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Dynamic expansion of alert responses to incoming painful stimuli following tool use

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ABSTRACT

Peripersonal space is the region closely surrounding our bodies. Within its boundaries, avoidance of threatening objects is crucial for surviving. Here we explored autonomic responses to painful stimuli with respect to the dynamic properties of the peripersonal space in healthy individuals. To this aim, in a series of experiments, we measured the Skin Conductance Response (SCR) to a noxious stimulus approaching and touching the hand, or stopping at different distances (far, near) from it. Results showed that the anticipatory response to an incoming threat is reduced if the stimulus targets a spatial position far away from the body, as compared to a near or bodily location. However, responses to far stimuli change if the boundaries of reachable space are extended further away by active tool use. Noteworthy, SCR is not influenced by a training consisting of a spatial attention task, without active tool use. This evidence sheds novel light on the adaptive role of peripersonal space, showing its importance for the coding of incoming threatening stimuli and its plasticity induced by contingent experience, such as tool use.

Keywords:

Pain anticipation; peripersonal space; skin conductance response; tool use; vision.

1. INTRODUCTION

Pain anticipation is a crucial adaptive ability of humans as well as of many living beings. It allows us to understand potentially dangerous situations, in order to carry out appropriate defensive behavior. This function is particularly relevant with respect to the coding of potentially noxious stimuli that are within, and/or rapidly moving toward, the space surrounding our body (Graziano et al. 2002; Graziano and Cooke 2006). This sector of space, namely the peripersonal space (Rizzolatti et al. 1981a; Rizzolatti et al. 1981b), holds peculiar features due to its richness of multisensory interactions, especially with respect to body-related visual and tactile stimuli (Làdavas and Farnè 2004; Macaluso and Maravita 2010).

The neural substrate underlying the multisensory representation of peripersonal space comprises areas containing multisensory neurons with bimodal, visual and tactile, receptive fields (RFs) centered on body parts (Graziano and Gross 1993; Graziano and Gross 1995). These neurons hold a tactile RF on one body part (e.g., a hand) and typically increase their firing rate when a visual stimulus approaches the tactile RF, and decrease their response when the visual stimulus moves away (Graziano and Gross 1992). Interestingly, the visual RFs of bimodal neurons show dynamic properties. In his seminal study, Iriki et al. (1996) trained monkeys to retrieve bits of food placed in the extra-personal space, by means of a hand-wielded rake. They found that, after the training, the visual RF of parietal bimodal cells extended to the tip of the tool or to the space now reachable by the tool. This reorganization only occurred when monkeys actively used the rake, suggesting that this mechanism depends on voluntary action.

Several studies support the existence of similar mechanisms for body-related multisensory integration in humans (Maravita and Iriki 2004; Macaluso and Maravita 2010; Bolognini and Maravita, 2007). For instance, the investigation of right brain-damaged (RBD) patients with left tactile extinction has provided strong support to the existence of an integrated visuo-tactile representation of peripersonal space in humans. These patients can typically detect a single touch on the left or right hand in isolation, but they fail to report the contralesional, left-sided, touch when it is presented simultaneously with an ipsilesional, right-sided, stimulus of the same (Bender

1952) or different sensory modality (di Pellegrino et al. 1997; Mattingley et al. 1997; Làdavas et al. 1998; Farnè and Làdavas 2000). Crossmodal extinction of contralesional touch to the hand by an ipsilesional visual stimulus is usually more pronounced when the visual stimulus is presented close to the ipsilesional hand (Làdavas et al. 1998). However, after a brief period of training with a tool allowing to reach for objects in the space far from the body, crossmodal extinction emerges even for visual stimuli placed far from the body, but near the tip of the tool (Farnè and Làdavas 2000; Maravita et al. 2001; Farnè et al. 2007), suggesting an expansion of crossmodal visuo-tactile interactions to the far space. Studies in healthy subjects using the Crossmodal Congruency Task (CCT) (Driver and Spence 1998a; Driver and Spence 1998b; Maravita et al. 2003; Spence et al. 2004b) have provided further evidence for the efficacy of tool use for expanding crossmodal responses to the far space (Maravita et al. 2002b; Holmes et al. 2004; Spence et al. 2004a; Holmes et al. 2007a; Macaluso and Maravita 2010).

The functional meaning of having such a peculiar representation of peripersonal space is likely due to its importance for object manipulation, but also for the avoidance of incoming threats. The latter aspect, in particular, is reminiscent of the notion of "defensive flight zone", proposed in the 1950s by the Swiss zoologist Heini Hediger as the urge to protect the zone near the body as the primary goal of any creature, more important than food or sex. He defined this zone as the "flight distance", and later as "flight zone". Graziano and colleagues further corroborated Hediger' idea in non-human primates, by showing the occurrence of avoidance behaviors in response to visual stimuli rapidly approaching the body or to air puffs directed to single bodily regions (Graziano et al. 2002; Cooke and Graziano 2003). These authors also found that the electrical stimulation of the ventral intraparietal area (VIP) and of a polysensory area in the precentral gyrus (PZ) elicits a set of defensive behaviors, such as squinting, ducking and blocking, as if the monkey was defending the portion of the body that is spatially coded by the stimulated neurons. These findings suggest that areas VIP and PZ could represent the neural substrate that coordinates defensive responses by maintaining a sort of safety barrier around the body (Graziano et al. 2002; Graziano and Cooke 2006). A recent study in humans also supports the existence of a hand-centered coding system of the visual space in humans, where approaching objects can rapidly modulate corticospinal excitability in hand-centered coordinates (Makin et al. 2009). This mechanism may allow anticipating the impact of approaching objects as if peripersonal space acted as a protective safety barrier to incoming threats (Cardinali et al. 2009a).

Given the plasticity of peripersonal space for action, as shown in the case of tool use, the present work investigates whether also the boundaries of such a "safety barrier" may be dynamically modulated by tool use experience. Notwithstanding the critical importance of the defensive role assumed by the peripersonal space, this issue has not yet been investigated. To this aim, we first assessed the spatial organization of automatic, physiologic responses to the vision of approaching noxious stimuli by measuring the Skin Conductance Response (SCR), and then we assessed the possibility of modulating the spatial pattern of such responses following tool use.

