1***	***ULA2***	***ULA3***	***ULA4***	***ULA5***
Sex	Female	Male	Male	Male	Male
Age	60-65	36-40	50-55	20-25	40-45
Dominant Side	Right	Right	Right	Right	Left
Amputation Side	Left	Left	Left	Right	Left
Amputation Level	Transradial	Transcarpal	Transradial	Transcarpal	Transradial
Amputation Cause	Aorta Dysfunction	Elective Decollement Injury	Trauma	Trauma	Trauma
Years Since Amputation	1	10	8	8	24
Relevant Conditions	No	No	No	Amputation of left digits	No
Perception of The Missing Limb	Yes	No	Yes	Yes	Yes

II. MATERIALS AND METHODS

A. Participants

Seventeen able-bodied participants (mean age 26.2 $\pm$ 4.1 years, 6 females) with no limb differences (AB), and five participants (mean age 44.4 $\pm$ 16.1 years, 1 female) with upper-limb amputations (Table I) were recruited for this study. Thirteen of the able-bodied participants participated in both tSCS and the brachial plexus stimulation (BPS) experiments, two participants took part in tSCS experiments only and the remaining two only participated in the BPS experiment. Informed consent was obtained from all participants before the experiment. Experiments were conducted in accordance with the Declaration of Helsinki and procedures were approved by the Imperial College Research Ethics Committee (reference number 20IC5945).

B. Study Design

The study comprised three scientific aims: (1) to evaluate whether tSCS can elicit sensations in the distal upper limb; (2) to map the effect of three core stimulation parameters (stimulation location, carrier and burst frequencies) to the quality, location and success of evoked sensations; (3) to evaluate the effect of stimulation on the force-modulation aspect of motor control for upper-limb prosthesis users. The study was conducted in two experimental phases. Phase one included two sub-studies with AB participants: the first sub-study included two experimental sessions run on separate days and addressed scientific aims (1) and (2), the second sub-study acted as a control condition to compare tSCS to a semi proximal approach, brachial plexus stimulation. The aim of this control condition was to test if the effects induced by tSCS were comparable to those obtained by stimulating peripheral nerves. Upon analysing the results of the AB participants (phase 1), the experimental protocol for the subsequent phase, phase two, was selected and conducted with ULA participants,

with the addition of an experiment addressing scientific aim (3), thereby reducing the total experimental duration to one day. The experimental protocol was repeated (repeated measures) with ULA participant 3 (ULA3) one week after the initial experiment to assess the consistency of tSCS. For a graphical representation of the study design and experimental protocols, see Fig. S1 in the supplementary information.

C. tSCS

To evaluate the effect of stimulation parameters on the quality and location of the evoked sensation in the targeted limb, we employed kilohertz burst-modulated alternating current [33]. This high-frequency modulated current waveform was selected because it allows for high amplitude stimulation without discomfort and potentially deeper stimulation penetration by reducing tissue impedance [29], [34], [35]. As a result, tSCS can penetrate to the dorsal root [28]. The effects of burst frequency (50 Hz, 100 Hz, 150 Hz), carrier frequency (6 kHz, 10 kHz), and stimulation location (C5-C7 and C6-T1) and their twelve combinations were tested. Those frequencies were selected to span the range used in conventional SCS and kilohertz-modulated neurostimulation protocols [28], [36]. Stimulation was delivered in 1 ms bursts of biphasic rectangular pulses with widths of 40 μs at 10 kHz and 70 μs at 6 kHz with a constant current stimulator (DS8R, Digitimer). Participants sat comfortably on a chair with both of their arms resting at 120 degrees on a table in front of them during the experiment. The stimulation electrode serving as cathode (5×5 cm^2, Axelgaard Pals Platinum) was placed over the skin over either spinous process C5-C7 or C6-T1, and two stimulation electrodes (4×9 cm^2, Axelgaard Pals Platinum) serving as anodes were placed over the clavicle of the dominant side for AB participants and the side of the amputation for ULA participants. During the study, the choice of stimulation parameters was randomised, and participants were blinded to those choices. The cathode was placed either over C5-C7 or C6-T1. The cathode placement was changed mid-session while the anode remained fixed. The order in which the cathode was placed was also randomised. The stimulation amplitude was set as 90% of discomfort or motor threshold (depending on which was detected first) per protocol and per participant. Discomfort threshold was defined as the stimulation amplitude that the participant felt would be just tolerable if they had to endure for 5 minutes. Given the lack of standardised motor threshold criteria for tSCS [37], motor threshold was determined using methods appropriate to each participant group, whilst limiting the experimental duration.

For AB participants, motor threshold was estimated as the stimulation current that produced a visible contraction in any of the upper-limb muscles, consistent with established methods in tSCS literature [38]. For ULA participants, motor threshold was defined as the lowest stimulation current required to elicit a motor-evoked potential of at least 50 μV in a minimum of 50% of ten consecutive pulses, adapted from transcranial magnetic stimulation criteria [39]. Resting motor threshold in ULA participants was assessed using bipolar EMG recordings from the biceps brachii, triceps brachii, wrist flexors and wrist extensors. Motor threshold was not measured when discomfort threshold was reached first.

To verify that the stimulation amplitude remained sub-motor threshold during active contractions (and throughout the EMG modulation experiment), stimulus-triggered averaging (STA) of EMG activity from the wrist flexors was calculated for the ULA participants during sustained wrist flexion tasks at 5%, 15%, and 25% of maximum voluntary contraction (MVC) while receiving tSCS at their optimal stimulation parameters. Here, STA refers to the time-locked average EMG waveform computed across all stimulation pulses, representing the typical EMG response pattern following each stimulus.

The EMG was recorded during the EMG modulation task during the no visual feedback condition (see methods in Force Proprioception in ULA Participants), to avoid any compensation by the participant. The EMG signals were digitally notch filtered (50 Hz, Q = 37.5) and band-pass filtered (10–500 Hz). For each stimulation pulse, an EMG window was extracted starting 4 ms after the stimulus onset (to exclude the stimulation artifact) and ending one sample before the next stimulus pulse. The STA was computed by averaging these windows across all stimulation pulses:

$$STA[m] = \frac{1}{N}\sum_{k=1}^{N} x[n_k + M_a + m], m = 0, 1, \ldots, M-1 \quad (1)$$

where $x[n]$ is the discrete EMG signal, n_k are the stimulus onset sample indices, N is the total number of stimulation pulses,$M_a = 4\ ms \cdot f_s$ is the artifact duration in samples, f_s is the sampling frequency, M is the window length in samples.

