



THE UNIVERSITY *of* EDINBURGH

Edinburgh Research Explorer

Tool use modulates early stages of visuo-tactile integration in far space

Evidence from event-related potentials

Citation for published version:

Forsberg, A, O'Dowd, A & Gherri, E 2019, 'Tool use modulates early stages of visuo-tactile integration in far space: Evidence from event-related potentials', *Biological Psychology*, vol. 145, pp. 42-54.
<https://doi.org/10.1016/j.biopsycho.2019.03.020>

Digital Object Identifier (DOI):

[10.1016/j.biopsycho.2019.03.020](https://doi.org/10.1016/j.biopsycho.2019.03.020)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Peer reviewed version

Published In:

Biological Psychology

General rights

Copyright for the publications made accessible via the Edinburgh Research Explorer is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

The University of Edinburgh has made every reasonable effort to ensure that Edinburgh Research Explorer content complies with UK legislation. If you believe that the public display of this file breaches copyright please contact openaccess@ed.ac.uk providing details, and we will remove access to the work immediately and investigate your claim.



Tool Use Modulates Early Stages of Visuo-Tactile Integration in Far Space: Evidence from event-related potentials

Alicia Forsberg*, Alan O'Dowd* & Elena Gherri

**Human Cognitive Neuroscience, Psychology,
University of Edinburgh, UK**

***These authors contributed equally to this work.**

Corresponding author:
Dr. Elena Gherri
Department of Psychology
The University of Edinburgh
7 George Square
Edinburgh EH8 9JZ
Tel.: +44 (0)131 650 3340
E-mail: elena.gherri@ed.ac.uk

Abstract

The neural representation of multisensory space near the body is modulated by the active use of long tools in non-human primates. Here, we investigated whether the electrophysiological correlates of visuo-tactile integration in near and far space were modulated by active tool use in healthy humans. Participants responded to a tactile target delivered to one hand while an irrelevant visual stimulus was presented ipsilaterally in near or far space. This crossmodal task was performed after the use of either short or long tools. Crucially, the P100 components elicited by visuo-tactile stimuli was enhanced on far as compared to near space trials after the use of long tools, while no such difference was present after short tool use. Thus, we found increased neural responses in brain areas encoding tactile stimuli to the body when visual stimuli were presented close to the tip of the tool after long tool use. This increased visuo-tactile integration on far space trials following the use of long tools might indicate a transient remapping of multisensory space. We speculate that performing voluntary actions with long tools strengthens the representation of sensory information arising within portions of space (i.e. the hand and the tip of the tool) that are most functionally relevant to one's behavioural goals.

Keywords:

Visuo-tactile integration, near/far space, tool use, Event-Related Potentials

1. Introduction

To facilitate everyday interaction with a complex and ever-changing world, the primate brain constructs distinct representations of the surrounding space which are defined by their relative proximities to the body. There is evidence that the processing of sensory information arising from the space within reach of the body, termed peripersonal space (Rizzolatti, Fadiga, Fogassi, & Gallese, 1997), is enhanced to facilitate both the rapid detection of potential threats to the body (Graziano & Cooke, 2006; Sambo & Iannetti, 2013) and the execution of actions towards reachable objects (Brozzoli, Cardinali, Pavani, & Farnè, 2010; Làdavvas & Serino, 2008). Early neurophysiological work with non-human primates suggested that peripersonal space is encoded by a specific population of visuo-tactile neurons located in the ventral premotor cortex, intraparietal sulcus and putamen (e.g. Graziano & Gross, 1993; Gross & Graziano, 1995). The visual receptive fields of these bimodal neurons are anchored to a specific body part (e.g. the hand) so that when this body part moves, visual and tactile receptive fields shift in parallel while remaining in spatial register with each other (Fogassi, Gallese, Fadiga, Luppino, Matelli, & Rizzolatti, 1996; Graziano, Yap, & Gross, 1994; Rizzolatti et al., 1997). Because these neurons respond robustly to visual stimuli presented close to – but not far away from – the relevant body part, their activity defines the boundary of the multisensory peripersonal space. Intriguingly, this boundary exhibits a degree of plasticity in response to an individual's experience, as first evidenced in a seminal study by Iriki, Tanaka and Iwamura (1996). These researchers trained macaque monkeys to utilise a rake with the goal of retrieving food pellets located beyond reach of the monkey's hand whilst concurrently recording the electrical activity of visuo-tactile neurons encoding peripersonal space within the intraparietal sulcus. Following repetitious tool use, the visual receptive fields of these bimodal neurons were physically elongated, suggesting that the representation of peripersonal space had extended so as to encompass the newly accessible space and the target objects as well as the entire length of the manipulated tool (Iriki et al., 1996; see Maravita & Iriki, 2004 for a review; however, note that Iriki et al.'s (1996) conclusions rely exclusively on qualitative data; quantitative evidence for neurophysiological changes in neuronal structure post tool-use is, to the authors' knowledge, non-existent).

The idea of a plastic representation of near peripersonal space is further supported by converging neuropsychological and behavioural evidence in humans. For example, patients

with crossmodal extinction often fail to report a contralesional tactile stimulus when presented simultaneously with an ipsilesional visual stimulus (e.g. Heilman, Bowers, Valenstein & Watson, 1993). The severity of visuo-tactile extinction is determined by the spatial separation between visual and tactile stimuli as shown by reduced extinction deficits when the visual stimulus is presented in far as compared to near ipsilesional space (Làdavas, Di Pellegrino, Farnè, & Zeloni, 1998; Làdavas, Zeloni, & Farnè, 1998). Importantly, the extinction deficit worsens again when the visual stimulus is presented in far space but close to the tip of a tool after it was actively used (Berti & Frassinetti, 2000; Farnè, Iriki, & Làdavas, 2005; Farnè, Serino, & Làdavas, 2007; Maravita, Husain, Clarke, & Driver, 2001). Thus, the active manipulation of tools can affect the core multisensory mechanisms that define the representation of peripersonal space in the brain.

In healthy humans, systematic evidence for the effect of tool use on visuo-tactile peripersonal space is provided by behavioural studies employing the visuo-tactile crossmodal congruency task (hereafter referred to as the CCT) which measures the influence of task-irrelevant visual stimuli on the localization of touches delivered to the hand (Maravita, Spence, & Driver, 2003; Spence, Pavani, & Driver, 2004a; Spence, Pavani, Maravita, & Holmes, 2004b). Specifically, participants make an elevation discrimination of a tactile target presented to one hand (at a top or bottom location) while a simultaneous visual distractor is presented from the same or opposite elevation. Responses to tactile targets are typically faster and more accurate when task-irrelevant distractors are presented at congruent than incongruent vertical locations. The magnitude of this crossmodal congruency effect (CCE) changes as a function of the horizontal spatial separation between tactile and visual stimuli, with larger CCEs when visual distractors are located close to the tactually stimulated hand and smaller effects when the distractors are presented farther away, thus providing a behavioural measure of the strength of the visuo-tactile interactions in near and far space (see for example Maravita & Iriki, 2004; Maravita et al., 2003; Spence, 2011, for reviews). Importantly, behavioural studies have also provided consistent evidence that far-space visual stimuli can also interact strongly with touches to the hand when presented on or around the tips of actively manipulated tools, confirming that tool use modulates the multisensory dynamics of peripersonal space as measured by the CCT (e.g. Bassolino, Serino, Ubaldi, & Làdavas, 2010; Berti & Frassinetti, 2000; Farnè et al., 2007; Holmes, Calvert, & Spence, 2004; Maravita, Spence, Kennett, & Driver, 2002; Maravita et al., 2003).

The fact that stronger visuo-tactile interactions are typically observed in near (peripersonal) space than in far space is in line with the canonical spatial rule of multisensory

integration, which specifies that independent sensory signals from different modalities are more likely to be integrated if they arise from the same location in space (Holmes & Spence, 2005; Meredith & Stein, 1986; Stein, Huneycutt, & Meredith, 1988; Stein & Meredith, 1990; Valdès-Conroy, Sebastià, Hinojosa, Romàn, & Santaniello, 2014). In contrast, the presence of stronger visuo-tactile interactions in far space following the use of tools clearly defies this multisensory integration rule, given that the presence of tools does not change the physical location of far-space visual stimuli which remain distal to the body. Thus, tool use appears to revise the principles under which crossmodal interactions typically occur in space.

The behavioural evidence for increased visuo-tactile interactions in far space following tool use is often interpreted as an expansion of peripersonal space boundaries around the actively manipulated tool, in line with the neurophysiological recordings by Iriki and colleagues (1996). However, the idea of an extension of near peripersonal space after tool use is only one of the possible interpretations of the existing evidence in humans (e.g. Holmes et al., 2004; Holmes, Sanabria, Calvert, & Spence, 2007b). While there are impressive analogies between the results of single cell recordings in monkeys and behavioural studies of both neurotypical and neurologically-impaired humans regarding the interplay between peripersonal space and tool use, it is problematic to directly collate these findings due to the different level of information that these methodologies can provide (see Quinn et al., 2014 for a recent discussion of the gap between behavioural and neurophysiological work in the context of visuo-tactile integration). Surprisingly, despite the increasing number of behavioural studies demonstrating tool-induced changes in visuo-tactile interactions in near and far space (see Spence, 2011, for a recent review), the neural mechanisms underlying this effect remains scarcely investigated in healthy humans (but see Holmes, Spence, Hansen, Mackay, & Calvert, 2008, for a neuroimaging study on the effect of tool use on visuo-tactile integration).

The purpose of the present study was to investigate the effect of tool use on visuo-tactile interactions in near and far space with electrophysiological measures. Event-Related Potentials (ERPs) can track the effect of tool-use with high temporal resolution, and thus provide direct evidence relative to the specific processing stage(s) during which modulations of visuo-tactile integration by tool use occur. Importantly, existing ERP evidence has shown systematic differences between visuo-tactile integration in near and far space (Sambo & Forster, 2009). Their participants were instructed to respond to tactile targets to the attended hand whilst ignoring touches to the unattended hand. On each trial a task-irrelevant visual

distractor was presented simultaneously with the tactile target, either within near or far space. Responses to tactile targets were faster when visual distractors were presented in near than in far space. In addition, ERPs elicited by these visuo-tactile stimuli were characterized by enhanced somatosensory P100 components when the simultaneous visual distractors were presented in near than in far space, irrespective of which hand was attended (see also Mahoney et al., 2015; Piesco, Molholm, Sehatpour, Ritter, & Foxe, 2005; Schürmann, Kolev, Menzel, & Yordanova, 2002, for other studies investigating the additive properties of visuo-tactile stimuli with ERP measures). In line with the spatial rule of multisensory integration, these findings suggest that tactile processing within somatosensory areas is modulated by crossmodal interactions with vision, with stronger behavioural and electrophysiological responses when visual and tactile stimuli are presented within near peripersonal space (i.e. are spatially congruent).

Based on the task used in Sambo and Forster's study (2009), which provided reliable electrophysiological measures of visuo-tactile integration in near and far space, we developed a non-spatial visuo-tactile cross-modal task. In the present study, participants responded to the identity of a tactile target (single or double tap) delivered to the left or right hand while ignoring a simultaneous double or single flash of light from a visual distractor (a set of LEDs) presented on the same side of spaceⁱ, either next to the stimulated hand (i.e. in near space) or beyond peripersonal space boundaries, in far space (see Figure 1, right panel; hereafter referred to as the non-spatial CT). To test whether tool-use modulates multisensory integration, participants completed a short motor task (20 trials) using long or short tools (see Figure 1, left top and bottom panels) before each block of the non-spatial CT, pressing a left or right key with the ipsilateral tool in response to an auditory stimulus. While tool use was involved in both forms of motor training, the active use of short tools (*control condition*) to reach response keys in near space was not expected to extend reachable space (indeed, the same action could have been performed without tools). In contrast, long tools allowed for the physical extension of reachable space into far-space where the response keys were located (*experimental condition*).

To investigate the effect of tool use on visuo-tactile integration, we compared ERPs elicited by visuo-tactile stimuli on near and far space trials in the crossmodal task as a function of tool type (long vs. short tools), specifically focusing on modulations of visuo-tactile processing within somatosensory areas where crossmodal spatial effects have been observed in previous electrophysiological studies (e.g. Sambo & Forster, 2009). Following

the active use of short tools (control condition), we expected to observe faster responses and enhanced somatosensory processing during early stages of processing when visual and tactile stimuli were presented in near than in far space in line with the spatial rule of multisensory integration and similar to previous studies without tools (e.g. Sambo & Forster, 2009). If the use of long tools (experimental condition) induces a remapping of the space near the hand, visual distractors presented in far space should be represented as if they were close to the tactually stimulated hand, resulting in stronger visuo-tactile integration.