The SCR is a measure of the electrical conductance of the skin due to sweating and represents a reliable, direct measure of sympathetic nervous system activation following psychological or physiological arousal (Mordkoff et al. 1967; Deltombe et al. 1998). When the body is threatened by an incoming dangerous stimulus, the SCR can be used as a measure of fear and pain anticipation (Armel and Ramachandran 2003; Hägni et al. 2008; Guterstam et al. 2011). Furthermore, previous evidence has showed that SCR increases in response to affective stimuli (Armel and Ramachandran 2003; Forgiarini et al. 2011), pain perception (Rhudy et al. 2009; Williams and Rhudy 2009; Romano et al. 2014b) and cognitive conflict (Kobayashi et al. 2007). In particular, here we adopted a protocol recently designed to elicit reliable anticipatory responses to the vision of threatening stimuli approaching the body (Romano et al. 2014a; Romano and Maravita 2014). Using this paradigm we explored whether SCR to incoming threatening stimuli can be modulated by the expansion of peripersonal space boundaries that follows tool use. This occurrence would be an indication that the safety region surrounding our body has not a fixed extension, but can be plastically expanded following contingent experience.

2. EXPERIMENT 1

The aim of the first experiment is to uncover whether SCR anticipatory responses to approaching threatening stimuli depend upon the distance of the stimuli from the body. Since, traditionally, studies regarding the peripersonal space were conducted considering only the horizontal, radial dimension, while the peripersonal space also extends along the vertical axis, the latter axis was also considered in the present experimental paradigm. We expect larger autonomic responses as the needle approached the hand and the nearest positions, as compared to the middle and far positions, regardless of its direction (namely, no interaction between axis and stimulus distance).

2.1 MATERIAL AND METHODS

2.1.1. Participants

Fourteen right-handed participants took part in this experiment (4 males, mean age: 26±11). All participants gave written informed consent; they were naïve to the experimental procedure and to the purpose of the study and none of them reported neurological, psychiatric, or other relevant medical problems. The protocol was carried out in accordance with the ethical standards of the Declaration of Helsinki (BMJ 1991; 302: 1194) and was approved by the ethical committee at the University of Milano-Bicocca.

2.1.2. Experimental procedure

Participants sat on a chair in a floodlit room with the experimenter sitting in front of them. Two electrodes were attached on the middle finger and ring finger of left hand (Figure 1a) in order to record SCR, as described below. During the experiment, participants were asked to relax, and carefully fixate the approaching stimulus, namely a 4cm long medical needle. On each trial, the experimenter manually moved the stimulus from behind the table (where it was invisible to the participant) towards the hand, in four spatial conditions: 1) touch, the needle eventually touched the right index fingertip; 2) near 1cm, the needle placed at 1cm from the fingertip; 3) near 5cm:

the needle placed at 5cm-distance from the finger; 4) far 40cm: the needle at 40cm from the fingertip. The reliability of noxious stimuli to be considered as painful was validated by previous studies from other groups (Cheng et al. 2007; Höfle et al. 2012), and from our lab using the same stimulus set (i.e., Romano and Maravita 2014, Romano et al. 2014a; 2014b). Specifically we showed that when the needle was applied to the hand, the participant experienced pain, and showed reliable SCR, while control, neutral, non-painful tactile stimuli (cotton swab) do not induce pain experience nor any detectable SCR (Romano and Maravita, 2014). Hence, based on such previous evidence, here only painful stimuli, which proved to provide significant SCR, were used.[1] The painful stimulus was moved towards the hand along two directions (Figure 1b): horizontal (H) and vertical (V). In the H condition, the experimenter raised the needle for 2cm from the table, and then approached the table at the given radial distance from the hand for each trial, or touched the hand itself; in the V condition the needle was raised at 50cm above the hand, and then, once aligned with the hand, was manually lowered towards the hand, stopping at the given distance for each single trial, or touching the hand. Two rulers were fixed close to participants' hand, one for each axis, shielded from participants view by a cardboard box, and were used as reference for the stimulations by marking the four spatial distances upon them. The experimenter received a training in order to be able to deliver manually the stimuli at a speed as constant as possible. Eight blocks of stimuli were given, each comprising 8 trials, one for each distance and axis, for a total of 64 stimuli. Within every block of trials, the axis direction varied in a counterbalanced fixed order (HV or VH), while the spatial distance was randomly chosen. The total duration of the experimental session was about 30 min.

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[1] Additionally, in a pilot experiment (published in the PhD thesis of DR) the reliability of SCR as a measure of experienced pain was assessed.

Twenty noxious stimuli were given to 21 volunteers by means of the same needle used in the present study, while recording their SCR. Participants were asked to judge the unpleasantness and intensity of the stimulation through a scale ranging from 0 (no pain at all) to 10 (worst pain ever experienced). The response was given ten seconds after the stimulation to avoid affecting SCR. During the entire experiment the needle and the target hand were never visible to avoid contextual interference.

We tested in two separate models whether the SCR can predict the rating expressed for a specific stimulus, using an ANOVA with random effect (linear mixed model) design, that showed that the SCR predicts significantly both ratings: Intensity rating: $F=21.078$, $p<.01$, $r^2= .347$; Unpleasantness rating: $F=20.303$, $p<.01$, $r^2= .342$.

2.1.3. SCR Hardware and Software

SCR was measured through a SC-2071 device (Bioderm, UFI, Moro Bay, California, Figure 1a) following standard guidelines (Dawson et al. 2007). Two Ag–AgCl electrodes (1081FG Skin Conductance Electrode) with a constant voltage (.5 Volt) were attached to subjects' proximal phalanges of their left middle and ring fingers. Saline conductor gel was used to ensure adequate adherence and improve the signal-to-noise ratio. The SCR device was connected to a dedicated PC to digitalize data through the SC-2701 software. The gain parameter was set at 10 µSiemens (µS)/Volt, the A/D resolution was 12 bit, allowing to record responses ranging from .1 to 100µS, with a sample rate of 10Hz.

For each trial, the peak-to-base value was computed (Rhudy et al. 2010), namely the difference between the maximum value of SCR within a time window of 6 seconds post-stimulus (Forgiarini et al. 2011), and the average value of the 300-millisecond pre-stimulus interval (see Romano et al. 2014a; Romano and Maravita 2014).

Manual markers identifying each stimulus type were added to the SCR trace by the computer keyboard, at the moment that the stimulus became visible to the participant.