The mean STA amplitude was then calculated as:

$$\overline{STA} = \frac{1}{M}\sum_{m=0}^{M-1} |STA[m]| \quad (2)$$

As a control validation, $\overline{STA}$ values during tSCS were compared with those obtained during the sham condition (stimulation of the upper trapezius muscle). Comparable $\overline{STA}$ values between conditions would confirm that tSCS was not directly eliciting motor-evoked potentials in the wrist flexors, as upper trapezius stimulation would not be expected to produce such responses in the distal upper-limb musculature. The mean $\overline{STA}$ across all conditions during tSCS was 4.26 ± 1.85 % MVC and during Sham it was 4.79 ± 1.85 % MVC, indicating that tSCS was below motor threshold during steady contractions as well as during rest (for more detailed graphic representation $\overline{STA}$ amplitude see Fig. S2 in Supplementary Information).

D. Evaluating Evoked Sensory Percepts

For each stimulation protocol (stimulation location * carrier frequency * burst frequency), participants were subjected to 2.5 minutes of stimulation and were asked, using a psychophysical questionnaire [40] and dermatome image (see Fig. 1), to identify the quality and location of the evoked sensation, the overall perceived stimulation intensity, and the overall perceived comfort at the onset of stimulation and again 2.5 minutes later. Participants could report multiple sensations,

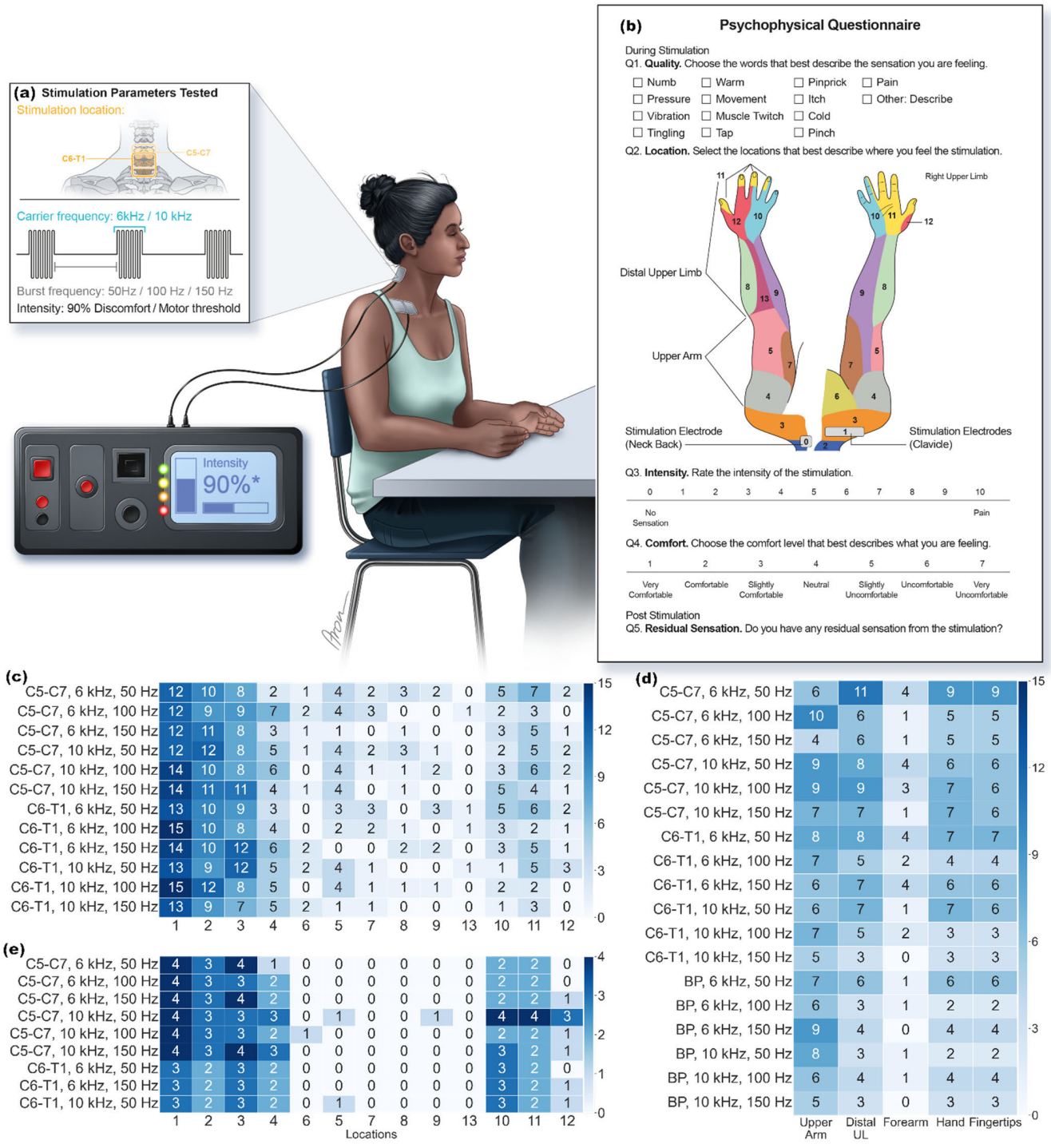

Fig. 1. Experimental set-up and locations of evoked sensations during tSCS in AB and ULA participants. **(a)**, tSCS parameters and participant's position during the experiment. **(b)**, psychophysical questionnaire including the dermatome image used for selecting location of evoked sensations, and the regions these locations are classified under. **(c)**, locations of evoked sensations during each tSCS protocol in AB participants. **(d)**, region of evoked sensations during each tSCS and BPS protocol for AB participants. **(e)**, locations of evoked sensations during each tSCS protocol in ULA participants. The number in each cell indicates the number of participants that reported a sensation in each location during each protocol. Each experiment, tSCS and BPS, had fifteen participants, with thirteen mutual to both. The distal upper limb (locations 8-13) includes the forearm (locations 8,9, and 13), and the hand (locations 10-12). The hand includes the fingertips (locations 10-11). Participants were only counted once in each cell in the heatmaps (c), (d), and (e); thus, if a participant reported sensations in locations 10, 11, and 12 in heatmap (c), then in heatmap (d) they would be counted for once under Fingertips and once under Hand.

and multiple locations simultaneously. They could also use descriptors and locations that were not in the questionnaire. It is worth noting that the stimulation was delivered while the questionnaire was asked the second time and was only turned

off after they finished reporting. Psychophysical measurements such as detection threshold and just noticeable difference were recorded in a pre-experiment session (See Supplementary Methods for more information). Participants were informed to consider the neutral level of comfort as that experienced before stimulation. A washout period of four minutes was followed between protocols. After each protocol, the participant was required to report on any persistent sensory percepts after stimulation ceased, and if any, the washout period was extended until any persistent sensations completely faded.