2. Method

2.1. Participants

Twenty-nine paid volunteers gave informed consent to participate in the experiment. Five were excluded from the analysis due to an insufficient number of trials after artefact rejection (less than 50% of the trials remaining) and one due to poor performance in the behavioural task (less than 65% of correct trials). The 23 remaining participants (11 male, 12 female; average CT accuracy 90%, range 74 - 99%), aged between 19 and 35 years (average age = 26.0), were all right-handed and reported having normal or corrected-to-normal vision. The study was approved by the Psychology Research Ethics Committee at the University of Edinburgh.

2.2. Stimuli and Apparatus

Participants sat at a table in a dimly lit, sound-attenuated experimental chamber. Four ensembles of green LEDs, used to present visual stimuli, were mounted on a custom made cardboard panel (59.5 cm x 84.0 cm) secured to the table. Each of these ensembles was composed of nine circular segments (each 0.5 cm) arranged in a square (side: 1.7 cm x 1.7 cm, three segments on three rows) and fixed on a black cube (side: 3.2 cm). Two green plastic toy golf clubs were positioned on this board so that two of the LEDs were located next to the tools' handles (near LEDs) while the other two were positioned next to the tools' tips (far LEDs), see Figure 1 (right panel). The horizontal distance between the left and right LEDs was 35 cm, while near and far LEDs on the same side were 44 cm apart. A white fixation circle (0.4 cm diameter) positioned equidistantly from the four LED ensembles was used as a fixation point. Tactile stimuli were presented using 12-V solenoids, driving a metal rod with a blunt conical tip. The solenoids were attached to the radial side of the middle phalanx of the index fingers with white medical tape. Whenever a current was passed through

the solenoids, the tip made contact with the finger. White noise (65 dB SPL) was presented throughout the non-spatial CT to mask any sound made by the tactile stimulators.

During the non-spatial CT long tools were always placed on the board in front of the participants regardless of the specific type of training performed (long vs. short tools) and participants rested their hands on the handles of these golf clubs, as if holding them. By using an identical set-up following both long and short tool training we eliminated the possibility that differences in performance on the non-spatial CCT following training were simply due to the physical presence of different types of tools (long vs. short) in front of the participants. The distance between the participants' index fingers was approximately 40 cm and their hands were placed about 20 cm in front of the near edge of the table. Two loudspeakers positioned beyond the board (90 cm away from the table edge) were used to present auditory stimuli during the tool training. An infrared camera was used to monitor participants during the experiment.

In the non-spatial CT, a bimodal visuo-tactile stimulus was presented (200 ms duration) on each trial. The task relevant tactile stimulus was either a *single tap* (the rod continuously contacting the skin for 200 ms) or a *double tap* (skin contact interrupted for 100 ms after a duration of 50 ms), presented to their right or left index finger, simultaneously with an irrelevant visual distractor; either a single flash (200 ms illumination of one of the four LED lights) or a double flash (the illumination was interrupted for a period of 100 ms after a 50 ms period). Participants responded to the identity of the tactile stimuli by pressing one of two foot-pedals, positioned under the heel and the toes of the same foot (bottom and top pedals, respectively).

In the *tool training*, a sound file (either a high pitch or a low pitch sound) was played at the beginning of each trial (50 ms duration, 65 dB SPL). Participants responded to the pitch of the auditory stimulus by pressing a left or right target key (keys 1 and 5, respectively, of the Serial Response Box, Psychology Software Tools, Inc.) with long or short tools in different blocks of trials. The long tools were the previously mentioned toy golf clubs (66 cm long), while the short tools consisted of toy golf club handles (12 cm long). The target keys were positioned close to the near visual distractors (and the hands) in the short tool training and close to the far visual distractors (and the tip of the tools) in the long tool training, see Figure 1 (left top and bottom panels). Tactile, visual, and auditory stimuli were presented electronically using E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA).

2.3. Procedure

The experiment consisted of 16 blocks (each consisting of 96 trials) of the *non-spatial CT*. Each one of these blocks was preceded by 20 trials of *tool training*. Before starting the experiment, each participant completed 40 practice trials of the visuo-tactile task, to ensure that they understood the task and could distinguish between the single and double taps.

2.3.1. Tool Training

During the tool training, participants hit the left target key with the left tool (operated by the left hand) in response to a high-pitched tone, or the right target key with the right tool (operated by the right hand) for a low-pitched tone. Each block of tool training consisted of 20 trials (10 requiring a left tool movement and 10 requiring a right tool movement) presented in random order. Participants completed eight consecutive blocks of tool training (each followed by the corresponding eight blocks of the non-spatial CT) with a given tool length (either long or short tools, see Figure 1, left top and bottom panels), before performing the remaining eight blocks with the other tools. Tool order was counterbalanced across participants (half started with long tools and the other half started with short tools). Each trial of the tool training block started with the presentation of a sound followed by a 1500 ms interval used to record responses. The inter-trial interval was 300 ms. Participants were instructed to execute the tool movement as quickly and accurately as possible and to return their hand and the tool to the initial resting position after each movement.

2.3.2. Non-spatial Crossmodal Task

Each block of the tool training was followed by one block of the non-spatial CT (96 trials). On each trial, a task-relevant tactile target (single or double taps) was delivered with equal probability to the right or the left hand. A simultaneous task-irrelevant visual distractor (single or double LED light flashes) was presented randomly and with equal probability at one of the four possible locations (left or right, near or far, see Figure 1, right panel). Thus, on 48 trials per block tactile and visual stimuli were congruent (both single or both double) while on the remaining 48 trials they were incongruent (one stimulus was single and the other double). Following the 200 ms stimulus presentation, a 1200 ms interval was used to collect foot responses. The inter-trial interval (ITI) was randomly varied between 300 and 400 ms. Participants were instructed to keep their gaze on the central fixation point throughout each block. Their task was to respond as quickly and accurately as possible to single tactile stimuli with the top pedal and to double stimuli with the bottom pedal, while ignoring the visual stimuli. To avoid motor contamination of the visuo-tactile ERPs, the responding foot (left vs.

right) was counterbalanced within participants. After four consecutive blocks of the non-spatial CT the pedals were positioned under the opposite foot and participants were instructed to use the corresponding foot to respond (stimulus-response mapping was not changed). Thus, each participant completed four consecutive blocks of trials for the different combinations of tool length and responding foot (e.g. Short tool training – Right foot; Short tool training – Left foot; Long tool training – Right foot; Long tool training – Left foot).

2.4. EEG Recording, Pre-Processing and Data Analysis

EEG was recorded using a BIOSEMI system including 64 active electrodes (Fpz, Fp1, Fp2, AFz, AF7, AF3, AF4, AF8, Fz, F7, F5, F3, F1, F2, F4, F6, F8, FCz, FT7, FC5, FC3, FC1, FC2, FC4, FC6, FT8, Cz, T7, C5, C3, C1, C2, C4, C6, T8, CPz, TP7, CP5, CP3, CP1, CP2, CP4, CP6, TP8, Pz, P9, P7, P5, P3, P1, P2, P4, P6, P8, P10, POz, PO7, PO3, PO4, PO8, Oz, O1, O2, Iz) positioned according to the 10-20 placement system, distributed over the head surface in a cap fitted to each participant's head size. A total of six unipolar external electrodes were used. Two electrodes attached to the earlobes were used as offline references. The electrooculogram (EOG) was recorded from four facial electrodes: two were placed on the outer canthi of each eye to record horizontal eye movements (HEOG), and two were positioned above and below the right eye to record vertical eye movements (VEOG). The EEG and EOG were sampled at a 512 Hz digitization rate.

Off-line EEG data analysis was performed using Brain Vision Analyzer software, version 2.0.4.368 (Brain Products, Gilching, Germany). The bipolar EOG signal was computed offline by averaging the left and right facial electrodes for the HEOG and the top and bottom facial electrodes for the VEOG. EEG was digitally re-referenced to the average of the left and right earlobe, and was digitally filtered offline (high-pass filter 0.53 Hz, low-pass filter 40 Hz and notch filter 50 Hz). EEG was epoched into 600ms periods, starting 100ms before and ending 500ms after the onset of tactile stimuli. Trials with eye blinks (voltage exceeding $\pm 60\mu\text{V}$ relative to baseline on the VEOG channel), horizontal eye movements (voltage exceeding $\pm 40\mu\text{V}$ relative to baseline, on the HEOG channel) and other artefacts (voltage exceeding $\pm 80\mu\text{V}$ relative to baseline, at all other electrode sites) were excluded from further analysis.

Previous studies have shown that the location of the task-irrelevant visual distractor (far vs. near) modulates the processing of tactile stimuli within the somatosensory cortex, as suggested by spatially-specific modulations of the somatosensory P100 component (Sambo & Forster, 2009). Here we investigated whether this effect of distractor position is modulated by

tool use. Accordingly, statistical analyses were conducted on the ERPs waveforms measured over and near the somatosensory cortex (FC1/2; FC3/4; FC5/6; Fcz; C1/2; C3/4; C5/6; Cz; Cp1/2; Cp3/4; Cp5/6; Cpz; P1/2; P3/4; P5/6; Pz) where the crossmodal spatial effect was expected based on existing electrophysiological evidence in humans (Sambo & Forster, 2009; 2011). ERP mean amplitudes were computed within four successive time windows centred on the latencies of the somatosensory P100 (95 - 125 ms) and N140 (130 - 180 ms) components. In addition, longer latencies effects were investigated in the time interval of the P2 (185 - 235 ms) and N2 (240 - 290 ms) components. Four separate ANOVAs were carried out, one for each of these time windows. These ANOVAs included the within-subjects factors *tools* (long tools vs. short tools motor training), *distractor position* (visual stimuli presented in near vs. far space), and *electrode cluster* (fronto-central cluster - pooled across FC1/2, FC3/4, FC5/6 and FCz - vs. central cluster - pooled across C1/2, C3/4, C5/6 and Cz - vs. centro-parietal cluster - pooled across Cp1/2, Cp3/4, Cp5/6, and Cpz - vs. parietal cluster - pooled across P1/2, P3/4, P5/6 and Ppz). Preliminary analyses including the factor laterality (hemisphere ipsilateral vs. contralateral to the stimulated hand) revealed no significant interactions with the factors of interest. Therefore, this factor was not included in the analyses reported here.

To investigate the possibility that the effects of interest measured over central electrodes were instead driven by modulations of sensory processing over visual areas, additional analyses were carried out over pooled *occipital electrodes* (O1/2; Oz; PO3/4; PO7/8, Poz). These were carried out separately due to the different numbers of electrodes included in the central and occipital electrode clusters. Analyses of occipital electrodes included the factors *tools* (long tools vs. short tools motor training) and *distractor position* (visual stimuli presented in near vs. far space) and were carried out for the same time windows centred on the somatosensory ERP components of interest.

Relevant for the main question of interest were significant interactions between tool and distractor position indicating that the training with long tools had systematic effects on the way in which visuo-tactile information was integrated in near and far space (crossmodal spatial effect). Whenever significant tool \times distractor position interactions were observed, the presence of a spatial crossmodal effect (i.e. difference between ERPs on near and far visuo-tactile trials) was assessed after long and short tools use with planned paired t-tests (contrasts shown in Fig. 2A and 2B). In addition, to investigate whether the effect of long tool use was present for both near and far stimuli we also compared the effect of tool (short vs. long) separately for ERPs elicited on near and far trials (contrasts shown in Fig. 2C and 2D). The

alpha level for these four contrasts was adjusted with the Bonferroni method. Note that in the manuscript we reported the non-corrected p-values, and specifically stated whenever these did not survive the Bonferroni correction. Partial eta squared (η^2) was reported as a measure of effect size for main effects and interactions in the ANOVAs while Cohen's d was calculated for the paired t-tests. Wherever appropriate, Greenhouse-Geisser corrections were applied.

In the behavioural analyses, mean response times and accuracy rates were submitted to repeated measure ANOVAs with tools (long tools vs. short tools motor training) and distractor position (visual stimuli presented in near vs. far space) as within-subjects factors. Trials with omissions (no responses) and outliers (responses on trials exceeding ± 2.5 standard deviations from the mean calculated separately for each participant and each factor) were excluded from the RT analyses.