-Insert Figure 1 about here-

2.2. STATISTICAL ANALYSIS

Data were analyzed using Statistica for Windows (release 6.0, StatSoft). To verify whether a threatening stimulus induced a different pattern of activation due to its distance from the observer's body, the mean SCR values in the different experimental conditions were compared using a repeated-measure analysis of variance (rmANOVA), with 2 within subjects factors: axis (Horizontal/Vertical) and distance (touch, near 1cm, near 5cm, far 40cm). When appropriate, post-hoc comparisons were performed using the Fisher test. The effect size in the ANOVA were measured by calculating the partial Eta Squared (η^2), which measures the degree of association between an effect and the dependent variable, namely the proportion of the total variance that is attributable to a main factor or to an interaction (Cohen 1973).

2.3. RESULTS

The ANOVA showed a significant main effect of the factor axis ($F_{1,13}=8.35$, $p<.05$, $\eta^2=.39$): the SCR was overall higher when the stimulus moved along the vertical axis (.43μs ± standard error .09), as compared to the horizontal axis (.34±.08μs). Crucially, the main factor distance reached significance ($F_{3,39}=24.15$, $p<.001$, $\eta^2=.65$), showing that SCR was modulated by the distance of the needle from the observer's body (see Figure 2). Indeed, when the needle touched the subject's index finger, the SCR was significantly higher (.62±.1μs) as compared to all other conditions (1cm=.38±.08μs; 5cm=.32±.07μs; 40cm=.21±.04μs; all ps<.001). There was no difference between the two near conditions (i.e., stimulus presented at 1cm and at 5cm, p=.22). Instead, SCR was significantly lower when the needle was presented at 40cm from the body as compared with all other distances (all ps<.05). The axis by distance interaction did not reach significance ($F_{3,39}=.7$, $p=.5$, $\eta^2=.05$).

-Insert Figure 2 about here-

2.4. DISCUSSION

Experiment 1 shows that pain anticipatory responses depend on the distance of the threatening stimulus from the hand. First, we found an overall greater SCR when the stimulus was presented along the vertical axis. This result might be explained by the fact that stimuli delivered along this axis were closer to the rest of the body (e.g., head and trunk) and thus it could have increased the autonomic response to the threat.

Crucially, the more the painful stimulus approached the hand, the greater the SCR. The response was indeed maximal when the needle touched the hand, but it was also higher for the positions immediately near the hand (1cm, 5cm), as compared to the far distance (40cm).

Taken together, these results show that when a threatening stimulus enters into the space close to the hand, it increases the level of arousal in the observer.

3. EXPERIMENT 2

Experiment 2 tested the hypothesis that extending the reaching space by means of a motor training with a long tool increases the alert response to incoming noxious stimuli presented far away from the body, but close to the tool. Since in the previous experiment, the trajectory of the stimulus (along the vertical vs. horizontal axis) did not affect SCR as function of the distance of the stimulus from the body (i.e., no significant axis by distance interaction), in the following experiments only the horizontal (radial) axis was tested. We expected a different effect of the training for different distances of stimulation, namely an increased response to stimuli targeting the tip or middle part of the tool, but no increase, or else a decreased response due to habituation for stimuli targeting the hand or the nearest position.

3.1. MATERIALS & METHODS

3.1.1. Participants

Twelve right-handed participants took part in Experiment 2 (2 males, mean age: 24±6), after giving their informed consent (see Experiment 1).

3.1.2. Experimental procedure

Stimulus type, presentation and SCR recording were identical to Experiment 1, but now stimuli were only presented along the horizontal axis, while participants passively held a tool during the task (Figure 1c). The tool was a 45cm long wooden stick, with a diameter of 2.5cm. At the tip of the stick a 5cm long nail was placed, which made the tool useful to collect objects during the following training phase (see below). Stimulation conditions were identical to Experiment 1. However, since in Experiment 1 no difference was found between the two nearer (i.e., 1cm and 5cm) distances from the hand, now the nearest position was shifted from 1cm to 2cm from the hand (near condition), while the 5cm position was shifted at 20cm (medium condition). The latter spatial location was chosen in order to clarify whether the training with the tool induces a complete embodiment of the entire tool, or whether its effects are limited to the tip of the tool, which represents the active part of the tool, as proposed by attentional accounts of tool-use based modulation of peripersonal space (Holmes et al., 2004).

The far condition, with the 40cm distance, remained unchanged. Eight blocks of stimuli were given, each one containing one stimulus per condition, for a total of 32 stimuli.

To assess the effect of active tool use on SCR to approaching noxious stimuli, the task was delivered to subjects under two sessions, namely before (pre-training) and after a training during which the subjects were trained to use the held stick to act in the extrapersonal space (post-training).

3.1.2.1. Tool training

Following the procedure adopted in a previous study (Sposito et al. 2012), four different tool use tasks were used during the training in order to have participants performing a prolonged tool training, while avoiding a decrease of sustained attention due to habituation to a single task (Sposito et al. 2012). All subjects performed the training with their right hand.

Task 1: 15 polystyrene targets were placed at a distance of about 100 cm from the participant's body, featuring a well-visible colored number. On each trial, participants were instructed to pick one of the targets displaying a number written in the color named by the experimenter, using the nail fixed at the tool tip to target the correct trial at the center of a cross drawn on the top face of the target. Once they hooked the target they had to bring it close to the body, pick it up with the left hand and place it on a grid drawn on the table, at the spatial position displaying the same number. Participants were instructed to make a continuous, fluid movement and to place the arm back on the arm-rest placed on their right side, at the end of each trial.

Task 2: The procedure was similar to the previous task, but now, on each trial, participants were instructed to pick up the target objects displaying the number named by the experimenter and put them into one of two boxes placed on the table, depending on their odd/even status.

Task 3: Now the stick was used as a rake in order to retrieve the target objects. To this aim a 15 X 10 X 1cm plastic plate was fixed on the distal nail. The targets were placed close to the participant's body in a random order. Participants had to push the target cubes, starting from number 1, over a paper template, fixed on the table, displaying the numbers from 1 to 15 in a domino-like sequence. There was no time constraint, but participants were required to be as accurate as possible.

Task 4: During this task participants were blindfolded. The experimenter scattered the targets all over the table and participants were asked to explore the space in front of them, trying to retrieve the targets and move them close to their body midline, using the same rake-tool as in the previous task.

The four tasks were given in the fixed order described above. Each task lasted 5 minutes, for a total of 20 minutes of training.