All twelve stimulation protocols were tested with AB participants without repetitions across two sessions over two days with six protocols on each day. Subsequent to analysis of the results of AB participants, the experimental protocol was adapted for the ULA participants to reduce the experimental time to one day. For the ULA participants, the nine most effective protocols at targeting the distal upper limb in AB participants were selected.

Additionally, one protocol per ULA participant was designated as optimal, defined as the protocol that elicited the most naturalistic sensation in the missing limb with the highest comfort rating, and was tested twice. This resulted in ten protocol instances per ULA participant (nine unique protocols plus one repeat of the optimal protocol). Each administration of the psychophysical questionnaire is referred to as a trial; thus, AB participants completed twelve trials each and ULA participants completed ten trials each. For ULA participants, within-participant statistical comparisons of individual stimulation parameters (cathode placement, burst frequency, or carrier frequency) were conducted only between matched protocol pairs that differed in a single parameter; protocols without a corresponding match were excluded from these analyses. Both cohorts were asked to avoid voluntary upper-limb movements during testing. To help ULA participants describe functional sensations evoked by tSCS in their missing limb, they were asked to mirror its perceived kinematic state using their intact limb before stimulation and again at 2.5 minutes, including movement and location, while being video recorded. Sensations (e.g., perceived movement) reported during mirroring were categorised and incorporated into the questionnaire.

E. Comparison With Peripheral Nerve Stimulation: Brachial Plexus Stimulation

A peripheral nerve stimulation approach was also evaluated by testing the same combinations of stimulation parameters over the brachial plexus in AB participants only. The aim of this control study was to test if the effects induced by tSCS are comparable to those of peripheral nerve stimulation. Given the proximity of the tSCS anode (placed on the clavicle) to the brachial plexus, this control condition also aimed to determine whether the effects induced by tSCS arise from spinal circuit activation or from incidental stimulation of peripheral nerves at the brachial plexus. In a pre-experiment session, the electrode location for BPS was identified as the site eliciting the most distal contraction in the upper limb during four 2 ms biphasic rectangular stimulation pulses, delivered 50 ms apart, across two round electrodes (3.2 cm diameter, Axelgaard Pals Platinum) applied over the supraclavicular fossa of the dominant side. The BPS study included six protocols (BPS * carrier frequency * burst frequency) tested in one session on one day. The experimental setting for the BPS study was otherwise identical to that of the tSCS study with AB participants. To compare the effectiveness of BPS and tSCS at targeting the distal upper limb, a Cochran's Q test with three repeated measures (C5-C7, C6-T1, BPS) was conducted on the thirteen mutual AB participants. Pairwise comparisons were performed using Dunn's procedure with Bonferroni correction for multiple comparisons.

F. Force Proprioception in ULA Participants

To investigate the effects of tSCS on force proprioception, we assessed ULA participants' ability to differentiate between contraction levels (5%, 15%, and 25% of MVC) under three conditions: tSCS, no stimulation (noStim), and a sham condition (stimulation of the trapezius). The previously optimized tSCS protocol for evoking naturalistic sensations in the missing limb was employed for the tSCS condition. The tSCS amplitude remained the same as the one used in psychophysical study. The sham stimulation condition utilized the same stimulation parameters as tSCS but targeted the trapezius muscle, using two square stimulation electrodes (5×5 cm^2, Axelgaard Pals Platinum) as anode and cathode (See Fig. 4). The testing of the sham condition allows controlling for the potential disruption of force proprioception due to the recruitment of cutaneous fibres without the activation of spinal interneurons targeted in the tSCS condition. Similar to tSCS, the stimulation current of the sham condition was set to 90% of the motor threshold of the trapezius.

Surface EMG activity was recorded and amplified with a sampling frequency of 2048 Hz (Quattrocento, OT Bioelettronica) with bipolar electrodes placed along the wrist flexors (ULA1, ULA3, ULA4, ULA5) maintaining a 2-cm inter-electrode distance. At the start of the session, participants performed two maximum contractions of the primary muscles used for prosthesis control to estimate their MVC. The average of these measurements served as a reference for subsequent tests. Participants were seated before a screen displaying visual feedback. The feedback was generated using the root mean square (RMS) of the EMG signal, calculated in sliding windows of 250 ms with 125 ms overlap. The RMS signals were normalized using participants' EMG levels at rest and estimated MVC, providing a visual representation of contraction level. Prior to the experiment, participants underwent a 30-second familiarization period using visually-guided force feedback. The experiment comprised three blocks, one for each targeted contraction level. Individual trials (training or test) lasted 10 seconds, consisting of 2 seconds of rest, 1 second of ramp-up, a constant (steady) phase of 4 seconds at the target contraction level, 1 second of ramp-down, and finally, a 2-second rest. Each block was subdivided into three condition-specific sub-blocks (noStim, Sham, tSCS). Sub-blocks commenced with a training trial (no stimulation, visual feedback), followed by three test trials with the respective