Existing literature suggests that the difference between near and far visuo-tactile trials is reduced after long tool use (see Maravita & Iriki, 2004 for a review). In order to interpret this null effect, Bayes factors (Rouder, Speckman, Sun, Morey, & Iverson, 2009) were calculated with the software JASP (JASP team, 2016) for the pairwise comparisons between near and far trials after long and short tool use in both the RT and ERP analyses. BF values can indicate support for the null hypothesis, the alternative hypothesis, or neither (Dienes, 2014), and arguably provide a better foundation for probabilistic inference than null hypothesis significance testing (Raftery, 1995; Wagenmakers, 2007). BF_{10} values larger than 3 are often considered as 'substantial' support for the alternative hypothesis (Wetzels & Wagenmakers, 2012), value smaller than .33 indicate 'substantial' support for the null hypothesis. BF_{10} values between .33 and 3 are considered as providing inconclusive evidence, supporting neither hypotheses.

Preliminary analyses including the within-subject factor non-spatial congruency were carried out. For completeness, these are reported in full in Footnote 2ⁱⁱ. The task-relevant feature of the tactile target was the stimulus identity (single vs. double taps) and the simultaneous visual distractor was either congruent or incongruent with respect to this non-spatial tactile feature. RT analyses revealed the presence of a congruency \times distance \times tool interaction showing that tool use did not affect visuo-tactile multisensory integration in near and far space on incongruent trials. Because the aim of the present study was to investigate the electrophysiological correlates of the effects of tool use on visuo-tactile integration in near and far space, the analyses reported in the results section of the manuscript were restricted to congruent trials where the behavioural effect of tool use was stronger (see

Marini, Romano, & Maravita, 2016, for a recent explicit suggestion to investigate multisensory integration in the absence of response conflict).

Finally, the behavioural performance measured in the training with long and short tools was analysed and summarised in the result section. Paired *t*-tests were used to compare mean RTs and mean accuracy rates observed in the long and short tool motor training.

3. Results

3.1. Behavioural data

Tool training task

Pairwise comparisons revealed that the execution of movements (including both reaction times – from the onset of the auditory stimuli to the initiation of the movement – and movement times – from movement onset to target key press) during the training with tools took longer when participants hit the target keys in far space with long tools than when they pressed target keys in near space with short tools ($t(22) = 2.1, p = .047; M = 858$ ms and $SD = 229$ ms for long tool training; $M = 776$ ms and $SD = 200$ ms for short tool training). Similarly, accuracy rates were higher with short ($M = 858$ ms and $SD = 229$ ms) than long tools ($M = 858$ ms and $SD = 229$ ms), $t(22) = 7.5, p < .001$).

Non-spatial Crossmodal Task

The analysis of response times revealed a main effect of distractor position ($F(1, 22) = 7.3, p = .013, \eta^2 = .25, d = .56$). Across tool conditions, responses were faster when the visual distractor was presented in near space ($M = 632.5$ ms, $SD = 91.8$ ms) as compared to far space ($M = 638.4$ ms, $SD = 95.2$ ms), that is when visuo-tactile stimuli were spatially congruent, in line with the spatial rule of multisensory integration. The distractor position \times tool interaction failed to reach statistical significance ($F(1, 22) = 3.1, p = .09; \eta^2 = .12$)ⁱⁱⁱ. Planned comparisons between near and far distractor trials conducted separately for the experimental and control conditions revealed the presence of a significant crossmodal spatial effect after short tool use ($t(22) = 2.9, p = .008, d = .6, BF_{10} = 5.95$). Responses to visual distractors near the tactile targets were faster as compared to responses to visual distractors in far space (Near: $M = 635.9$ ms, $SD = 88.9$ ms; Far: $M = 645.5$ ms, $SD = 95.2$). In contrast, no difference between near and far distractors was observed after long tool use (Near: $M = 629.2$

ms, $SD = 106.1$ ms; Far: $M = 631.2$ ms, $SD = 108.7$ ms; main effect of distractor position, $t(22) = .7$, $p = .4$, $d = .1$, $BF_{10} = 0.276$, null hypothesis favoured over the alternative hypothesis by $1/ BF_{10} = 3.62$).

The analysis of error rates did not yield any significant results, both for main effects of distractor position ($F(1, 22) = .12$, $p = .72$, $\eta^2 = .006$) and tools ($F(1, 22) = 2$, $p = .16$, $\eta^2 = .08$) as well as the distractor position \times tools interaction ($F(1, 22) = 1.6$, $p = .2$, $\eta^2 = .07$; for short tools, near distractors ($M = 8.38\%$, $SD = 5.30\%$), far distractors ($M = 7.70\%$, $SD = 4.77\%$). For long tools, near distractors ($M = 9.35\%$, $SD = 5.56\%$), far distractors ($M = 9.74\%$, $SD = 6.14\%$).

3.2. ERP results

Visuo-tactile ERPs over central electrodes

Figure 2 (top panels) illustrates grand-averaged ERP waveforms elicited by tactile targets pooled over fronto-central (FC1/2; FC3/4; FC5/6; Fcz), central (C1/2; C3/4; C5/6; Cz), centro-parietal (CP1/2; CP3/4; CP5/6; Cpz) and parietal (P1/2; P3/4; P5/6; Pz) electrodes when visual distractors were presented in near (solid lines) and far (dashed lines) space following training with short and long tools, respectively. These pooled electrodes will be referred to as ‘central’. Differences between ERPs elicited on near and far space trials were apparent during both early sensory-specific and later processing stages. This crossmodal spatial effect was characterised by enhanced N140 components for near as compared to far space trials and by a sustained negativity for far space trials in the N2 time range (between 190 and 290 ms post-stimulus). Figure 3 shows the voltage distribution measured over the scalp for these difference waveforms computed separately for the different time-windows considered (95 - 125 ms; 130 - 180 ms; 185 - 235 ms; 240 - 290 ms) and the different tool trainings. As can be observed in figures 2 and 3, the crossmodal spatial effect appeared to be modulated by tool use. Differences between near and far trials during early processing stages (e.g. the P100 and N140 time windows) appeared earlier and were stronger following long tool use. In contrast, modulations of the following P2 and N2 components observed over central electrodes appeared to be less affected by the use of tools.

In the time range of the P100 component (95 - 125 ms), a significant distractor position \times tools interaction was present over central electrodes ($F(1,22) = 5.1$, $p = .033$, $\eta^2 = .19$). As can be seen in Figure 2 (Panel B), following training with long tools, the P100 component

was characterised by an enhanced positivity for far distractor trials as compared to near ones. Figure 4 (top panel) shows the average amplitudes of ERPs elicited in the P100 time window by near and far distractors (light and dark blue bars, respectively) after short and long tool training. Paired comparisons between ERPs elicited by near and far visuo-tactile stimuli were conducted separately for the long and short tool training conditions. Significant differences in the P100 time range were observed between near and far visuo-tactile trials ($t(22) = -2.96$, $p = .007$, $d = 0.6$, $BF_{10} = 6.47$; Near trials after long tools: $M = 1.6 \mu V$, $SD = 2.4 \mu V$; Far trials after long tools: $M = 2.33 \mu V$, $SD = 2.5 \mu V$). No such difference was present after short tool use ($t(22) = 0.35$, $p = .7$, $d = 0.07$, $BF_{10} = 0.23$, null hypothesis favoured to the alternative hypothesis by $1/ BF_{10} = 4.35$; Near trials after short tools: $M = 1.54 \mu V$, $SD = 2.78 \mu V$; Far trials after short tools: $M = 1.43 \mu V$, $SD = 2.67 \mu V$).

The systematic effect of long tool use in far space can be further appreciated in the bottom panels of Figure 2 in which visuo-tactile ERPs elicited over central electrodes after short (solid line) or long tool use (dashed line) are directly contrasted separately for near (left panels) and far trials (right panels). Note that in panels C and D of Figure 2 visuo-tactile stimuli are physically identical so that the only difference between the ERP waveforms is the effect of tool use. This figure suggests that the use of long tools in the P100 time range primarily affected ERPs elicited by far distractors, in line with the hypothesis of increased brain activity in far space after long tool use. Pairwise comparisons revealed that ERPs on far visuo-tactile trials were more positive after long compared to short tool training (main effect of tool, $t(22) = 3.4$, $p = .003$, $d = 0.7$, $BF_{10} = 15.24$). No such difference was present for near distractor ERPs ($t(22) = 0.16$, $p = .87$, $d = 0.03$, $BF_{10} = 0.22$, null hypothesis favoured to the alternative hypothesis by $1/ BF_{10} = 4.55$).

In the following time window (130 - 180 ms), the N140 ERP component was more negative for near as compared to far space distractor trials, as revealed by the main effects of distractor position observed at central electrodes ($F(1,22) = 15.4$, $p < .001$, $\eta p^2 = .4$; Near: $M = -1.98 \mu V$, $SD = 3.23 \mu V$; Far: $M = -0.9 \mu V$, $SD = 3.2 \mu V$). No other interactions involving the factors distractor position and tools were observed in this time window.

Results of the ANOVAs carried out for later time windows centred on the P2 and N2 components (185 - 235 ms and 240 - 290 ms, respectively) revealed significant main effects of distractor position (P2 time range: $F(1, 22) = 8.5$, $p = .008$, $\eta p^2 = .27$; Near: $M = 4.3 \mu V$, $SD = 3.7 \mu V$; Far: $M = 3.5 \mu V$, $SD = 3.5 \mu V$; N2 time range: $F(1, 22) = 16.3$, $p = .001$, $\eta p^2 = .4$; Near: $M = 3.8 \mu V$, $SD = 3.4 \mu V$; Far: $M = 2.6 \mu V$, $SD = 3.4 \mu V$). As can be seen in Figure 2, between 185 and 290 ms ERPs elicited on far distractor trials were more negative than

those measured on near distractor trials. No other significant interactions involving the factors distractor position and tools were present.

Visuo-tactile ERPs elicited over occipital electrodes

Figure 5 (top panels) illustrates grand-averaged ERP waveforms elicited by visuo-tactile targets pooled over occipital electrodes (Po7/8; Po3/4; O1/2; Poz; Oz) when visual distractors were presented in near (solid lines) space and far (dashed lines) space following training with short and long tools (panels A and B, respectively). In panels 5C and 5D, ERPs elicited after short (solid line) and long tools (dashed lines) are contrasted separately for near and far distractor trials (panels C and D, respectively).

Analyses over occipital electrodes were carried out to investigate the possibility that the effects of interest measured over central electrodes were instead driven by modulations of sensory processing over visual areas. Thus, the same time windows chosen for the visuo-tactile ERP components elicited over central electrodes were used for the analysis of ERPs elicited over occipital electrodes, even though visual and somatosensory ERP components are characterised by different time-courses with earlier peaks for the somatosensory as compared to the visual ERP components.

In the time windows centred on the somatosensory P100 and N140 components (95 - 125 and 130 - 180 ms respectively), significant main effects of distractor position were observed over occipital electrodes (P100 time range: $F(1, 22) = 5.6$, $p = .027$, $\eta^2 = .20$; Near: $M = 1.8 \mu\text{V}$, $SD = 1.9 \mu\text{V}$; Far: $M = 1 \mu\text{V}$, $SD = 1.9 \mu\text{V}$; N140 time range: $F(1, 22) = 5.8$, $p = .024$, $\eta^2 = .21$; Near: $M = 0.24 \mu\text{V}$, $SD = 2.1 \mu\text{V}$; Far: $M = 1 \mu\text{V}$, $SD = 1.66 \mu\text{V}$). Both these differences are likely to be driven by the physical differences between near and far visual distractors. Visual stimuli presented in the upper and lower visual fields are known to elicit C1 components of opposite polarity which in turn affect the onset time of the P1 component. Thus, near and far visual distractors (falling on the lower and upper visual fields, respectively) will contribute differently to the visual component of the visuo-tactile ERPs recorded over occipital electrodes in these two types of trials. Importantly, no significant distractor position \times tools interactions were observed in these time windows (P100 time range: $F(1, 22) = .053$, $p = .82$, $\eta^2 = .002$; N140 time range: $F(1, 22) = 2.1$, $p = .15$, $\eta^2 = .089$).

Neither a main effect nor relevant interactions involving the factor distractor position were observed in the 185 - 235 ms time window, which encompassed the peak of the visual

N1 component and part of the P2 component. In the final 240 - 290 ms interval, overlapping with the P2 and N2 components, a significant distractor position \times tools interaction was observed ($F(1, 22) = 5.2$, $p = .031$, $\eta^2 = .19$). Paired comparisons between near and far distractor trials revealed no significant difference after short tool use ($t(22) = -0.38$, $p = .7$, $d = 0.08$, $BF_{10} = 0.23$, null hypothesis favoured to the alternative hypothesis by $1/ BF_{10} = 4.35$; Near short tools: $M = -0.96 \mu V$, $SD = 3.1 \mu V$; Far short tools: $M = -0.83 \mu V$, $SD = 2.7 \mu V$). After long tool use the difference between near and far distractor trials did not survive the Bonferroni correction ($\alpha < .0125$), $t(22) = -2.5$, $p = .02$, $d = 0.52$, $BF_{10} = 2.79$; Near long tools: $M = -1.17 \mu V$, $SD = 2.8 \mu V$; Far long tools: $M = -0.24 \mu V$, $SD = 3.4 \mu V$).