3.1.3. STATISTICAL ANALYSIS

We analyzed the mean SCR (μs) via a two-way repeated-measure ANOVA with distance (touch, near, middle, far) and session (pre-training, vs post-training) as main factors, the partial Eta Squared (η^2) was calculated as measure of effect size. Then, for each spatial position, we calculated the difference (Δ) in SCR before and after the training (i.e., post-training minus pre-training values) to investigate the interaction between distances and training in an easier to read way. Post-hoc comparisons were performed using the Fisher test.

Furthermore, the confidence intervals (CI), (Cohen 1990, 1994; Masson and Loftus 2003; Cumming 2013) were used to explore effects on Δ SCR, setting at 95% the confidence level.

3.2. RESULTS

The ANOVA showed a significant effect of distance ($F_{3,33}$=13.762, $p<.01$ η^2=.43), and, of major interest for this study, a significant interaction of distance by session ($F_{3,33}$=4.568, $p<.01$ η^2=.29).

To better clarify the meaning of the significant interaction, Fisher post-hoc test was calculated for the Δ SCR. Post-hoc comparisons showed no significant differences (p=.85) between the SCR difference in the touch condition (ΔSCR -.16±.07μs) and the near condition (2cm= ΔSCR -.14±.06μs). Moreover, the SCR difference for the middle (20cm= ΔSCR .07±.08μs) and the far (40cm= ΔSCR .1±.06μs) conditions showed average positive values, and were significantly different from the touch and the near conditions (each p<.05).

Confidence Intervals (CIs) of the interaction showed a decrease of the SCR, after the training, for touch 95% CI [lower limit = -.311, upper limit =-.009], and near conditions [-.285, .001], and a tendency to increase in medium [-.098, .234] and far [-.046, .238] conditions.

-Insert Figure 3 about here-

3.3. DISCUSSION

Experiment 2 shows that the spatial pattern of SCR to noxious stimuli can be significantly altered by active tool use. After the training, there was no significant increase in SCR amplitude to a threatening stimulus presented near or on the hand: the slight reduction in SCR values, instead, hypothetically reflects habituation that normally affects galvanic responses for constant stimulation (Levinson and Edelberg 1985; Elie and Guiheneuc 1990). Conversely, a different pattern of SCR was found in the post-training session for the middle and far locations: in spite of the likely habituation process, a tendency to SCR increase was observed. A direct comparison between pre and post-training values at each position was not performed, since any increase at far positions may be masked by underlying habituation. However, the critical statistical interaction witnesses the different direction of the SCR pattern for touch and near conditions as compared to middle and far conditions, according to the working hypothesis. These results may indicate that, following the use of the rake, alertness responses to approaching stimuli expanded as to include all the space occupied by the tool.

4. EXPERIMENT 3

Experiment 3 aimed at investigating whether the increased SCR to far stimuli induced by tool-use is related to the presence of the tool itself during the testing session, or it can emerge even in its absence. The working hypothesis is that the absence of the tool may reduce, but not completely abolish, the autonomic response to the presentation of noxious stimuli to the spatial position occupied by the tool during the training, witnessing a change of representation of that space sector in the monitoring of incoming threat, partially independent from the saliency of the tool as an attention capturing object.

4.1 MATERIALS & METHODS

4.1.1 Participants

Twelve naive participants took part in Experiment 3 (all right-handed, 5 males, mean age: 25±6), giving their informed consent and according to international and local ethic standards (see Experiment 1).

4.1.2 Experimental procedure

The experimental procedure was the same outlined in Experiment 2. The only difference was that now the tool was held during the training only, while during the pre-training and post-training SCR recordings, participants were asked to keep the hand closed as if they were still grasping the tool, but the tool was not present.

4.2 RESULTS

Data were analyzed with the same statistical models used in Experiment 2.

The ANOVA on SCR showed a significant effect of the main factor distance ($F_{3,33}=27.503$, $p<.01$, $\eta^2=.61$), and the interaction distance by session ($F_{3,33}=6.025$, $p<.05$, $\eta^2=.35$).

The Fisher post hoc analysis of Δ SCR, highlighting the meaning of the significant interaction, showed that ΔSCR for touch condition was significantly different (ΔSCR -.21±.06 μs) from all the other conditions (2cm= ΔSCR -.09±.05 μs, $p<.05$; 20cm= ΔSCR -.02±.07 μs, $p<.01$; 40cm= ΔSCR .02±.03 μs, $p<.001$) which did not differ from themselves (each $p>.05$).

CIs of the interaction showed the smallest ΔSCR for touch condition [-.349, -.079], while ΔSCR in near [-.195, .025], medium [-.174, .132], and far [-.041, .089] conditions was always around 0.

-Insert Figure 4 about here-

4.3 DISCUSSION

Experiment 3 shows that, even in the absence of the tool, there is still a differential modulation of SCR habituation to incoming threats directed to the space occupied by the tool during the training between the hand and the extracorporeal positions. However, the difference between near and far positions was no more detectable, suggesting that the presence of the tool during the testing session enhances the modulation of visual responses to incoming stimuli targeting the far space.

5. EXPERIMENT 4

The last experiment aimed at confirming that the spatial remapping of SCR depends on the active use of the tool during the training, rather than on a pure attentional effect due to the prolonged monitoring of far positions for task execution. Hence we recorded SCR before and after the participants were submitted to an attentional training during which they passively held the tool but, critically, they did not use it. We predict that no difference between pre- and post training in spatial response to threatening stimuli should be induced.

5.1 MATERIALS & METHODS

5.1.1. Participants

Twelve naïve, right-handed participants took part in Experiment 4 (5 males mean age: 25±6), giving their informed consent (see Experiment 1).

5.1.2. Experimental procedure

The procedure was similar to that of Experiment 2, with the only difference that now the training did not require the use of the tool (Figure 1c). Participants were blindfolded and held the tool passively. The experimenter displaced only 14 out of 15 cubes on the table, in random order, at about 45cm away from the subjects. The blindfold was then removed, and participants were asked to report which one of the cubes was missing, after silently reading the number labeling each single cube. This procedure was repeated for 15 minutes.