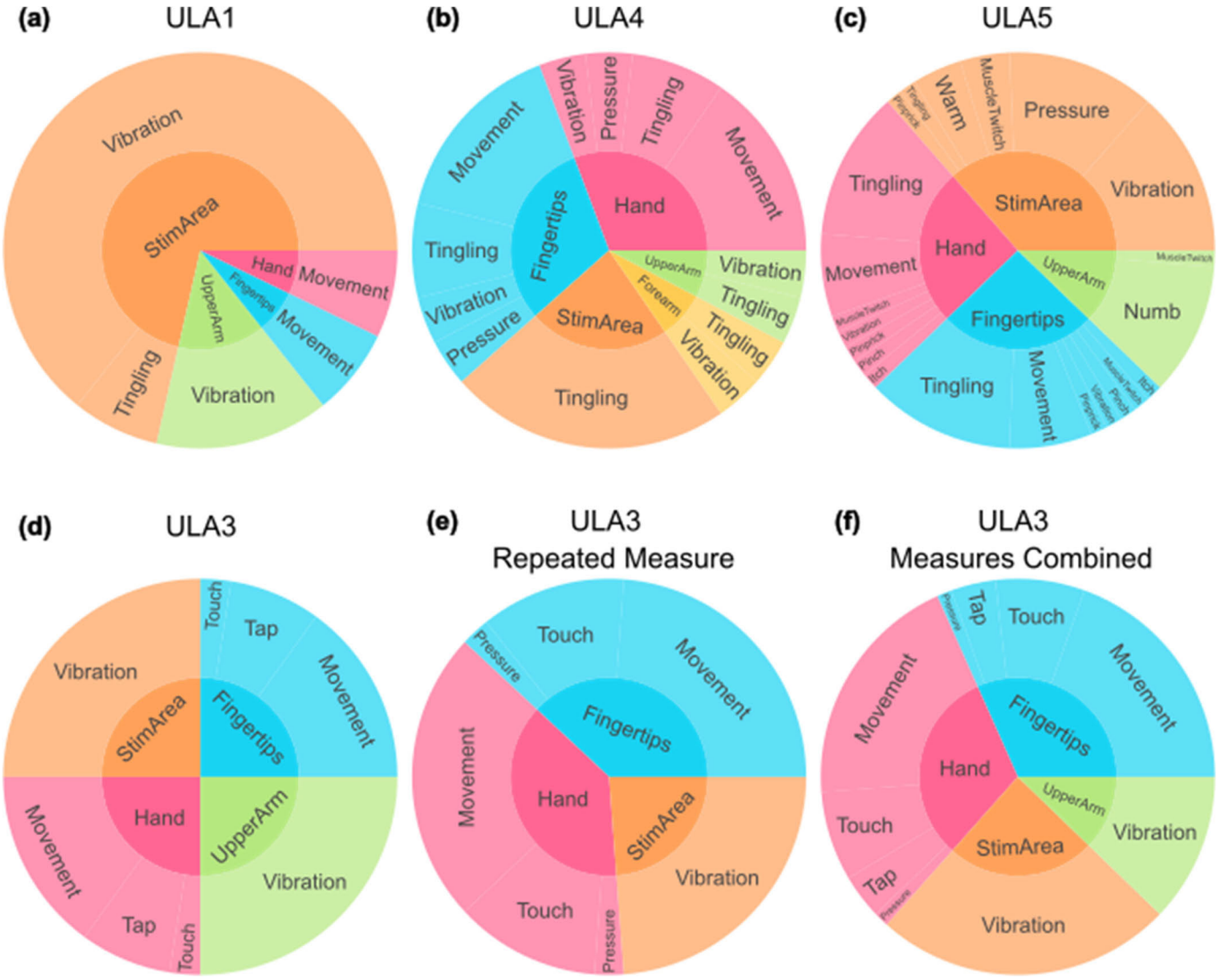

Fig. 2. Sunburst plots showing the location (inner ring) and type (outer ring) of evoked sensations during all tSCS protocols in ULA participants. The subplots show the location and quality of sensations evoked during tSCS for: **(a)**, ULA1; **(b)**, ULA4; **(c)**, ULA5; **(d)**, ULA3–in the first session; **(e)**, ULA3 in the second session; **(f)**, ULA3 in both sessions. For a word cloud representation of the type of movement each ULA participant reported during tSCS, see Fig. S7.

stimulation condition and no visual feedback. During test trials, the researcher provided verbal cues ("Get ready" at ramp-up, "Go" at constant phase onset) based on the visual feedback. The order of target contraction levels and conditions was randomised, and participants were blinded to these selections. A 4-minute rest period followed each sub-block, with extensions provided if participants reported fatigue.

G. EMG Modulation Analysis

The EMG signals were digitally notch filtered (50 Hz, Q = 37.5), and band passed filtered (10–500 Hz). For the tSCS and Sham conditions, to remove the stimulation artifact, the signals were blanked $\pm$ 2 milliseconds around each stimulus. This brief blanking window does not affect EMG decoding performance [46]. Then, the signals were rectified and low-pass filtered at 3 Hz to obtain the EMG envelope. The mean of the steady contraction phase (second 4 to 7) was calculated. To formally address whether the relationship between the mean steady contraction level achieved and target contraction level was unique to tSCS with single trial EMG data, we performed linear mixed models (LMM) fit by REML, with target level contraction and condition as fixed factors, and subject and trials as random effects to control for subject and trial variability.

III. Results

A. Stimulation Elicits Sensations in The Missing Hand

The first aim of this study was to ascertain the extent of sensation elicitation in the distal upper limb by tSCS applied at sub-motor threshold and to correlate various stimulation parameters—including stimulation location, burst frequency, and carrier frequency —with the quality and location of the evoked sensations. For this purpose, we designed twelve stimulation protocols of burst-modulated alternating current consisting of combinations of different stimulation locations (C5-C7, C6-T1), carrier frequency (6 kHz, 10 kHz), and burst