4. Discussion

Existing electrophysiological evidence suggest that the location of a task-irrelevant visual distractor (far vs. near) modulates the processing of tactile stimuli within the somatosensory cortex (Sambo & Forster, 2009). Here we investigate whether this effect of distractor position is modulated by tool use. Interactions between vision and touch were measured in a non-spatial crossmodal task (CT) in which participants responded to the identity of a tactile stimulus delivered to the left or right hand while ignoring an irrelevant visual distractor presented either in proximity to the stimulated hand or beyond reach (in near and far space respectively; see Sambo & Forster, 2009, for a similar task). Thus, the present non-spatial crossmodal task measured the integration of visuo-tactile information in near and far space when space was completely task-irrelevant. Importantly, before each block of the non-spatial CT, participants completed a motor training task either using short tools to hit target keys located in near space (control condition) or long tools to act upon far space targets (experimental condition).

As expected based on Sambo and Forster's study (2009), after the use of short tools (i.e. our control condition), responses to tactile targets were faster when visual distractors were presented within the space close to the body rather than far away from it. This finding provides further evidence for the existence of stronger multisensory integration of proximal visuo-tactile stimuli, in line with previous studies (e.g. Bolognini & Maravita, 2007; see Holmes & Spence; 2004, Longo, Musil, & Haggard, 2012; Macaluso & Maravita, 2010; and

Sambo & Forster, 2009, for reviews) and with the spatial rule of multisensory integration (Meredith & Stein, 1986; Stein et al., 1988; Stein & Meredith, 1990). This difference between near and far space trials was not observed after long tool use (i.e. in the experimental condition), suggesting increased multisensory processing in far space after the participants manipulated tools that extended into this spatial region (e.g. Bassolino et al., 2010; Farnè et al., 2007; Maravita et al., 2002). Overall, the pattern of results observed in the RT analysis confirmed that visuo-tactile multisensory dynamics can be revealed using a non-spatial task (e.g. Holmes, Sanabria, Calvert, & Spence, 2006; Poole, Couth, & Gowen, 2015) with stimulus identity as the target-relevant stimulus feature rather than spatial elevation. In line with existing behavioural studies (e.g. Holmes et al., 2004; 2007), the use of tools of varying lengths has differential effects on visuo-tactile integration in near and far space. However, in the present study, the behavioural differences between near and far visuo-tactile stimuli were relatively small (10 ms in the short tool condition) and their modulations by tool use weaker as compared to the classic CCT, as suggested by the fact that the interaction between distractor position and tools was not statistically significant in the RT analysis.

The task used in the present study was developed to investigate the electrophysiological correlates of visuo-tactile processing in near and far space after different tool conditions. While the classic CCT provides robust behavioural effects, task demands (i.e. response requirements; Gallace, Soto-Faraco, Dalton, Kreukniet, & Spence, 2008) and response conflict (Forster & Pavone, 2008; Marini et al., 2016; Spence et al., 2004a; Shore, Barnes & Spence, 2006) rather than multisensory integration have been suggested to play a fundamental role in the occurrence of the CCE. This was further shown in an ERP study using the classic CCT in which no spatial modulation of visuo-tactile processing was observed during early processing stages, suggesting that crossmodal visual distractor effects were largely due to response conflicts (Forster & Pavone, 2008). For these reasons, we choose a non-spatial task that was sensitive not only to the ERP differences between visuo-tactile integration in near and far space but also proved to be sensitive to their modulations by tool use, as discussed below.

Electrophysiological results revealed the presence of a crossmodal spatial effect in the control condition (after short tool use) with systematic differences between ERPs elicited over central electrodes on near and far distractor trials during both sensory-specific as well as later processing stages. More specifically, the earliest difference between ERPs elicited by tactile targets presented in synchrony with either near or far visual distractors was observed in

the time window of the sensory-specific N140 component (see Figure 2, panel A). Enhanced N140 components were observed for near than far distractor trials, suggesting increased integration of spatially congruent tactile and visual stimuli in line with the spatial rule of multisensory integration (Meredith & Stein, 1986; Stein et al., 1988; Stein & Meredith, 1990). Using a comparable task, Sambo and Forster (2009) observed a similar pattern of results, with enhanced ERP components when the visual distractor was presented in close proximity to the tactually stimulated hand. However, in their study, this visuo-tactile spatial effect was observed in the earlier P100 time range. This time difference could be explained by the fact that Sambo and Forster (2009) directly manipulated tactile spatial attention by instructing participants to attend to one of their hands and to respond exclusively to attended stimuli. By contrast, the tactile target in our paradigm was presented unpredictably to either hand, forcing participants to spread their attentional resources between the two possible target locations (their left or right hand). This ‘diffused attentional state’ might have delayed visuo-tactile integration processes, resulting in differences across spatial regions arising during the time range of the following N140 component. Thus, the enhanced N140 component observed on near as compared to far visuo-tactile trials in the present study might suggest increased multisensory integration in near space, in line with previous ERP studies (e.g. Sambo & Forster, 2009).

In the control condition, differences between ERPs elicited over central electrodes by visuo-tactile stimuli in near and far space were also present in the following P2/N2 time-range (measured between 185 and 290 ms post-stimulus onset) with enhanced negativities for ERPs elicited on far than near distractor trials. That is, an enhanced N2 component was observed for spatially incongruent far visuo-tactile stimuli (i.e. when the tactile signal is presented within near space and the visual signal from far space). A similar N2 modulation is also visible in Sambo and Forster’s (2009) ERP data, between approximately 250 and 350 ms post stimulus, but this late time window was not analysed. Because perceptual conflict has been linked to modulations of the N2 component (e.g. Wang et al., 2003; Wang, Cui, Wang, Tian & Zhang, 2004), N2 differences on spatially congruent and incongruent trials (near and far distractor trials, respectively) observed in the present study might reflect the perceptual mismatch between the location of visual and tactile stimuli. Support for this hypothesis comes from recent ERP evidence reporting reduced N2 amplitudes for spatially congruent visuo-tactile stimuli in personal space as compared to spatially incongruent ones (Longo et al. 2012), although it is worth noting that the visual and tactile stimuli manipulated by Longo

and colleagues are considerably different from the ones used in our study (visual stimuli consisted of visual information about the touched body part manipulated through the mirror box technique). Taken together, the electrophysiological results observed in the short tool condition replicate previous observations of systematic differences between visuo-tactile processing in near and far space (e.g. Sambo & Forster, 2009) and extend them by demonstrating the presence of similar effects in a task in which tactile spatial attention was not directly manipulated (in the present study the location of the tactile target was unpredictable).

In summary, after the use of long tools (in the control condition) responses to tactile targets were faster when the visual distractor was presented in near as compared to far space. This difference between near and far distractor trials (spatial crossmodal effect) was also evident in the ERP waveforms as revealed by systematic enhancement of the N140 component followed by reduced N2 for spatially congruent as compared to spatially incongruent visuo-tactile stimuli (i.e. near and far respectively).

After the use of *long tools* (experimental condition), visuo-tactile ERPs elicited over central electrodes between 130 and 290 ms post stimulus onset in the near and far conditions followed a pattern similar to that observed in the control condition. Specifically, the somatosensory N140 component was enhanced for near compared to far stimuli. In addition, post-perceptual ERPs measured in the P2/N2 time range over central electrodes were more negative for far as compared to near space trials. Thus, similar spatial crossmodal effects were observed after the use of long and short tools over central electrodes between 130 and 290 ms post-stimulus. Crucially, however, our findings also revealed systematic changes in near and far visuo-tactile interactions as a function of tool use. In contrast to the control condition in which the earliest effect of distractor position on visuo-tactile integration was observed in the N140 time range (from about 130 ms post-stimulus), in the experimental condition – after long tool use - differences between ERPs elicited by tactile stimuli coupled with visual distractors in near or far space had already emerged between 90 and 125 ms post-stimulus (see Figure 2 panel B). This difference was driven by a selective enhancement of ERPs elicited by far visuo-tactile stimuli over central electrodes after long tool use, revealing that the active use of long tools increased neural responses to stimuli in far space during the early stages of visuo-tactile processing. The timing and scalp distribution of these ERP effects (see Figure 3) are consistent with a modulation of the somatosensory P100 component which originates bilaterally from the secondary somatosensory cortices (SII; e.g. Allison,

Wood, McCarthy, & Spencer, 1991; Allison, McCarthy, Wood, Darcey, Spencer, & Williamson 1989; Inui, Wang, Tamura, Kaneoke, & Kagigi, 2004; Mauguiere et al. 1997; Mima et al. 1997). This suggests that the effect of long tool use on far visuo-tactile processing emerged during processing stages classically considered as somatosensory-specific.

These findings demonstrate that long tools use resulted in the selective modulation of the P100 component elicited on far visuo-tactile trials, consistent with the hypothesis of increased visuo-tactile integration in far space after long tool use. This tool-induced modulation also affected the behavioural performance as suggested by the reduced RT difference between near and far visuo-tactile trials after long tool use as compared to short tool use. However, the statistical evidence indicated that this RT difference between tool conditions was quite weak. This could be at least in part due to the fact that tool-induced modulations of visuo-tactile processing were restricted to the early processing stages (e.g. P100 time range), while later stages remained unaffected by it (similar ERP differences between near and far visuo-tactile trials were observed after long and short tool use between 130 and 250 ms post-stimulus). Thus, behavioural results representing the final output of different processing stages only weakly reflected the earliest sensory modulations. This might suggest that ERP measures are more sensitive than behavioural ones to detect the subtle modulations of visuo-tactile integration induced by tool use.

At first, the finding that long tool use affects early processing stages (i.e. sensory-specific ERP components) might seem in contrast with neuroimaging studies showing multisensory representation of the space near the body in parietal and premotor higher-order cortices (e.g. Bremmer et al., 2001; Ehrsson, Spence, & Passingham, 2004; Gentile, Petkova, & Ehrsson, 2011; Macaluso & Driver, 2005; Makin et al., 2007; Sereno & Huang, 2006). However, it is worth noting that in the present study participants interacted with tools *before* they performed the non-spatial CT. Thus, under these experimental conditions changes induced by the use of tools are tonic, slowly building up during the tool training task. It is therefore possible that the P100 modulation observed in the present study was mediated by changes induced by tools during the training (that is before the crossmodal task) to the higher level spatial representations. These, in turn, might have top-down modulatory effects on somatosensory brain areas due to feedback projections from multisensory regions to sensory-specific brain areas (e.g. Driver & Noesselt, 2008). As our results provide the first electrophysiological evidence for the effect of tool use on visuo-tactile multisensory

integration in near and far space, these hypotheses are highly speculative and additional work is essential to fully elucidate this ERP effect.

Despite the growing body of studies suggesting that visuo-tactile integration in near and far space is modulated by tool use (Berti & Frassinetti, 2000; Farnè et al., 2005; Farnè et al., 2007; Iriki et al., 1996; Maravita et al., 2001; Maravita et al., 2002; Maravita et al., 2003), the exact mechanisms underpinning the plastic changes induced by the use of tools to these spatial representations remain poorly understood. In monkeys, the observation that following tool-use, bimodal visuo-tactile neurons located in the intraparietal sulcus show elongated receptive fields (e.g. Iriki et al., 1996; Hihara et al., 2006) has been interpreted as evidence that the representation of space surrounding the hand is extended by tool use (see Maravita & Iriki, 2004 for a review). According to the extension hypothesis, after long tool use far stimuli presented close to the tip of the tool are represented as if they are close to the body, resulting in increased visuo-tactile multisensory integration in far space. However, recent findings have suggested that long tools might perceptually ‘highlight’ far locations rather than extend the representation of near space. Tools are visually salient objects (e.g. Ambrosini & Costantini, 2017; Park, Strom, & Reed, 2013) and there is now evidence suggesting that visual attention captured by the tip of the tool in far space might play a relevant role in the effect of tool use on visuo-tactile integration (e.g. Holmes et al, 2004; 2007b; Holmes et al., 2008; Holmes, 2012). When the strength of visuo-tactile integration was probed not only in near and far space but also along the tool shaft, increased multisensory interactions after tool use were exclusively observed at the hand and at the tip but not in the middle of the tool (Holmes et al., 2004; 2007a). This might suggest that long tool use results in shifts of spatial attention away from the hands and towards the tip of the tools, highlighting specific regions of space rather than extending near space (Holmes, 2012). This hypothesis is further supported by a recent fMRI study by Holmes et al. (2008) showing a modulation of brain activity in early occipital areas in response to task-irrelevant visual stimuli presented close to the tip of a single, manipulated tool, consistent with an attentional account of tool use effects. Taken together these findings suggest that under certain experimental circumstances, the effects of tool use on visuo-tactile processing can be explained, at least partially, by shifts of spatial attention to the tool in far space which modulate visual processing in early occipital areas when visual distractors are presented close to the functional part of that tool. Interestingly, when endogenous tactile attention was explicitly directed to the tip of the tool, its crossmodal effects on unimodal irrelevant visual stimuli were unevenly spread along the

tool with crossmodal effects of tactile attention on irrelevant visual stimuli near the hand and tool tip but not along the tool shaft (Yue, Bischof, Zhou, Spence, & Röder, 2009).