5.2. RESULTS

Data were analyzed with the same statistical model used in Experiment 2 and 3. The ANOVA revealed a significant effect of distance ($F_{3,33}$=28.605, $p<.001$; η^2=.72), showing the same trend observed in Experiment 1. The main effect of session ($F_{1,11}$=7.363, $p<.05$; η^2=.40) showed that SCR was higher during pre-training session (pre-=.42±.38μs, post-=.31±.30μs). Differently from previous Experiments, and critical to our aim, the interaction distance by session did not reach significance ($F_{3,33}$=1.358, p=.28; η^2=.11). As shown in Figure 5, only an overall decrease in SCR emerged, likely due to habituation (touch=-.14±.08μs, near (2cm)=-.14±.06μs, medium (20cm)=-.04±.04μs, far (40 cm)=-.11 ±.05μs).

CIs show only an overall tendency to a decrease of SCR due to habituation: touch [-.335, .028], near [-.281, -.028], medium [-,127, .057], far [-.228, .000].

Insert Figure 5 about here

6.3. DISCUSSION

Experiment 4 shows that a task engaging attention at target locations in far space is not effective by itself in modifying the spatial pattern of anticipatory responses to approaching threatening stimuli. Although this result does not exclude a role of spatial attention in the effects induced by tool-training, which was shown to play a relevant role in tool-use effects (Holmes

2012; Holmes et al.,2007b), spatial attention cannot entirely explain the present results (see below). Here, what is observed is a general decrease of SCR, likely due to habituation, at all locations, exactly comparable to that found in Experiment 2 for the touch and near positions. The present experiment, therefore, suggests the importance of active tool use for the modulation of visual responses in the peripersonal space.

7. GENERAL DISCUSSION

The present work provides two main findings. First, it shows that physiological, anticipatory responses to the sight of a threatening, noxious stimulus approaching the observer's body depend on the distance of that stimulus from the body. Second, the spatial constrains of such anticipatory responses can be dynamically shaped, following the use of a tool that extends the space of action.

In particular, Experiment 1 shows that the response to noxious stimulation is highest when the stimulus actually touches the skin, however when the stimulus is close to the body, namely at 1cm and 5cm-distance, the SCR is still larger than those for stimuli at farther space (i.e., 40cm). This result clearly shows the existence of an area of space near the body, where threatening events are more likely to affect the observer's arousal level. Recent findings using the same paradigm in humans, confirm the result of a reliable anticipatory response to approaching noxious stimuli that do not touch the skin, likely related to the cognitive, emotional anticipation of threatening stimuli targeting one's own body (Romano et al. 2014a; Romano and Maravita 2014). This is reminiscent of evidence showing that somatosensory stimuli hitting the monkey's skin elicit avoidance movements, as recorded both at electromiographic and behavioral level (Cooke and Graziano 2003). These responses may reflect an automatic defensive reaction to potentially dangerous stimuli, likely mediated by the intraparietal VIP area and the premotor PZ area (Graziano et al. 2002; Cooke et al. 2003).

In this context, the present results are compatible with the existence of an area of safeguard in humans, which is close to the body and is reminiscent of the "flight zone" described by Hediger (1955; Graziano and Cooke 2006). Such a spatial system for coding approaching threats may be useful for preparing defensive responses for protecting one's own body, or for triggering prosocial behavior when others are in dangerous situations (Bufalari et al. 2007; Forgiarini et al. 2011).

A second novel finding is that, in humans, the spatial extension of such a protective space area is not fixed, rather it can be expanded by active tool use. As shown in Experiment 2, after a training with a tool expanding the reachable space far from the body, SCR to far extra-personal threatening stimuli changes its pattern, contrasting the rapid SCR habituation that typically affect SCR following repeated stimulations (Levinson and Edelberg 1985; Elie and Guiheneuc 1990).

Previous works showed the modulation of the response to visual non-painful stimuli in the peripersonal space, following tool use in monkeys (Iriki et al. 1996; Maravita and Iriki 2004) and in humans (Berti and Frassinetti 2000; Làdavas and Farnè 2004; Maravita and Iriki 2004). Longo and Lourenco (2006) reported that when performing a line bisection task, participants committed a rightward error which was progressively larger going from near (30cm) to far (120cm) space, suggesting the existence of a gradual shift of space representation from near to far space (Cowey et al. 1998). Critically, the spatial boundary between near and far space could be shifted more distally by the use of a long tool (Longo and Lourenco 2006). This reshaping of visual spatial processing in peripersonal space has been shown to be paralleled by a change in the brain representation of the body metrics, compatible with an extension of perceived arm length following tool-use (Cardinali et al. 2009b; Cardinali et al. 2011; Sposito et al. 2012). The present work goes beyond such previous results by showing that the use of a tool also plastically expands the space at which approaching threats induce an alert, protective response.

The modification of the body representation by tool use may represent a process of embodiment of the used tool, hence the acquisition of the tool as a functional extension of the body for perception and action (de Vignemont 2011). This process would bias both perceptual processing of stimuli delivered near the tool (Berti and Frassinetti 2000; Farnè and Làdavas 2000; Maravita et al. 2002a), as well as the kinematic parameters of reaching actions, which have been shown to change compatibly with a brain representation of a longer arm (Cardinali et al. 2009b), and the spatial range of alertness reactions to incoming stimuli, as shown here. The spatial reshaping of visual responses, therefore, brings along both perceptual and affective components of sensory processing, qualifying as a form of sophisticated and multi-componential plasticity of space processing that can be dynamically modulated by contingent factors.

In addition to the spatial modulation of alert responses, one may also speculate that a process of embodiment of the tool itself may occur, that extends to the affective domain (de Vignemont 2011), thus making the tool sensitive to the same anticipatory, protective physiological reactions that are usually produced to safeguard real body parts, or embodied fake body parts (Armel and Ramachandran 2003; Ehrsson et al. 2007; Hägni et al. 2008; Guterstam et al. 2011). Yet, previous studies in animals suggest that the feeling of care for an external object seems to be excluded when a tool is used (Povinelli et al. 2010). Povinelli and colleagues (2010) observed that chimpanzees did not develop any affective representation of the tool they were trained to use: under uncertainty, they always preferred to use the rake instead of their hand, avoiding exposing their body to a possible dangerous situation. However, a critical difference between the above reported studies in animals, and human studies showing emotional responses to alien objects (Armel and Ramachandran 2003; Ehrsson et al. 2007; Hägni et al. 2008; Guterstam et al. 2011) is that the experimental paradigms used in humans are typically designed to increase the sense of ownership of the alien objects, at odds with those in monkeys, which were actually allowed to choose between exposing their body or the object to a dangerous situation. In this respect, the novelty of the present study is that a putative affective embodiment was induced using an external object, which did not resemble a body part. Using an object to carry out some tasks seems to generate an affective bond with the object itself: when the tool is under menace it elicits a rapid warning response, analogous to those displayed when our own body is threatened. This finding would be crucial for research on brain augmentation devices (Di Pino et al. 2014) or prosthetics for amputees (Romano et al. 2014c). Indeed, ideal functional augmentation devices maybe charged of a sense of protection and emotional monitoring, besides their critical sensorimotor function (see Di Pino et al. 2014; Marini et al. 2014), body-space integration, as a complete and deep process of embodiment.