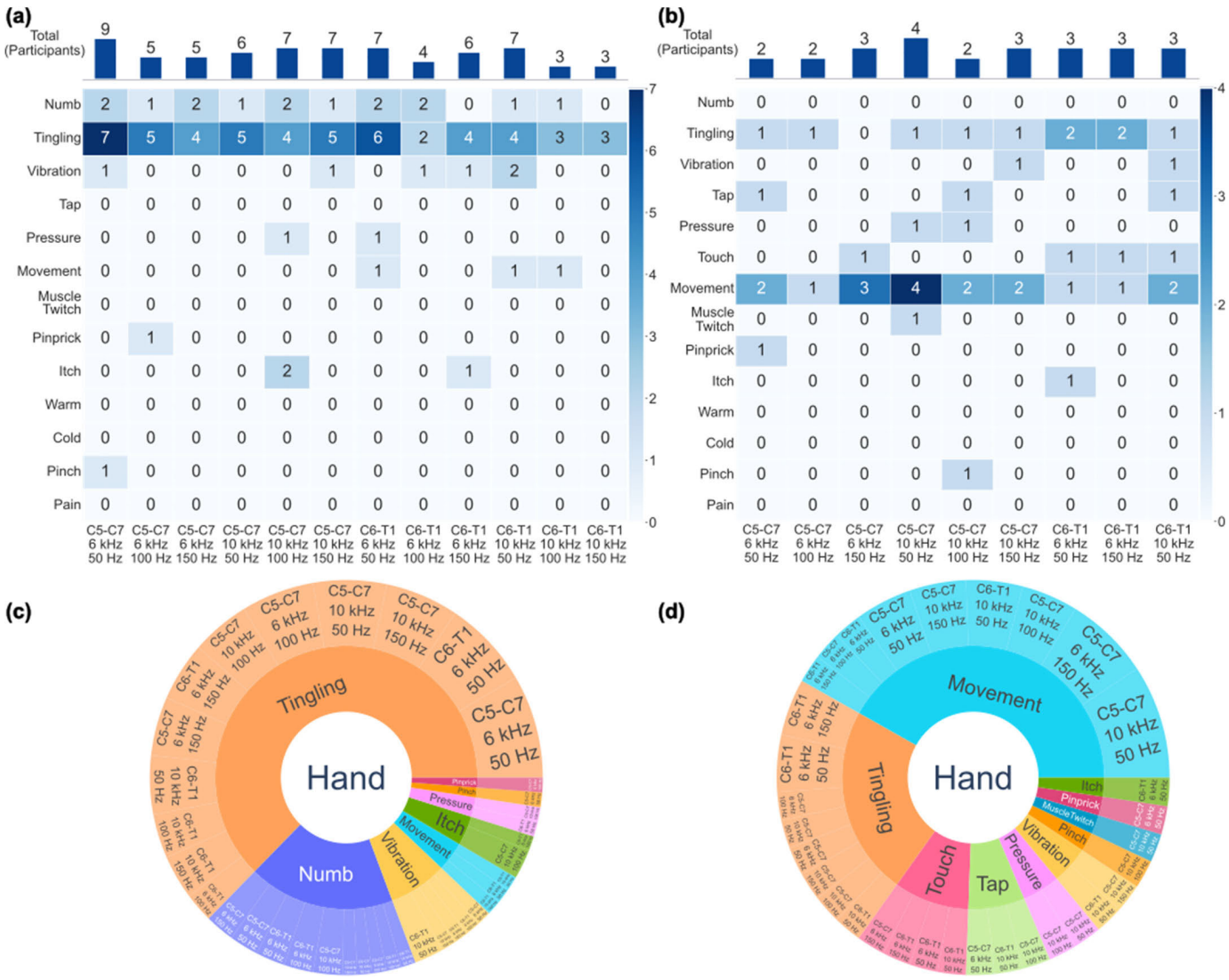

Fig. 3. Quality of evoked hand sensations in AB and ULA participants. **(a, b)** Heatmaps illustrating the frequency of reported sensations for each protocol in AB and ULA participants, respectively. **(c, d)** Sunburst plots depicting the types of evoked hand sensations (inner ring) and the corresponding evoking protocols (outer ring) for AB and ULA participants, respectively.

frequency (50 Hz, 100 Hz, 150 Hz) (Fig. 1). Subsequent retrospective analysis of the AB results identified nine out of twelve protocols that most effectively induced sensations in the distal upper limb while maintaining a relatively high comfort rating. These selected protocols were then tested on the five ULA participants, enabling the completion of the experimental procedure in each ULA within a single day. We also tested a control condition for tSCS by stimulating the brachial plexus in AB participants. The aim of this control condition was to test if the effects induced by tSCS were comparable to those obtained by stimulating peripheral nerves. The results of the psychophysical measurements evaluation of all the protocols tested are described in Supporting Results and Fig. S3-6.

With the optimal stimulation protocol for each participant (that being the protocol that elicited sensations perceived to emanate from the most distal part of the limb), tSCS elicited sensations in the fingertips of 93.3% of AB participants, and in the distal upper arm (forearm and hand) in 100.0% of participants, aside from eliciting sensations around the stimulation electrodes. In AB participants, location 11 (anterior lateral hand inc. digits 1-4, and posterior fingertip of digits 1-4, innervated by the median nerve, C6-C8) was the region of the hand mostly reported with evoked sensations (Fig. 1(c)). tSCS was able to target the hand without targeting the forearm (X^2 (1) = 55.000, p <0.001). Sensations evoked in the hand were accompanied by sensations in the forearm and upper arm in 20.3% and 63.8% of the cases, respectively. The most successful protocol in reaching farthest extremities was (C5-C7, 6 kHz, 50 Hz), eliciting sensations in the fingertips of 9/15 (60.0%) of AB participants (Fig. 1(d)). The least successful tSCS protocols in targeting the hand and fingertips were (C6-T1, 6 kHz, 100 Hz), (C6-T1, 10 kHz, 100 Hz), and (C6-T1, 10 kHz, 150 Hz), which were therefore excluded from the experiments with participants with amputations, (Fig. 1(d)).

Five participants with a unilateral upper-limb amputation from 1 to 24 years prior to the study, with causes of amputations ranging from trauma to vascular disease, also took part in the study. Four of the participants (ULA1, ULA3, ULA4,