Results of the present study showed enhanced ERP amplitudes for far visuo-tactile stimuli after long tool use, consistent with the idea of increased multisensory integration on far space trials following interactions with long tools. Before these findings can be considered as evidence of tool-induced remapping of space, it is necessary to test the possibility that they are instead mediated by shifts of attention to the functionally and perceptually relevant tip of the tool. If spatial attention was directed to *far space* after long tool use, ERP attentional modulations induced by the tip of the tools should be a) present on far but not near trials because no stimulus was presented at far ‘attended’ locations on near trials, and b) particularly evident over occipital electrodes where visual information is initially processed because visual but not tactile stimuli were presented at far ‘attended’ locations. In the time window of the somatosensory P100 component (measured between 95 and 125 ms post-stimulus), ERPs elicited over occipital electrodes were more positive on near as compared to far trials regardless of tool condition (see Figure 5, panels A and B). The observation that occipital ERPs were enhanced on near as compared to far trials, together with the fact that tool use did not modulate this main effect of distractor position, suggests that no selective modulation of *visual* processing in far space was present between 95 and 125 ms post-stimulus (see Figure 4, bottom panel). It is therefore unlikely that visuo-spatial attention directed to the tip of the tool in far space was the main factor responsible for the effect of tool use observed over central electrodes in the P100 time range (Fig. 4, top panel). Nevertheless, it is worth pointing out that a weak effect of tool use on visuo-tactile integration was present over occipital electrodes during later processing stages (240-290 time window). Because this effect was not predicted, we will not discuss it further here. Future studies should *directly* investigate the consequences of tool use on visuo-tactile integration in near and far space over occipital brain areas. This is additionally warranted by the fact that that visual and somatosensory ERP components are characterised by different time-courses (as indicated by the earlier peaks of the somatosensory ERP components), and that the time windows chosen in the present study were centred on the somatosensory components of interest rather than on visual ERP components.

While shifts of ‘spatial attention’ to far locations cannot explain the pattern of results observed here, at least another possible attentional explanation should be considered. Enhancements of the somatosensory P100 component are typically reported in studies of

unimodal *tactile* spatial attention in which participants are explicitly instructed to covertly attend to one of their hands while ignoring the other (e.g. Desmedt & Robertson, 1977; Eimer & Forster, 2003; Michie, Bearparic, Crawford, & Glue, 1987). Does spatial attention shift to (the hands in) *near space* after long tool use? Performing actions with long tools is arguably more attentionally demanding in comparison to short tools, as it forces participants to divide their cognitive resources between two different relevant locations: the hand that has to operate the tool and the functionally-relevant tip of the tool. Thus, it is possible that after the use of long tools, increased attentional resources were directed to the hands (as suggested by the behavioural performance during the motor task – more errors and longer RTs associated with long tool use). However, if increased attentional resources were directed to the hands in near space after long tool use, enhanced processing of tactile events should be observed regardless of trial type (near or far distractor trials), as the tactile target was presented within the attended near space on each trial after long tool use. In contrast to this hypothesis, the use of long tools (as compared to short tools, see Figure 4) modulated brain responses to *tactile targets in near space* exclusively when these were presented with *visual distractors in far space*, ruling out a general attentional effect due to the difficulty of the motor task.

Overall, our results support the idea that interacting with long tools modulates crossmodal dynamics between vision and touch in far space. We found increased neural responses in brain areas encoding tactile stimuli to the body when visual stimuli were presented close to the tip of the tool after long tool use. Thus, increased visuo-tactile interactions emerged when functionally relevant but spatially disparate sectors of space were simultaneously stimulated. This might suggest that the deliberate use of a set of tools, extending into an otherwise unreachable part of space, reinforces the representation of sensory information from spatial locations that are relevant for this goal-directed action, namely the hand and the tip of the tool. The use of long tools appears to modify the coding or mapping of far space in a manner that is functionally determined by the action performed with the tools. The idea of action-dependent changes to the encoding of space is not new (see Làdavas & Serino, 2008, for a review) and there is evidence that the on-line planning and execution of goal-directed movements induce a temporary remapping of near space (Brozzoli, Pavani, Urquizar, Cardinali, & Farnè, 2009; Brozzoli et al. 2010). Specifically, when participants executed a reaching movement towards a distal object, increased multisensory interactions were found between hand-centred touches to the moving hand and visual stimuli embedded on this target object (such an effect was not apparent in a static

control condition; Brozzoli et al., 2009). This is further supported by recent studies demonstrating that movement planning and execution are linked to changes in the perceptual processing of stimuli presented within action-relevant regions of space (e.g. Baldauf & Deubel, 2010; Deubel & Schneider, 2004; Eimer, van Velzen, Gherri, & Press, 2007; Gherri & Eimer, 2008, 2010; Gherri & Forster, 2012a, 2012b; Gherri, Van Velzen, & Eimer, 2007; Juravle, Deubel, Tan, & Spence, 2010; Mason, Linnell, Davis, & Van Velzen, 2015). As tool use constitutes a form of goal-directed action, it is possible that the planning and execution of reaching movements with long tools might represent a special case of action-induced remapping of space. Importantly, the effect of tool use on crossmodal dynamics measured in the present study persisted beyond the on-line execution of the motor action and could therefore be considered as ‘off-line’ (see for example Holmes et al., 2007a for a similar point). Future studies should focus on elucidating the temporal boundaries of the effects of tool use on multisensory visuo-tactile integration in near and far space and directly contrast the on-line and off-line effects of tool use on the multisensory coding of near and far space.

In conclusion, the present electrophysiological findings demonstrate that even in the absence of response conflicts the active manipulation of long, hand-held tools augments interactions between visual stimuli located close to the tips of these tools and ipsilateral tactile stimuli delivered to the hands holding the tools. Visuo-tactile ERPs recorded from electrodes close to the somatosensory cortex in the P100 time range were enhanced for far as compared to near trials following manipulation of long tools while no such difference was observed after short tool use. Our findings suggest that the way in which far visuo-tactile stimuli are processed changes as a function of tool use, providing the first electrophysiological evidence that the active use of long tools modulated neural responses to stimuli in far space during the early stages of visuo-tactile processing. This is consistent with the idea that the use of long tools induces a transient remapping of space, creating a ‘link’ between near and far space which bridges these functionally-relevant spatial locations in a manner that is most likely attuned to action-centred goals.

Acknowledgements

We are grateful to Dr Michael Allerhand for his advice on the Bayesian Analysis. This study was supported by a University of Edinburgh PPLS internal grant to E.G..

References

- Allison, T., McCarthy, G., Wood, C. C., Darcey, T. M., Spencer, D. D., & Williamson, P. D. (1989). Human cortical potentials evoked by stimulation of the median nerve. II. Cytoarchitectonic areas generating short-latency activity. *Journal of Neurophysiology*, *62*(3), 694-710. Retrieved from: <http://www.physiology.org/doi/abs/10.1152/jn.1989.62.3.694>
- Allison, T., Wood, C. C., McCarthy, G., & Spencer, D. D. (1991). Cortical somatosensory evoked potentials. II. Effects of excision of somatosensory or motor cortex in humans and monkeys. *Journal of neurophysiology*, *66*(1), 64-82. Retrieved from: <http://www.physiology.org/doi/abs/10.1152/jn.1991.66.1.64>
- Ambrosini E, Costantini M. (2017). Body posture differentially impacts on visual attention towards tool, graspable, and non-graspable objects. *Journal of Experimental Psychology: Human Perception & Performance*, *43*(2), 360-370. doi: 10.1037/xhp0000330.
- Baldauf, D., & Deubel, H. (2010). Attentional landscapes in reaching and grasping. *Vision Research*, *50*(11), 999-1013. doi: <https://doi.org/10.1016/j.visres.2010.02.008>
- Bassolino, M., Serino, A., Ubaldi, S., & Làdavas, E. (2010). Everyday use of the computer mouse extends peripersonal space representation. *Neuropsychologia*, *48*(3), 803-811. doi: 10.1007/s00221-013-3532-2
- Berti, A., & Frassinetti, F. (2000). When far becomes near: Remapping of space by tool use. *Journal of Cognitive Neuroscience*, *12*(3), 415-420. doi:10.1162/089892900562237
- Bolognini, N., & Maravita, A. (2007). Proprioceptive alignment of visual and somatosensory maps in the posterior parietal cortex. *Current Biology*, *17*(21), 1890-1895. doi: <https://doi.org/10.1016/j.cub.2007.09.057>
- Bremmer, F., Schlack, A., Shah, N. J., Zafiris, O., Kubischik, M., Hoffmann, K. P., & Fink, G. R. (2001). Polymodal motion processing in posterior parietal and premotor cortex: a human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron*, *29*(1), 287-296. doi: [https://doi.org/10.1016/S0896-6273\(01\)00198-2](https://doi.org/10.1016/S0896-6273(01)00198-2)
- Brozzoli, C., Cardinali, L., Pavani, F., & Farnè, A. (2010). Action-specific remapping of peripersonal space. *Neuropsychologia*, *48*(3), 796-802. doi: <http://dx.doi.org/10.1016/j.neuropsychologia.2009.10.009>
- Brozzoli, C., Pavani, F., Urquizar, C., Cardinali, L., & Farne, A. (2009). Grasping actions remap peripersonal space. *Neuroreport*, *20*(10), 913-917. doi: 10.1097/WNR.0b013e32832c0b9b
- Desmedt, J. E., & Robertson, D. (1977). Differential enhancement of early and late components of the cerebral somatosensory evoked potentials during forced-paced cognitive tasks in man. *The Journal of Physiology*, *271*(3), 761-782. Retrieved from: <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC1353632/>

- Deubel, H., & Schneider, W.X. (2004). Attentional selection in sequential manual movements, movements around an obstacle and in grasping. In G.W. Humphreys, & M.J. Riddoch (Eds.), *Attention in action* (pp. 69–91). Hove, East Sussex: Psychology Press.
- Dienes, Z. (2014). Using Bayes to get the most out of non-significant results. *Frontiers in psychology*, 5, 781.
- Driver, J., & Noesselt, T. (2008). Multisensory interplay reveals crossmodal influences on ‘sensory-specific’ brain regions, neural responses, and judgments. *Neuron*, 57(1), 11-23. doi: <https://doi.org/10.1016/j.neuron.2007.12.013>
- Ehrsson, H. H., Spence, C., & Passingham, R. E. (2004). That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb. *Science*, 305(5685), 875-877. doi: 10.1126/science.1097011
- Eimer, M., & Forster, B. (2003). Modulations of early somatosensory ERP components by transient and sustained spatial attention. *Experimental Brain Research*, 151(1), 24-31. doi: 10.1007/s00221-003-1437-1
- Eimer, M., Van Velzen, J., Gherri, E., & Press, C. (2007). ERP correlates of shared control mechanisms involved in saccade preparation and in covert attention. *Brain Research*, 1135, 154-166. doi: <https://doi.org/10.1016/j.brainres.2006.12.007>
- Farnè, A., Iriki, A., & Làdavas, E. (2005). Shaping multisensory action–space with tools: evidence from patients with cross-modal extinction. *Neuropsychologia*, 43(2), 238-248. doi: <https://doi.org/10.1016/j.neuropsychologia.2004.11.010>
- Farnè, A., Serino, A., & Làdavas, E. (2007). Dynamic size-change of peri-hand space following tool-use: determinants and spatial characteristics revealed through cross-modal extinction. *Cortex*, 43(3), 436-443. doi: [http://dx.doi.org/10.1016/S0010-9452\(08\)70468-4](http://dx.doi.org/10.1016/S0010-9452(08)70468-4)
- Fogassi, L., Gallese, V., Fadiga, L., Luppino, G., Matelli, M., & Rizzolatti, G. (1996). Coding of peripersonal space in inferior premotor cortex (area F4). *Journal of Neurophysiology*, 76(1), 141-157. Retrieved from: <https://jn.physiology.org/content/76/1/141.short>
- Forster, B., & Pavone, E. F. (2008). Electrophysiological correlates of crossmodal visual distractor congruency effects: Evidence for response conflict. *Cognitive, Affective, & Behavioral Neuroscience*, 8(1), 65-73. doi: 10.3758/CABN.8.1.65
- Gallace, A., Soto-Faraco, S., Dalton, P., Kreukniet, B., & Spence, C. (2008). Response requirements modulate tactile spatial congruency effects. *Experimental Brain Research*, 191(2), 171-186. Retrieved from: <https://link.springer.com/article/10.1007/s00221-008-1510-x>
- Gentile, G., Petkova, V. I., & Ehrsson, H. H. (2011). Integration of visual and tactile signals from the hand in the human brain: an fMRI study. *Journal of Neurophysiology*, 105(2), 910-922. doi: <https://doi.org/10.1152/jn.00840.2010>
- Gherri, E., & Eimer, M. (2008). Links between eye movement preparation and the attentional processing of tactile events: an event-related brain potential study. *Clinical Neurophysiology*, 119, 2587–2597. doi: <https://doi.org/10.1016/j.clinph.2008.07.214>