Along this line, the results of Experiment 3, showing only a general reduction of habituation between the hand and the extracorporeal positions, without a clear difference between near and far positions, may suggest that the presence of the tool in the visual scene increases the affective component of space monitoring, thus driving stronger anticipatory responses at spatial positions where the tool body moves and the tool tip operates.

An alternative (or additional) explanation for our results would be that the training with the tool has induced a shift of spatial attention from the effector to the tip of the tool (Holmes et al. 2004; Holmes et al. 2007b), more than an expansion of the visual responses across the peripersonal space, up to the far space. However, it is worth noting that our results do not fully support a sheer attentional account: although spatial attention takes part in the effects caused by tool training (Holmes et al. 2004; Holmes 2012), our data support the idea that SCR changes cannot be caused exclusively by spatial attention. First, because the critical change in SCR values were found not only at the tip of the tool, but also along the tool shaft as compared to touch and near condition in Experiment 2, as predicted by an attentional account (Holmes 2012); second, the results of Experiment 4 suggest that a pure attentional task does not lead to a distance-dependent change in the arousal responses, as compared to the critical active tool use task. One way in which the tool may drive the participant's attention is by its mere presence on the visual scene at the time of testing, as shown by Experiment 2. However, the purposeful, active use of the tool seems necessary to induce a change of arousal responses in extra-personal space.

It is worth mentioning, the anticipatory arousal response to incoming threats is a complex function that can be actively modulated by several factors that goes beyond tool use effects, like individual differences in emotional control of noxious stimuli (Rhudy et al. 2008), individual expertise in anticipating sensory stimuli (Cheng et al. 2007), or feeling of ownership for one’s own body (Romano et al. 2014a), suggesting for a complex relation between the representation of the self, the peripersonal space and the emotional valence of incoming stimuli (de Vignemont 2011).

In conclusion, the use of a tool to operate in extra-personal space not only expands the visual properties of the space surrounding our body, but the affective and defensive monitoring of the peripersonal space, in line with the key relevance of this sector of space for survival.

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Captions to figures

Figure 1. Equipment and Setting. Equipment and set up used for collecting the Skin Conductance Response (SCR). A) The biosignal amplifier was connected to a dedicated PC through a parallel port; the transducers (two passive Ag-AgCl electrodes) were applied to the first phalanx of the ring and the middle finger of the left hand. B) In Experiment 1 SCR was recorded in response to a needle presented at different distances. SC was collected in one session at four distances (touch, 1cm, 5cm, 40cm) along two different axes (horizontal/vertical) to establish the gradient of response in the peripersonal space. Here the horizontal axis is displayed. C) In Experiments 2 and 4 SC responses were collected at different distances, while participants held the tool in the right hand. In both experiments there were two sessions (pre/post training) and four distances (touch, 2cm, 20cm, 40cm) in order to investigate any modulation of the peripersonal space gradient response due to active trainings. Specifically in Experiment 2 we tested the effect of motor training using a 40cm long tool, while in Experiment 4 we aimed to verify the effect of attentional training in the same space sector as that involved in the tool training (see text for details). In Experiment 3 SCR was collected for the same stimulation of Experiments 2 and 4, but the tool was removed during the measurement phases.

Figure 2. Experiment 1: Results. Participants' response changed due to the distance of the needle from the hand. The Skin Conductance peak to baseline index was used as index of the SCR. Columns represent mean SCR, bars indicate the standard error and asterisks highlight significant differences.

Figure 3. Experiment 2: Results. Changes of SCR evoked by the approaching needle following tool training, at the four tested distances along the tool. Upper-side: columns represent the mean peak to base index of SCR (dark grey: mean SCR values for the pre-training sessions; light grey: mean SCR values for the post-training sessions). Lower-side: columns represent mean difference in the peak to base index of the SCR between post and pre training measurements (ΔSCR= post minus pre). Bars indicate standard errors and asterisks show significant differences.

Figure 4. Experiment 3: Results. Changes of SCR evoked by the approaching needle following tool training, without the presence of the tool during the exposure to the threat. Upper-side: columns represent the mean peak to base index of SCR (dark grey: mean SCR values for the pre-training sessions; light grey: mean SCR values for the post-training sessions). Lower-side: columns represent mean difference in the peak to base index of the SCR between post and pre training measurements (ΔSCR= post minus pre). Bars indicate standard errors and asterisks show significant differences.

Figure 5. Experiment 4: Results. Effects of the attentional training in the same space sector as that involved in the tool-use on the SCR to the approaching needle. Upper-side: columns represent the mean peak to base index of SCR (dark grey: mean SCR values for the pre-training sessions; light grey: mean SCR values for the post-training sessions). Lower-side: columns represent mean difference in the peak to base index of the SCR between post and pre training measurements (ΔSCR= post minus pre). Bars indicate standard error.