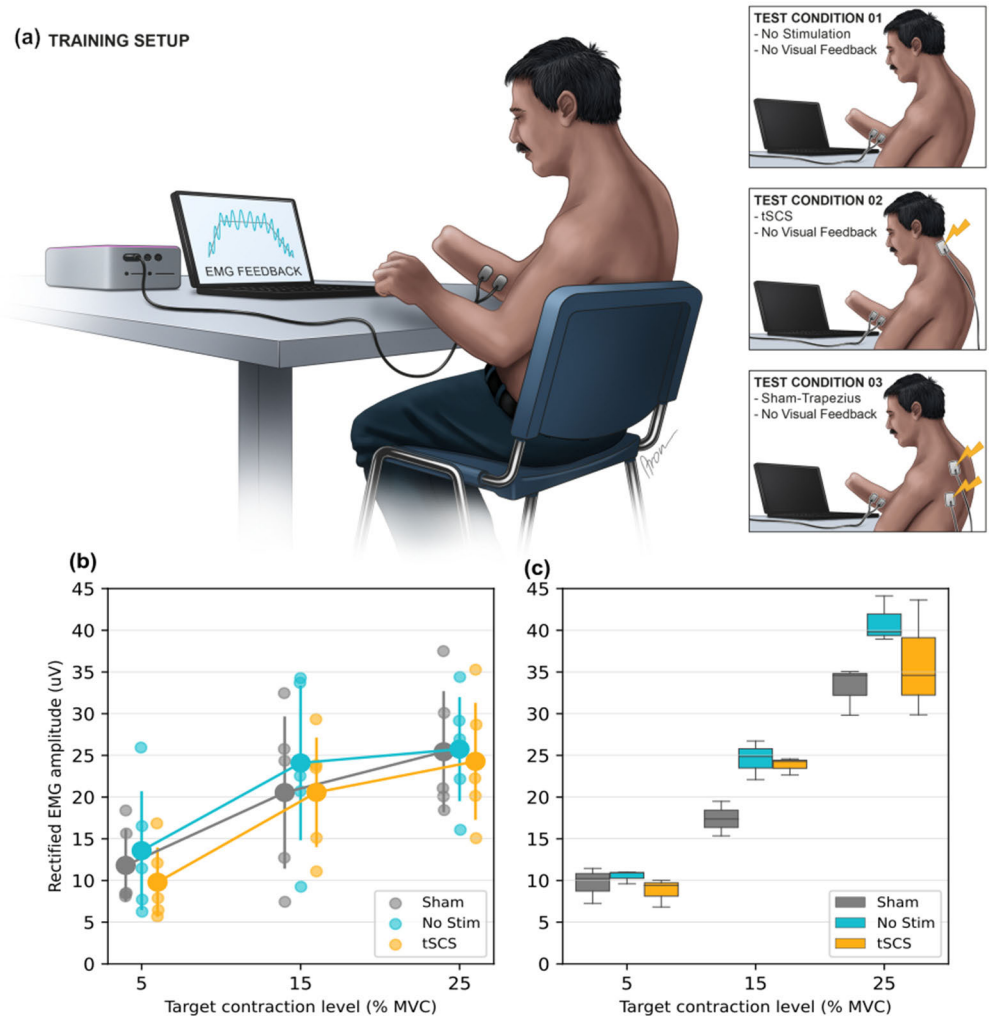

Fig. 4. tSCS preserves force proprioception. **(a)**, schematic of force proprioception experimental setup. **(b)**, effects plots showing the average rectified EMG amplitude during the steady contraction phase at target contraction levels of 5 %, 15 %, and 25 % of MVC for all ULA participants. This shows that the separability between the three levels of contraction is maintained during tSCS. **(c)**, example data from the EMG modulation tasks from subject ULA3 (repeated measure).

ULA5) had a cognitive perception of their missing limb, prior to the experiment, and reported being able to feel and slightly move their missing limb. All four ULA participants with baseline missing limb perception experienced induced sensations in the missing hand during the initial session of tSCS. Notably, ULA2 did not have any perception of their missing limb prior to the experiment and did not perceive their missing limb during the experiment. Thus, ULA2 was not considered in further analysis.

tSCS induced sensations perceived to originate from the missing limb without concurrent sensations in the stump in all ULA participants and in all trials (including repeated protocols), except in one out of ten trials reported by ULA4 (Fig. 2). However, in 85.7% of the trials, these sensations were accompanied by sensations under and around the stimulation electrodes. Within the missing hand, sensations were induced more often in locations 10 (medial part of the hand inc. digits 4 and 5, innervated by the ulnar nerve, C8-T1) and 11 (anterior lateral hand inc. digits 1-4, and posterior fingertip of digits 1-4, innervated by the median nerve, C6-C8) than in location 12 (posterior lateral part of the hand inc. digits 1-3, exc. fingertips, innervated by the radial nerve, C6-C8), X^2 (2) = 33.583, p <0.001. For ULA1, sensations in the missing limb were accompanied by sensations near the stimulation electrodes (Location 0,1,3) but not in the stump (Fig. 2(a)). Participant ULA3 undertook this experiment twice in two sessions across two weeks, to evaluate the changes in tSCS effects across sessions. In the first session, ULA3 reported sensations in the missing limb that were accompanied by sensations near the stimulation electrodes and deltoid (upper arm); while in the second session (repeated measures) ULA3 reported sensations in the missing limb were unaccompanied by sensations in the residual limb (Fig. 2(d), (e)). In three of nine protocols, ULA4, had sensations in the missing limb that were unaccompanied by any sensations in the residual limb or stimulation area (Fig. 2(b)). For ULA5, sensations in the missing limb were accompanied by sensations near the deltoid and bicep brachii in 80.0% of trials and always accompanied by sensations in the stimulation area (Fig. 2(c)).

In AB participants, configuring the stimulation electrode on C5-C7 was significantly more effective at targeting the distal upper limb (forearm and hand) compared to the C6-T1 placement (Cochran's Q (1) = 4.500, p = 0.03). In contrast, no statistically significant differences were observed in ULA participants. Stimulation consistently targeted the intended side, with no sensations elicited on the contralateral side in both participants with and without amputation. In AB and ULA participants, no significant differences in sensation quality or location were observed between reports at onset and at 2.5 minutes of stimulation. Persistent sensations after tSCS ceased were reported in 7.2% of trials in AB participants. For ULA, persistent sensations were only reported by ULA3. Those sensations lasted up to 10 seconds post-tSCS. There were no significant differences in persistent sensations between electrode locations, carrier or burst frequencies.

In AB participants, tSCS was also compared with the control condition, brachial plexus stimulation. This stimulation elicited sensations in the fingertips of 40.0% of the participants only (Fig. 1(d)). tSCS delivered at C5-C7 was more effective at targeting the distal upper limb than BPS (C5-C7> BP: p = 0.017, Bonferroni adjusted).

B. tSCS Evokes Perceptions of Movement of The Missing Hand

During tSCS, sensations elicited in the hand of AB participants were predominantly paraesthetic sensations. In fact, a sensation of movement in the hand was only reported in three trials across all AB participants (Fig. 3(a)). Tingling, numbness and vibration constituted 62.7%, 18.1% and 7.2% of reported sensations amongst this cohort, respectively (Fig. 3(c)). Sensations evoked during BPS were predominantly paraesthetic, such as tingling and vibration. Due to the ineffectiveness of BPS in targeting the distal upper limb, or eliciting non-paraesthetic sensations, this modality was excluded from testing with ULA participants.