- Gherri, E., & Eimer, M. (2010). Manual response preparation disrupts spatial attention: an electrophysiological investigation of links between action and attention. *Neuropsychologia*, *48*(4), 961-969. doi: <https://doi.org/10.1016/j.neuropsychologia.2009.11.017>
- Gherri E & Forster B. (2012)a. Crossing the hands disrupts tactile spatial attention but not motor attention: evidence from event-related potentials. *Neuropsychologia*, *50*(9), 2303-16. doi: 10.1016/j.neuropsychologia.2012.05.034.
- Gherri, E. & Forster, B. (2012)b. The orienting of attention during eye and hand movements: ERP evidence for similar frame of reference but different spatially-specific modulations of tactile processing. *Biological Psychology*, *91*(2), 172-184. doi: <https://doi.org/10.1016/j.biopsycho.2012.06.007>
- Gherri, E., Van Velzen, J., & Eimer, M. (2007). Dissociating effector and movement direction selection during the preparation of manual reaching movements: Evidence from lateralized ERP components. *Clinical Neurophysiology*, *118*(9), 2031-2049. doi: <https://doi.org/10.1016/j.clinph.2007.06.003>
- Graziano, M. S., & Cooke, D. F. (2006). Parieto-frontal interactions, personal space, and defensive behavior. *Neuropsychologia*, *44*(6), 845-859. doi: [10.1016/j.neuropsychologia.2005.09.009](https://doi.org/10.1016/j.neuropsychologia.2005.09.009)
- Graziano, M. S., & Gross, C. G. (1993). A bimodal map of space: somatosensory receptive fields in the macaque putamen with corresponding visual receptive fields. *Experimental Brain Research*, *97*(1), 96-109. Retrieved from: <http://link.springer.com/article/10.1007/BF00228820#aboutarticle>
- Graziano, M. S., Yap, G. S., & Gross, C. G. (1994). Coding of visual space by premotor neurons. *Science*, *266*, 1054 – 1056. Retrieved from: <http://monkeybiz.stanford.edu/nbio220/graziano1994.pdf>
- Gross, C. G., & Graziano, M. S. (1995). REVIEW: Multiple representations of space in the brain. *The Neuroscientist*, *1*(1), 43-50. Retrieved from: <http://nro.sagepub.com/content/1/1/43.short>
- Heilman, K. M., Bowers, D., Valenstein, E., & Watson, R. T. (1993). Disorders of visual attention. *Baillière's Clinical Neurology*, *2*(2), 389-413.
- Hihara, S., Notoya, T., Tanaka, M., Ichinose, S., Ojima, H., Obayashi, S., ... & Iriki, A. (2006). Extension of corticocortical afferents into the anterior bank of the intraparietal sulcus by tool-use training in adult monkeys. *Neuropsychologia*, *44*(13), 2636-2646. doi: <https://doi.org/10.1016/j.neuropsychologia.2005.11.020>
- Holmes, N. P. (2012). Does tool use extend peripersonal space? A review and re-analysis. *Experimental Brain Research*, *218*(2), 273-282. doi: 10.1007/s00221-012-3042-7
- Holmes, N. P., Calvert, G. A., & Spence, C. (2004). Extending or projecting peripersonal space with tools? Multisensory interactions highlight only the distal and proximal ends of tools. *Neuroscience Letters*, *372*(1), 62-67. doi: <https://doi.org/10.1016/j.neulet.2004.09.024>

- Holmes, N. P., Calvert, G. A., & Spence, C. (2007a). Tool use changes multisensory interactions in seconds: evidence from the crossmodal congruency task. *Experimental Brain Research*, 183(4), 465-476. doi: <https://doi.org/10.1007/s00221-007-1060-7>
- Holmes, N. P., Sanabria, D., Calvert, G. A., & Spence, C. (2007b). Tool-use: capturing multisensory spatial attention or extending multisensory peripersonal space? *Cortex*, 43(3), 469-489. doi: [https://doi.org/10.1016/S0010-9452\(08\)70471-4](https://doi.org/10.1016/S0010-9452(08)70471-4)
- Holmes, N. P., & Spence, C. (2004). The body schema and multisensory representation (s) of peripersonal space. *Cognitive Processing*, 5(2), 94-105. doi: 10.1007/s10339-004-0013-3
- Holmes, N. P., & Spence, C. (2005). Multisensory integration: space, time and superadditivity. *Current Biology*, 15(18), 762-764. doi: <http://dx.doi.org/10.1016/j.cub.2005.08.058>
- Holmes, N. P., Sanabria, D., Calvert, G. A., & Spence, C. (2007). Tool-use: capturing multisensory spatial attention or extending multisensory peripersonal space? *Cortex*, 43(3), 469-489. doi: [https://doi.org/10.1016/S0010-9452\(08\)70471-4](https://doi.org/10.1016/S0010-9452(08)70471-4)
- Holmes, N. P., Spence, C., Hansen, P. C., Mackay, C. E., & Calvert, G. A. (2008). The multisensory attentional consequences of tool use: a functional magnetic resonance imaging study. *PLoS One*, 3(10), e3502. doi: <https://doi.org/10.1371/journal.pone.0003502>
- Inui, K., Wang, X., Tamura, Y., Kaneoke, Y., & Kakigi, R. (2004). Serial processing in the human somatosensory system. *Cerebral Cortex*, 14(8), 851-857. doi: <https://doi.org/10.1093/cercor/bhh043>
- Iriki, A., Tanaka, M., & Iwamura, Y. (1996). Coding of modified body schema during tool use by macaque postcentral neurones. *Neuroreport*, 7(14), 2325-2330. Retrieved from: <http://europepmc.org/abstract/med/8951846>
- JASP Team (2018). JASP (Version 0.8.6)[Computer software].
- Jeffreys, H. (1961). Theory of probability In: 3rd New York: Oxford University Press.
- Juravle, G., Deubel, H., Tan, H. Z., & Spence, C. (2010). Changes in tactile sensitivity over the time-course of a goal-directed movement. *Behavioural Brain Research*, 208(2), 391-401. doi: <https://doi.org/10.1016/j.bbr.2009.12.009>
- Làdavas, E., Di Pellegrino, G., Farnè, A., & Zeleni, G. (1998). Neuropsychological evidence of an integrated visuotactile representation of peripersonal space in humans. *Journal of Cognitive Neuroscience*, 10(5), 581-589. doi:10.1162/089892998562988
- Làdavas, E., & Serino, A. (2008). Action-dependent plasticity in peripersonal space representations. *Cognitive Neuropsychology*, 25(7-8), 1099-1113. Retrieved from: <http://www.tandfonline.com/doi/abs/10.1080/02643290802359113>

- Làdavas, E., Zeloni, G., & Farnè, A. (1998). Visual peripersonal space centred on the face in humans. *Brain*, *121*(12), 2317-2326. doi: <http://dx.doi.org/10.1093/brain/121.12.2317>
- Longo, M. R., Musil, J. J., & Haggard, P. (2012). Visuo-tactile integration in personal space. *Journal of Cognitive Neuroscience*, *24*, 543-552. doi: [10.1162/jocn_a_00158](https://doi.org/10.1162/jocn_a_00158)
- Macaluso, E., & Driver, J. (2005). Multisensory spatial interactions: a window onto functional integration in the human brain. *Trends in Neurosciences*, *28*(5), 264-271. doi: <http://dx.doi.org/10.1016/j.tins.2005.03.008>
- Macaluso, E., & Maravita, A. (2010). The representation of space near the body through touch and vision. *Neuropsychologia*, *48*(3), 782-795. doi: <https://doi.org/10.1016/j.neuropsychologia.2009.10.010>
- Mahoney J. R., Molholm Sophie, Butler John S., Sehatpour Pejman, Gomez-Ramirez Manuel, Ritter Walter, Foxe John J. (2015). Keeping in touch with the visual system: spatial alignment and multisensory integration of visual-somatosensory inputs. *Frontiers in Psychology*, *6*, 1068. [https://doi: 10.3389/fpsyg.2015.01068](https://doi.org/10.3389/fpsyg.2015.01068)
- Makin, T. R., Holmes, N. P., & Zohary, E. (2007). Is that near my hand? Multisensory representation of peripersonal space in human intraparietal sulcus. *Journal of Neuroscience*, *27*(4), 731-740. doi: <https://doi.org/10.1523/JNEUROSCI.3653-06.2007>
- Maravita, A., & Iriki, A. (2004). Tools for the body (schema). *Trends in Cognitive Sciences*, *8*(2), 79-86. doi: <https://doi.org/10.1016/j.tics.2003.12.008>
- Maravita, A., Husain, M., Clarke, K., & Driver, J. (2001). Reaching with a tool extends visual-tactile interactions into far space: Evidence from cross-modal extinction. *Neuropsychologia*, *39*(6), 580-585. doi: [https://doi.org/10.1016/S0028-3932\(00\)00150-0](https://doi.org/10.1016/S0028-3932(00)00150-0)
- Maravita, A., Spence, C., & Driver, J. (2003). Multisensory integration and the body schema: close to hand and within reach. *Current Biology*, *13*(13), 531-539. doi: [http://dx.doi.org/10.1016/S0960-9822\(03\)00449-4](http://dx.doi.org/10.1016/S0960-9822(03)00449-4)
- Maravita, A., Spence, C., Kennett, S., & Driver, J. (2002). Tool-use changes multimodal spatial interactions between vision and touch in normal humans. *Cognition*, *83*(2), B25-B34. doi: [http://dx.doi.org/10.1016/S0010-0277\(02\)00003-3](http://dx.doi.org/10.1016/S0010-0277(02)00003-3)
- Marini, F., Romano, D., & Maravita, A. (2016). The contribution of response conflict, multisensory integration, and body-mediated attention to the crossmodal congruency effect. *Experimental Brain Research*, 1-15. doi: [10.1007/s00221-016-4849-4](https://doi.org/10.1007/s00221-016-4849-4)
- Mason, L., Linnell, K. J., Davis, R., & Van Velzen, J. L. (2015). Visual processing at goal and effector locations is dynamically enhanced during motor preparation. Visual processing at goal and effector locations is dynamically enhanced during motor preparation. *Neuroimage*, *117*, 243-249. doi: <https://doi.org/10.1016/j.neuroimage.2015.05.066>