Figure 1

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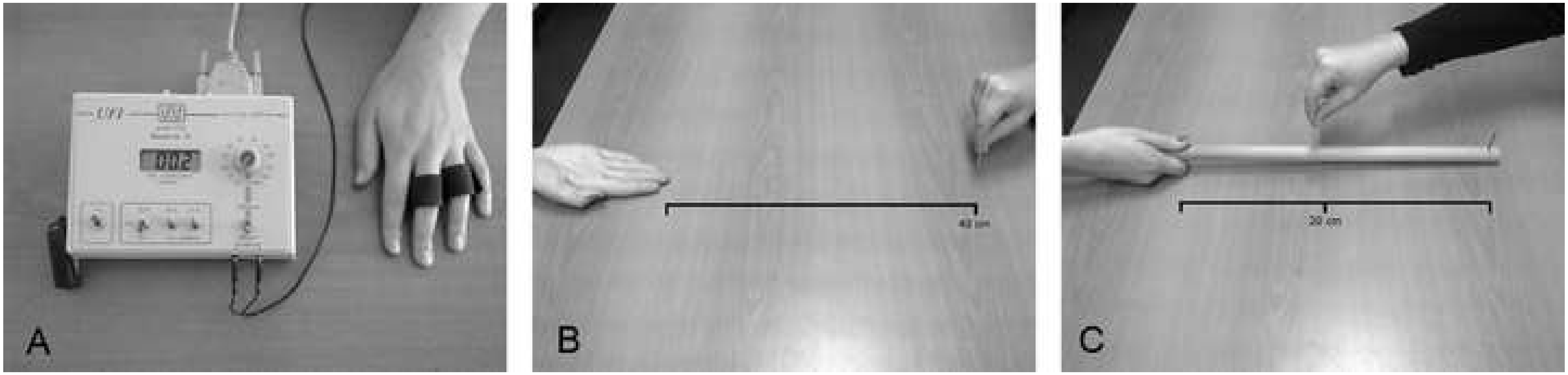

Figure 2

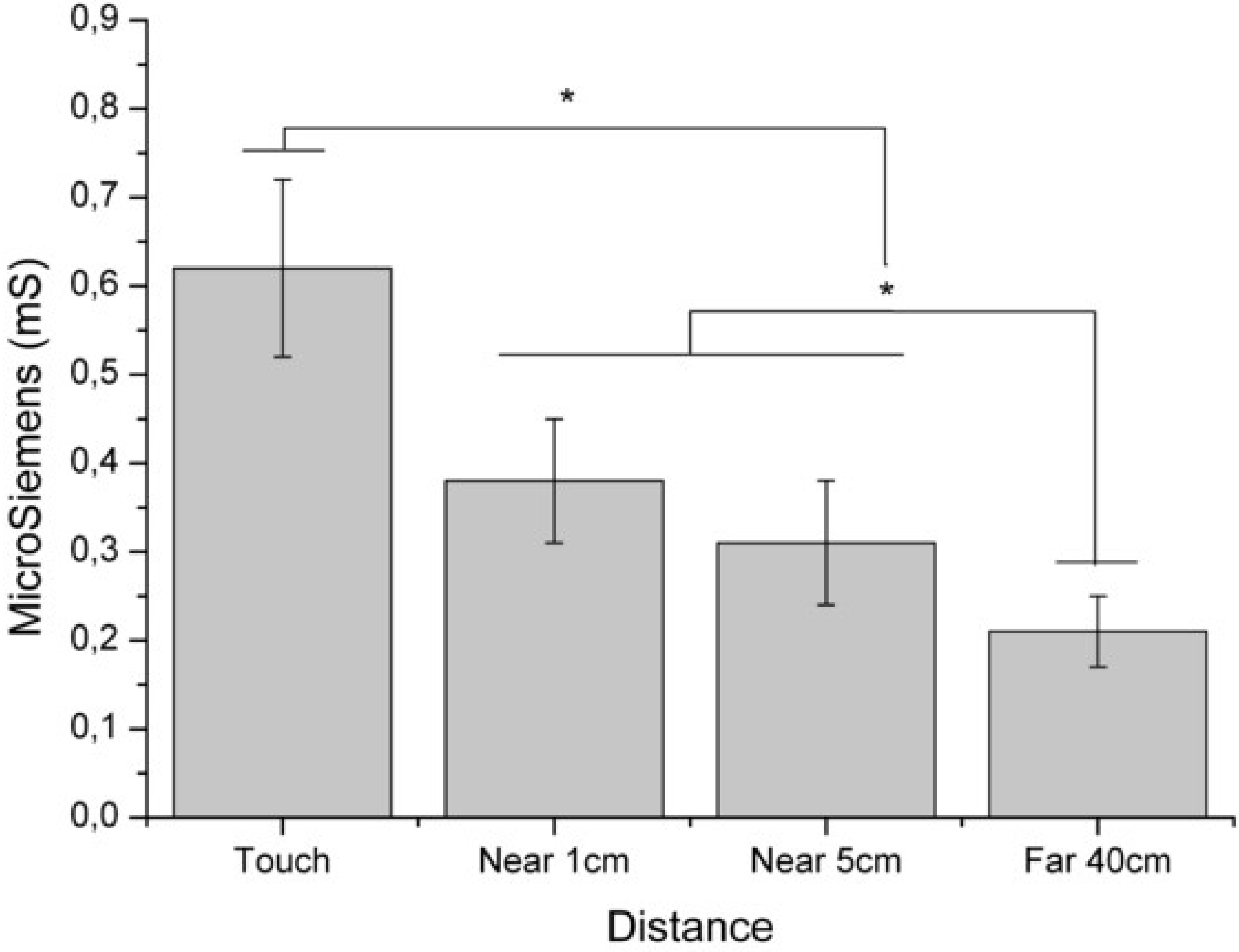
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Figure 3