All ULA participants with missing limb perception reported distinct sensations of their missing hand moving during tSCS (Fig. 2). For ULA 1, 3, 4 and 5, when their missing hand was targeted via tSCS, a perception of moving was evoked in 100.0%, 61.5%, 57.1%, and 50.0% of trials, respectively. For ULA3, movement perception rates were 60.0% in the first session and 62.5% in the repeated session. Participants reported experiencing dynamic proprioceptive-like sensations in the missing hand, including hand opening/closing and individual finger movements, induced by tSCS (Fig. S7.). Notably, ULA3, who occasionally experiences a restless state of continuous, sporadic movement of their absent fingers, reported that this perceived movement ceased during tSCS and resumed once the stimulation was discontinued. Similarly, ULA4, who typically perceive their missing hand in a persistently tight and uncomfortable fist, reported a slight opening of the hand during tSCS, leading to a sense of relief. All nine tSCS protocols tested on ULAs induced a perception of movement in the missing hand in at least one participant (Fig. 3). Among the different stimulation configurations, carrier frequency of 10 kHz, and burst frequency of 50 Hz was found to be the optimal configuration for ULA1, ULA5 (in combination with stimulation location of C5-C7), ULA3, and ULA4 (in combination with stimulation electrode at C6-T1). The protocol selected as optimal was tested twice during the experimental session for all participants with missing limb perception. The optimal protocol selected per participant was consistent in inducing sensation in the missing hand in ULA3, ULA4 and ULA5, but not ULA1.

In contrast to AB participants, ULAs predominantly experienced tactile and kinaesthetic sensations in their missing hand, including touch, tap, pressure, and perceived movement (Fig. 3(c), (d)). Stimulation protocol (C5-C7, 6 kHz, 150 Hz) successfully induced these sensations in ULA3, ULA4, and ULA5, without eliciting any paraesthetic sensations, such as tingling, in the missing hand. Across all trials of ULA participants, tSCS selectively induced perceived movement of location 12 (posterior lateral part of the hand inc. digits 1-3, excluding fingertips, innervated by the radial nerve, C6-C8), except for a single trial in which the sensation of pressure was also induced. tSCS never induced numbness in the missing hand (Fig. 3(b)). Neither group (AB or ULA) reported a sensation of pain, cold, or warmth in the hand during any of the stimulation blocks (Fig. 3(a), (b)).

C. tSCS Preserves Force Proprioception in ULAs

A key aim of this study was to evaluate whether tSCS preserves or disrupts the ULA participants' proprioception of force. For this purpose, we asked the participants to perform an EMG-modulation task, in which they attempted to produce three contraction levels (5%, 15%, 25% of MVC) under three conditions: during tSCS, without stimulation (No Stim), and with sham stimulation (stimulation on the upper trapezius muscle), without visually guided force feedback (Fig. 4). In this way, we aimed to assess whether the different conditions being compared led to changes in the separability of the various EMG levels produced. We recorded surface EMG from the wrist flexor muscles (ULA1, ULA3, ULA4, ULA5), based on the muscle the participants normally use for prosthesis control. The target contraction level, i.e. percentage of MVC, had a statistically significant impact on the average of the EMG envelope during the steady contractions ($F(2,122) = 103.12$, $p < .001$), indicating that the contraction levels were still separable using EMG in all conditions (Fig. 4(b)). Although there was a significant effect of the condition (tSCS, Sham, or No Stim) ($F(2,122) = 4.65$, $p = 0.011$) on the average of the EMG envelope level during the steady contraction, subsequent post-hoc tests did not reveal significant differences between conditions when tested for each contraction level as evidenced by the absence of a significant interaction effect between condition and contraction level. These results showed that the relationship between the achieved and target contraction levels was maintained during tSCS, suggesting that the participants' ability to perceive and differentiate between the different contraction levels during tSCS was maintained.

IV. Discussion

We have demonstrated that tSCS has the potential to be an effective approach for evoking sensations in the missing

limb of people with upper-limb amputations. Importantly, we observed that tSCS can restore tactile sensations such as touch, pressure and tapping, and evoke proprioception-like sensations, such as perceived movement of the missing hand, in people who had amputations from 1-24 years prior to the study, with causes of amputations ranging from trauma to vascular disease. Further, this restoration was achieved without compromising on natural force proprioception and preserving EMG-based control necessary for prosthesis use. Additionally, our study provides a comprehensive mapping of the effects of tSCS stimulation parameters (stimulation location, carrier and burst stimulation frequencies) to the location, quality, comfort and perceived intensity of evoked sensations, on both AB and ULA participants.

tSCS produced distinct, distal sensations in the upper limb, often evoking multiple concurrent sensations in a given body area. The technique successfully elicited sensations in the fingertips of nearly all AB participants (>90.0%) and in the missing hand of all ULA participants who had prior baseline perception of their missing hand. The greater effectiveness of tSCS compared to BPS at targeting the fingertips (93.3% vs 40.0% of AB participants) indicates that the two conditions activate different neural pathways; suggesting that tSCS may primarily activate spinal circuits rather than peripheral nerves. Although both the forearm and hand are innervated by C6-T1 dermatomes (with C5 also covering the forearm), tSCS was more effective at targeting the hand than the forearm in both AB and ULA participants. The reason for this apparent 'bypassing' of the forearm is not clear. It may suggest that the nerve branches serving the hand (ulnar, median, and superficial radial) are more excitable than those innervating the forearm (lateral and medial antebrachial, and radial nerve branches). However, it is important to note that the electrical field generated by tSCS could potentially interact with and stimulate both descending and ascending neural pathways [41], [42]. The interaction with the ascending pathways might explain the differences observed in sensations perceived as originating from the forearm versus the hand. Further research is required to understand what is causing these differences. While the locations of sensations produced by tSCS were similar in AB and ULA participants, the nature of these sensations differed markedly between the two groups. For ULAs who experienced missing limb sensations, tSCS triggered realistic sensations perceived to be originating from their missing hand, such as movement, pressure, touch, and tapping. Notably, when perceived movements of the missing hand were evoked, they were typically not accompanied by paraesthesia (unnatural sensations like tingling or prickling). In contrast, the sensations elicited in the hands of AB participants were predominantly paraesthetic. Sensations of movement in the hand were reported only in three instances across all trials with AB participants. The majority of sensations reported by this group were tingling (63%), numbness (18%), and vibration (7%). The disparities in sensations between AB and ULA participants may stem from the intricate interplay between electrical stimulation and neural circuits. tSCS can elicit bidirectional action potentials in the stimulated nerve fibres, resulting in both orthodromic and antidromic [43] signal propagation. This two-way transmission can potentially cause disruptions in the normal flow of neural information. In AB individuals, tSCS may recruit fibres involved in proprioceptive pathways, leading to interference with the natural sensory signals traveling along these same pathways. The collision between artificially induced antidromic action potentials and the naturally occurring proprioceptive action potentials could impede the transmission of the latter to the central nervous system, potentially altering sensory processing [44]. Conversely, ULA participants, lacking the peripheral sensory input from the missing limb, may not experience this interference phenomenon. The absence of ascending sensory information from the amputated extremity precludes the possibility of such collisions. The predominance of movement percepts in ULA participants may reflect the preferential activation of proprioceptive afferent pathways at the spinal level. With substantially reduced competing peripheral input from the missing limb, and without the signal collision that occurs in intact individuals, stimulation of these pathways may be more readily interpreted by the central nervous system as limb movement rather than cutaneous sensation. To fully comprehend the underlying mechanisms responsible for the observed sensory differences between AB and ULA participants during tSCS, additional research is necessary.