- Mauguiere, F., Merlet, I., Forss, N., Vanni, S., Jousmäki, V., Adeleine, P., & Hari, R. (1997). Activation of a distributed somatosensory cortical network in the human brain. A dipole modelling study of magnetic fields evoked by median nerve stimulation. Part I: Location and activation timing of SEF sources. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, *104*(4), 281-289. doi: [https://doi.org/10.1016/S0013-4694\(97\)00006-0](https://doi.org/10.1016/S0013-4694(97)00006-0)
- Meredith, M. A., & Stein, B. E. (1986). Spatial factors determine the activity of multisensory neurons in cat superior colliculus. *Brain Research*, *365*(2), 350-354. doi: [http://dx.doi.org/10.1016/0006-8993\(86\)91648-3](http://dx.doi.org/10.1016/0006-8993(86)91648-3)
- Michie, P. T., Bearparic, H. M., Crawford, J. M., & Glue, L. C. (1987). The effects of spatial selective attention on the somatosensory event-related potential. *Psychophysiology*, *24*(4), 449-463. doi: 10.1111/j.1469-8986.1987.tb00316.x
- Mima, T., Ikeda, A., Nagamine, T., Yazawa, S., Kunieda, T., Mikuni, N., ... & Shibasaki, H. (1997). Human second somatosensory area: subdural and magnetoencephalographic recording of somatosensory evoked responses. *Journal of Neurology, Neurosurgery & Psychiatry*, *63*(4), 501-505. doi: <http://dx.doi.org/10.1136/jnnp.63.4.501>
- Park, G. D., Strom, M., & Reed, C. L. (2013). To the end! Distribution of attention along a tool in peri-and extrapersonal space. *Experimental Brain Research*, *227*(4), 423-432. doi: 10.1007/s00221-013-3439-y
- Piesco, J., Molholm, S., Sehatpour, P., Ritter, W., & Foxe, J. J. (2005). *Dissociating the multiple phases of somatosensory–visual integrations in the human event-related potential: A high-density electrical mapping study*. Paper presented at the 6th International Multisensory Research Forum, Rovereto, Italy.
- Quinn, B. T., Carlson, C., Doyle, W., Cash, S. S., Devinsky, O., Spence, C. & Thesen, T. (2014). Intracranial cortical responses during visual–tactile integration in humans. *Journal of Neuroscience*, *34*(1), 171-181. doi: <https://doi.org/10.1523/JNEUROSCI.0532-13.2014>
- Raftery, A. E. (1995). Bayesian model selection in social research. *Sociological Methodology*, *25*, 11–163.
- Rizzolatti, G., Fadiga, L., Fogassi, L., & Gallese, V. (1997). The space around us. *Science*, *277*(5323), 190-191. Retrieved from: <http://search.proquest.com/openview/7302901212159c737f8c4c0faa3ca59b/1?pq-origsite=gscholar>
- Sambo, C. F., & Forster, B. (2009). An ERP investigation on visuotactile interactions in peripersonal and extrapersonal space: evidence for the spatial rule. *Journal of Cognitive Neuroscience*, *21*(8), 1550-1559. doi: 10.1111/j.1460-9568.2009.06791.x
- Sambo C. F., & Iannetti, G.D. (2013). Better safe than sorry? The safety margin surrounding the body is increased by anxiety. *Journal of Neuroscience*, *33*: 14225-30.
- Schürmann, M., Kolev, V., Menzel, K., & Yordanova, J. (2002). Spatial coincidence modulates interaction between visual and somatosensory evoked potentials. *NeuroReport*, *13*, 779–783. Retrieved from:

http://journals.lww.com/neuroreport/Abstract/2002/05070/Spatial_coincidence_modulates_interaction_between.9.aspx

- Sereno, M. I., & Huang, R. S. (2006). A human parietal face area contains aligned head-centered visual and tactile maps. *Nature Neuroscience*, *9*(10), 1337-1343. doi:10.1038/nn1777
- Spence, C. (2011). Tool use and the representation of peripersonal space in humans. In T. McCormack, C. Hoerl, & S. A. Butterfill (Eds.), *Tool use and causal cognition*. Oxford University Press.
- Spence, C., Pavani, F., & Driver, J. (2004)a. Spatial constraints on visual-tactile cross-modal distractor congruency effects. *Cognitive, Affective, & Behavioral Neuroscience*, *4*(2), 148-169. doi: 10.3758/CABN.4.2.148
- Spence, C., Pavani, F., Maravita, A., & Holmes, N. (2004)b. Multisensory contributions to the 3-D representation of visuotactile peripersonal space in humans: evidence from the crossmodal congruency task. *Journal of Physiology-Paris*, *98*(1), 171-189. doi: <http://dx.doi.org/10.1016/j.jphysparis.2004.03.008>
- Stein, B. E., & Meredith, M. (1990). Multisensory integration. *Annals of the New York Academy of Sciences*, *608*(1), 51-70. doi: 10.1111/j.1749-6632.1990.tb48891.x
- Stein, B. E., Huneycutt, W. S., & Meredith, M. A. (1988). Neurons and behavior: the same rules of multisensory integration apply. *Brain Research*, *448*(2), 355-358. doi: [http://dx.doi.org/10.1016/0006-8993\(88\)91276-0](http://dx.doi.org/10.1016/0006-8993(88)91276-0)
- Valdés-Conroy, B., Sebastián, M., Hinojosa, J. A., Román, F. J., & Santaniello, G. (2014). A close look into the near/far space division: a real-distance ERP study. *Neuropsychologia*, *59*, 27-34. doi: <http://dx.doi.org/10.1016/j.neuropsychologia.2014.04.009>
- Wagenmakers, E.-J. (2007). A practical solution to the pervasive problems of p values. *Psychonomic Bulletin & Review*, *14*, 779-804.
- Wetzels, R., & Wagenmakers, E. J. (2012). A default Bayesian hypothesis test for correlations and partial correlations. *Psychonomic bulletin & review*, *19*(6), 1057-1064.
- Yue, Z., Bischof, G. N., Zhou, X., Spence, C., & Röder, B. (2009). Spatial attention affects the processing of tactile and visual stimuli presented at the tip of a tool: an event-related potential study. *Experimental Brain Research*, *193*(1), 119-128. Retrieved from: <https://link.springer.com/article/10.1007/s00221-008-1599-y>

Figures:

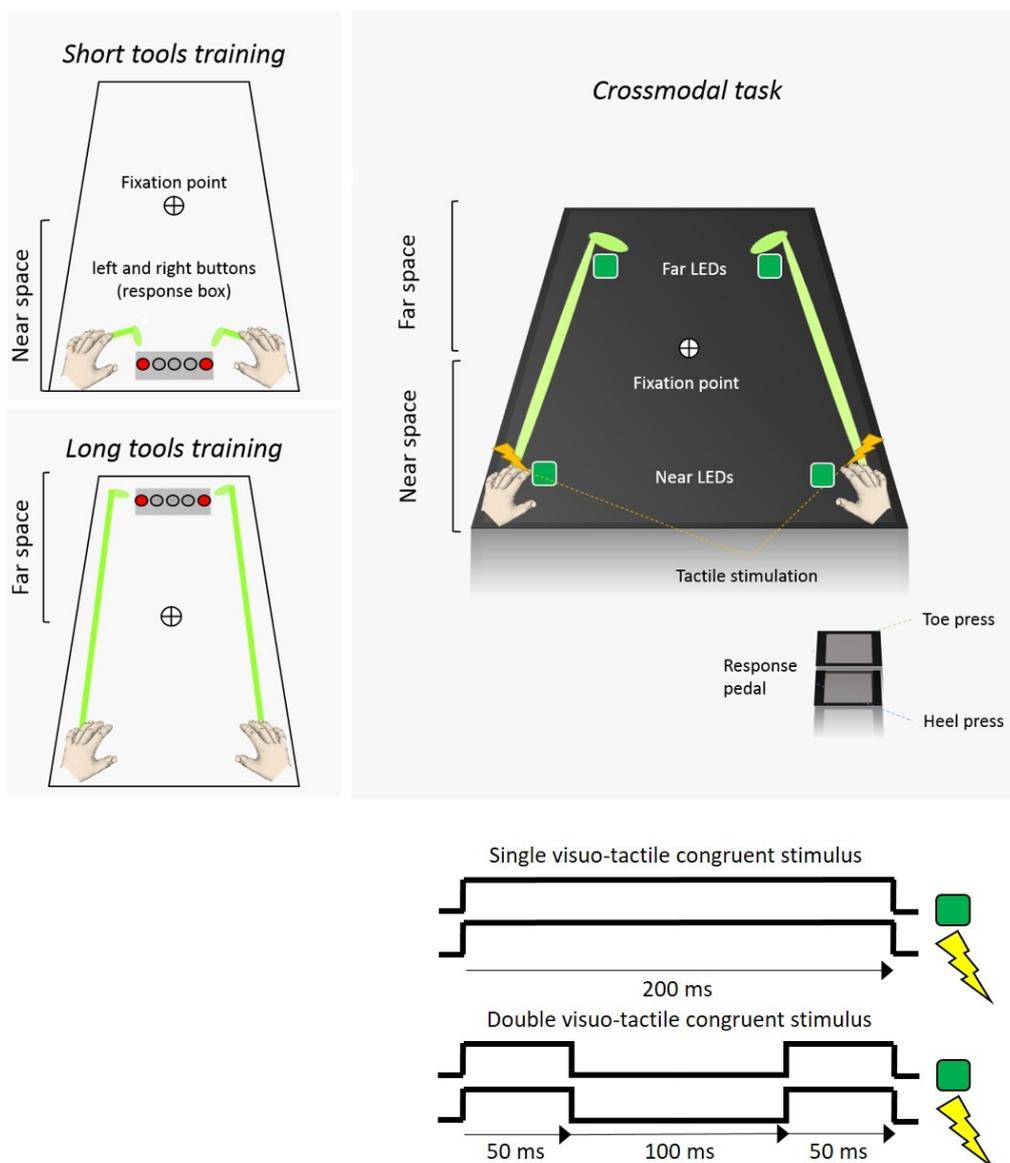


Figure 1. Schematic representation of the experimental setup for the non-spatial crossmodal task showing the sites of tactile stimulation, the four possible locations of visual stimuli in near space and far space (right panel) and the two types of training with short and long tools (left top and left bottom panels, respectively). The bottom panels show single and double visuo-tactile congruent stimuli presented during the Crossmodal task (green squares indicate visual stimuli, i.e. LEDs, while yellow flashes indicate tactile stimuli, i.e. vibro-tactile tappers). Note that measurements are not to scale but are for illustrative purposes only.

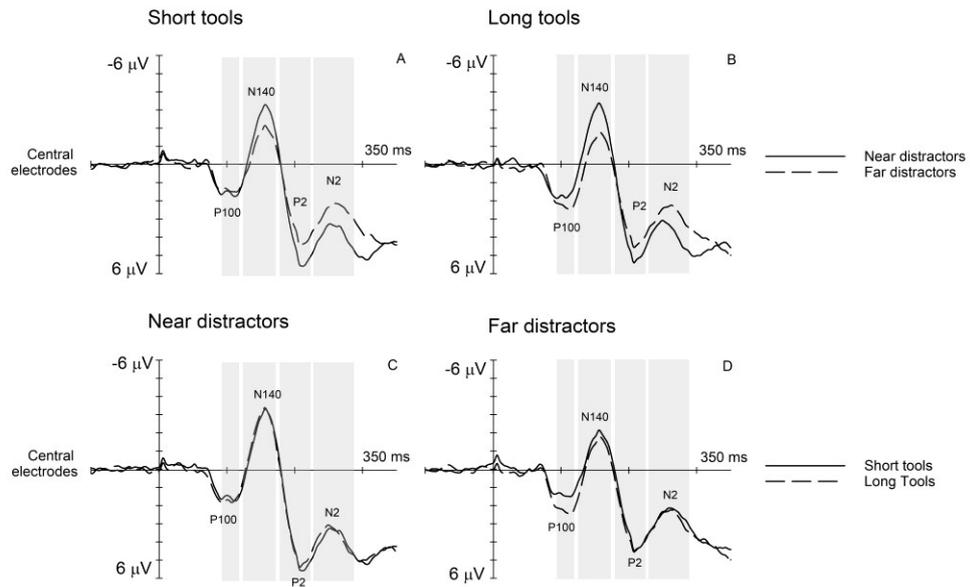


Figure 2. Grand-averaged visuo-tactile ERP waveforms elicited over central electrodes (pooled across FC1/2, FC3/4, FC5/6, Fcz, C1/2, C3/4, C5/6, Cz, CP1/2, CP3/4, CP5/6, Cpz, P1/2, P3/4, P5/6 and Pz) in the 350 ms post-stimulus. Panels A and B show the difference between ERPs elicited on near (solid lines) and far (dashed lines) distractor trials (i.e. the spatial crossmodal effect), after the use of short and long tools (panels A and B, respectively). The same ERPs waveforms are also shown in Panels C and D in which ERPs elicited after the use of short (solid lines) and long (dashed lines) tools are displayed separately for near and far distractor trials (panels C and D, respectively). Grey boxes indicate the time-windows during which the somatosensory ERP components of interest were measured for statistical analyses (95-125 ms, 130-180 ms, 185–235 ms and 240-290 ms).