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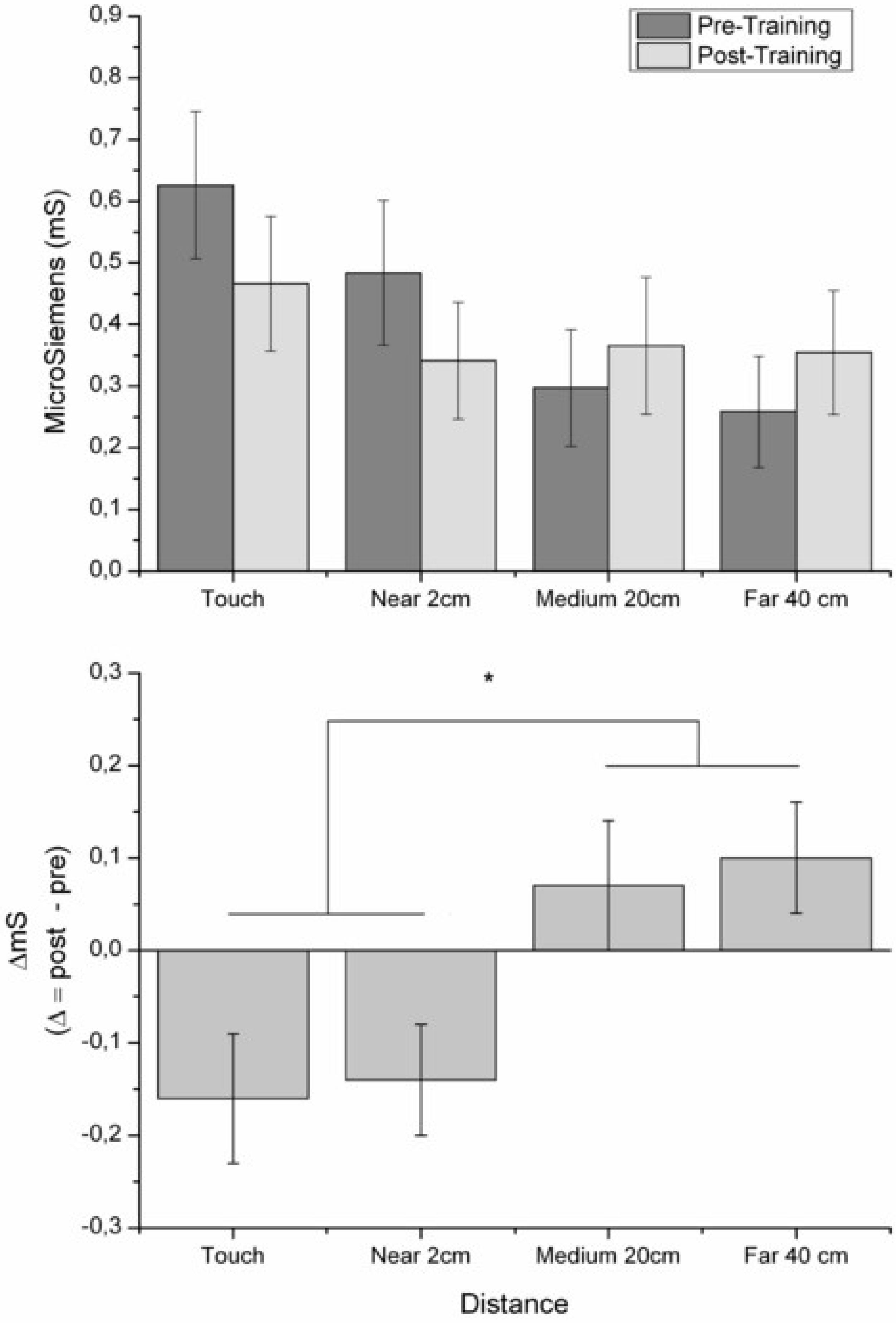
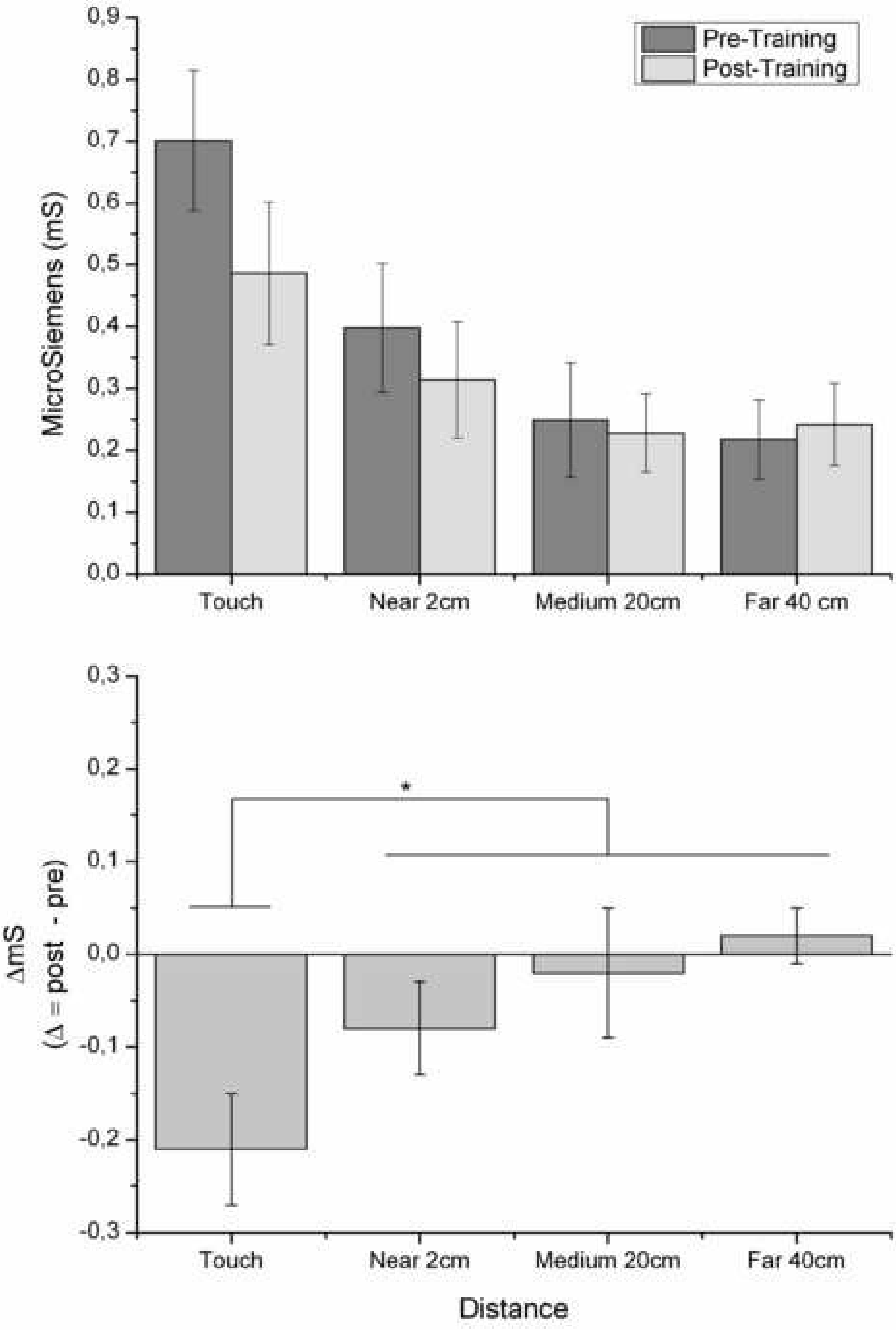


Figure 4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ΔmS
(Δ = post - pre)
Touch
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Far 40cm
Distance

Figure 5

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