By evoking distinct percepts of movement in the missing limb, tSCS enhances limb perception, which is fundamental to prosthesis embodiment. Heightened perception of the missing limb has been shown to improve prosthesis control [45]. Notably, in our study, tSCS not only evoked tactile and proprioceptive-like sensations in the missing limb, but also as a byproduct provided relief in the missing limb. For instance, participant ULA4 experienced relief after opening his missing hand, which is typically tightly closed to the point of discomfort, while ULA3 found that tSCS helped calm sporadic finger movements. These findings align with previous studies demonstrating that SCS can enhance comfort by reducing phantom limb pain [19], [20], suggesting potential for tSCS as a treatment for this condition.

The relationship between baseline phantom limb perception and responsiveness to tSCS may reflect the integrity of cortical and spinal representations of the missing limb. Participants without baseline phantom perception may lack a functional cortical 'target' for ascending tSCS input, whereas those with active phantom sensations, such as spontaneous movements, may experience modulation of residual peripheral nerve activity through inhibitory spinal mechanisms or antidromic signal collision [43], [44].

While eSCS has also been shown to elicit movement and tactile sensations in the missing limb [22], reduce phantom limb pain, and improve control [20], tSCS offers similar advantages [19] without the need for invasive surgery. This makes tSCS a more accessible and practical option for clinical and home use, or perhaps for first-line introduction into restoration of naturalistic sensations in the missing limb. However, while eSCS can be limited by lead migration, tSCS may be affected by electrode shifts between sessions, requiring consistent re-application for daily use which can be a limitation.

Although SCS has been shown to improve prosthesis control, further research is needed to specifically investigate how tSCS can utilize perceptions of movement as a sensory encoder in daily functional tasks. Additionally, the effect of stimulation amplitude on evoked sensations warrants investigation as a potential parameter for modulating sensory percepts. Understanding how these evoked sensations can be applied and integrated into prosthesis control for daily tasks is the next step to implementing this technique as a sensory feedback device.

The ability of prosthesis users to effectively control their artificial limbs is a critical factor in the successful integration of these devices into daily life. Central to this control is the user's capacity to modulate EMG signals, which serve as the primary interface between the user's intentions and the prosthetic device's actions. This modulation heavily relies on the user's intact perception of effort and force exerted. Without these sensory cues from the intact afferent pathways and muscles in the residual limb involved in prosthesis control, users would not be able to generate appropriate EMG signals, potentially leading to imprecise or erratic prosthesis control. Previous studies on eSCS have shown that stimulating the spinal circuits may disrupt proprioceptive or other afferent information due to collision between the naturally occurring orthodromic action potentials and antidromic action potentials induced by eSCS [44]. In this study, we have provided evidence that tSCS does not interfere with the ULA participants' ability to modulate and discriminate between different EMG contraction levels. This preservation of EMG control is crucial, as it ensures that the additional sensory information provided by tSCS does not come at the cost of disrupting the user's existing control strategies. Beyond preserving EMG modulation, tSCS also offers a practical advantage over peripheral stimulation paradigms: its shorter stimulation artifact requires only 4 ms of signal blanking, compared to 20–300 ms for peripheral nerve stimulation [46], [47]. This means less EMG data is lost per stimulation pulse, potentially enabling more robust decoding with reduced latency. Together, these findings suggest that tSCS could potentially be used in the future for supporting sensorimotor restoration, opening up new avenues for the development of more intuitive and responsive prosthetic limbs, potentially leading to improved functionality and user satisfaction.

As research in this field progresses, it is essential to continue investigating the interplay between neurostimulation techniques like tSCS, tactile and proprioceptive feedback, and EMG-based prosthesis control. Understanding these relationships will be key to developing the next generation of accessible prosthetic devices that can more closely mimic the sensorimotor capabilities of natural limbs.

Some limitations remain to be addressed in future studies. First, the cohort of ULA participants was relatively small and included participants with distal amputations only, including three participants with transradial amputations and two with transcarpal amputations. Future studies should include participants with shoulder-disarticulation and proximal amputations to understand the implications of such amputation levels on the efficacy of tSCS in evoking sensation from the missing limb. Further, the psychophysical measurements (i.e., detection thresholds, just noticeable differences, discomfort/motor thresholds, and perceived intensity) were measured based on sensations evoked anywhere in the body, including under the stimulation electrodes and were not measured from the effects local to the hand (See Supporting Methods and Supporting Results). The motor threshold was measured with different sensitivities for AB and ULA participants. For ULA participants, it was measured using surface EMG, whereas for AB participants it was measured based on visible contractions of the muscles (Supporting Methods). Moreover, the stimulation was administered for ~2 mins for psychophysical measurements and 2.5 minutes for evoked sensations questionnaire per trial/protocol, due to the time constraints, thus limiting the study to sensations evoked in that period.

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