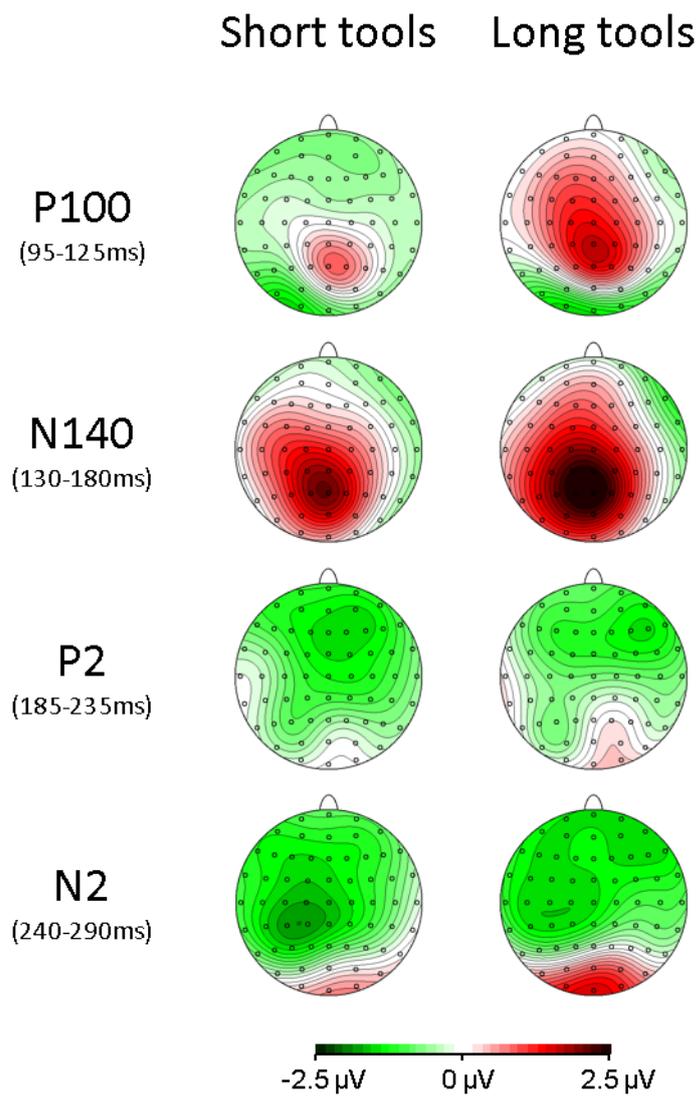


Figure 3. The scalp voltage distribution of the crossmodal spatial effect (calculated by subtracting ERPs elicited on near visuo-tactile trials from far visuo-tactile trials) computed separately for the 95-125 ms, 130-180 ms, 185–235 ms and 240-290 ms time-windows and for the different types of tool training (short vs. long tools).

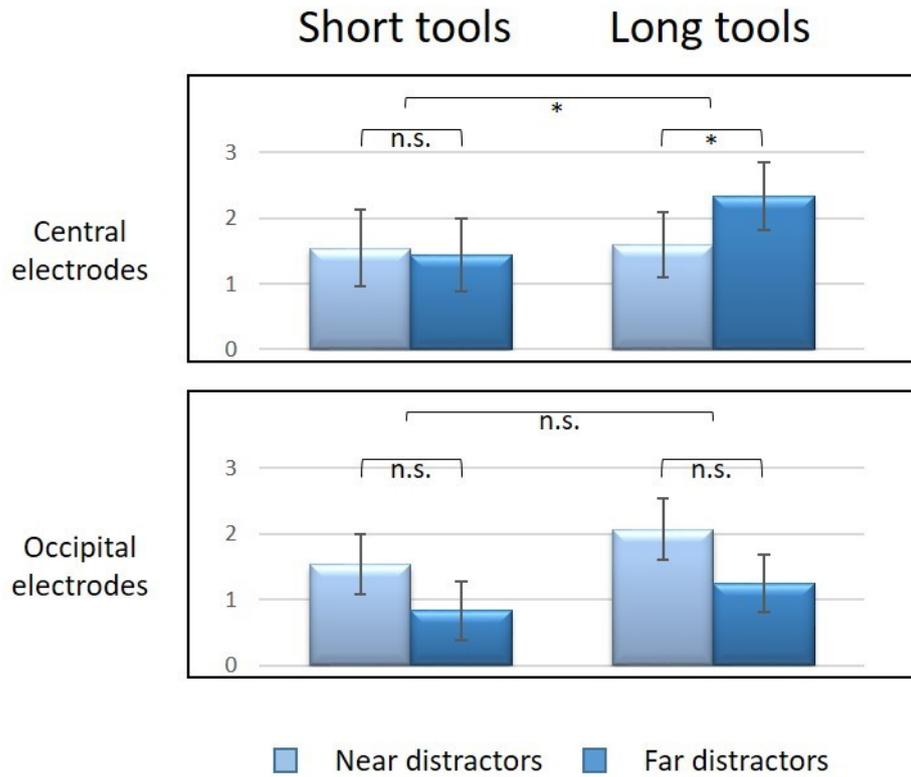


Figure 4. Average amplitudes of pooled ERPs over central and occipital electrodes (top and bottom panels, respectively) elicited in the P100 time window (95-125 ms) on near and far distractor trials (light and dark blue bars, respectively) after short and long tool training. Asterisks indicate the presence of significant differences between ERPs elicited on near and far distractor trials.

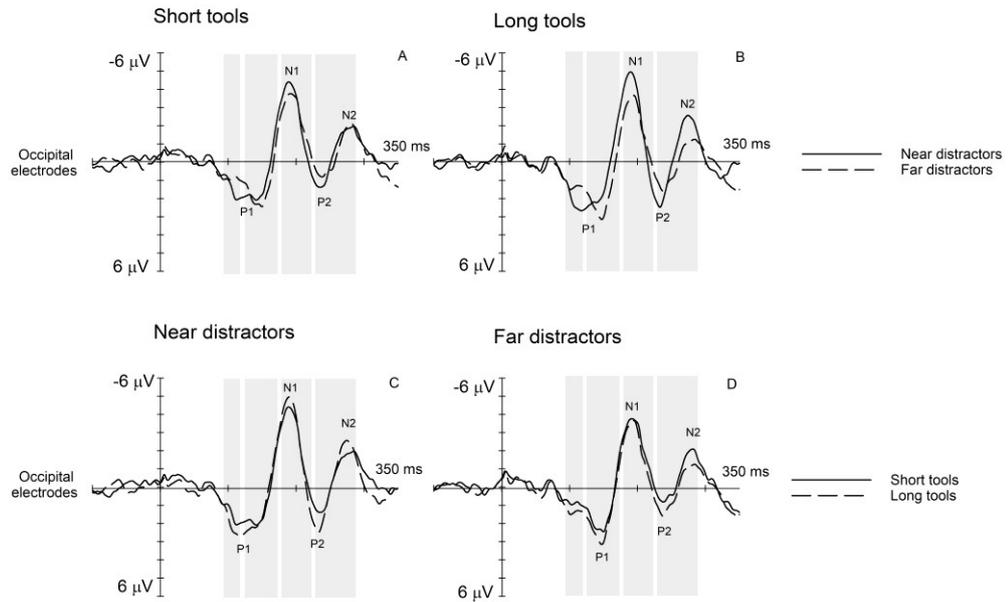


Figure 5. Grand-averaged visuo-tactile ERP waveforms elicited over occipital electrodes (pooled across Po7/8, Po3/4, O1/2, Poz and Oz) in the 350 ms post-stimulus. Panels A and B show the difference between ERPs elicited on near (solid lines) and far (dashed lines) distractor trials (i.e. the spatial crossmodal effect), after the use of short and long tools (panels A and B, respectively). The same ERPs waveforms are also shown in Panels C and D in which ERPs elicited after the use of short (solid lines) and long (dashed lines) tools are displayed separately for near and far distractor trials (panels C and D, respectively). Grey boxes indicate the time-windows during which the somatosensory ERP components of interest were measured for statistical analyses (95-125 ms, 130-180 ms, 185–235 ms and 240-290 ms).

Footnotes:

ⁱ Because the main aim of the present study was to investigate the effect of active tool-use on the spatial rule of visuo-tactile integration, visual and tactile stimuli were always presented on the same side of space. This allowed us to reduce the number of trials necessary to cover all possible combinations of stimuli locations and to avoid problematic ERP comparisons between same side and opposite sides visuo-tactile stimuli, given the lateralised nature of tactile processing.

ⁱⁱ A preliminary *behavioural analysis* was run including the within-subjects factors congruency, distractor position and tools. Congruent trials were faster than incongruent ones (645 and 667 ms, respectively, $F(1, 22) = 26.6$, $p = .001$, $\eta^2 = .54$). Responses were overall faster for near than far distractor trials ($F(1, 22) = 8.3$, $p = .009$, $\eta^2 = .23$). Importantly, we also observed a significant three-way interaction between congruency, distractor position and tools ($F(1, 22) = 4.9$, $p = .037$, $\eta^2 = .18$). For *congruent trials*, responses were faster when visual distractors were presented near than far to the tactually stimulated hand (636 ms and 646 ms, respectively; $t(22) = 2.9$, $p = .008$), while no distance effect emerged following long tool use (629 ms near and 631 ms far space trials $t(22) = .7$, $p = .48$). In contrast, there was a main effect of distractor position for *incongruent trials* ($F(1,22)=5.2$, $p = .03$, $\eta^2 = .19$) but this was not further modulated by tools (no distractor position x tools interaction, $F(1,22) = 1$, $p = .3$, $\eta^2 = .046$). On incongruent trials, responses were faster on near (653 ms) than far (660 ms) distractor trials regardless of tool condition.

The analysis of error rates revealed a main effect of congruency ($F(1, 22) = 19.6$, $p = .001$, $\eta^2 = .47$) with fewer errors for congruent (9%) than incongruent trials (18%). In addition, more errors were present on near than far distractor trials (14.5% and 12%, respectively, main effect of distractor position ($F(1, 22) = 10$, $p = .004$, $\eta^2 = .3$) and this effect was further modulated by congruency ($F(1, 22) = 6.8$, $p = .016$, $\eta^2 = .23$). Follow-up analyses showed that responses on incongruent trials were less accurate when visual distractors were presented near than far to the tactually stimulated hand (18.9% and 17.1%, respectively, $t(22) = -3.8$, $p = .001$), while no difference emerged between congruent trials (8.7% and 8.9%, $t(22) = -0.3$, $p = .7$).

Preliminary *ERP analyses* were carried out over central electrodes including the factors congruency (congruent vs. incongruent), distractor position (near vs. far), tools (long vs. short) and electrode cluster (fronto-central/central vs. centro-parietal/parietal) for each time window. In the P100 time window a significant distractor position x tools interaction was present ($F(1,22) = 4.8$, $p = .039$, $\eta^2 = .18$), revealing the presence of a distractor position main effect after long ($F(1,22) = 5.2$, $p = .033$, $\eta^2 = .19$), but not short tool training ($F(1,22) = .002$, $p = .9$, $\eta^2 = .0$). Between 130 and 235 ms post stimulus (time windows overlapping with the N140 and P2 components), a main effect of distractor position was present (130-180 ms time window: $F(1,22) = 10.9$, $p = .003$, $\eta^2 = .33$; 185-235 ms: $F(1,22) = 11.1$, $p = .003$, $\eta^2 = .33$). No other interactions involving distractor position were observed in these time windows. In the N2 time window (240-290 ms), a significant distractor position x tools x congruency x electrode cluster interaction emerged ($F(1,22) = 6.8$, $p = .016$, $\eta^2 = .2$). Separate ANOVAs carried out for congruent and incongruent trials, revealed that the distractor position x tools x electrode cluster interaction approached significance on incongruent ($F(1,22) = 4.25$, $p = .051$, $\eta^2 = .16$) but not on congruent trials ($F(1,22) = 2.2$, $p = .14$, $\eta^2 = .09$). However, follow up analyses carried out on incongruent trials showed the absence of reliable distractor position x tools interaction either at fronto-central/central or central/centro-parietal clusters (both $F(1,22) < 1$, both $p > .5$).

The first reliable main effect of congruency only emerged in a later time window measured between 300 and 400 ms post stimulus ($F(1, 22) = 7.3$, $p = .013$, $\eta^2 = .24$). This main effect of congruency did not interact with distractor position or tools. In line with previous ERP evidence of visuo-tactile crossmodal conflict tasks (Forster & Pavone, 2009), this effect of congruency was localized frontally and was characterised by enhanced negativities for incongruent as compared to congruent trials.

The analysis of occipital electrodes revealed main effects of distractor position in the 95-125 ms ($F(1,22) = 8.4$, $p = .008$, $\eta^2 = .27$) and 130-180 ms ($F(1,22) = 6.2$, $p = .021$, $\eta^2 = .22$) time windows. No other reliable main effects or interactions involving the factor distractor position were observed.

ⁱⁱⁱ A Bayesian repeated measures ANOVA (distractor position × tool on RTs), using the JASP default Cauchy prior width of .707 (JASP Team, 2018), and a non-directional hypothesis, was used to compare evidence for the model containing the two main effects and the interaction (M1) to the model containing the two main effects (M0):

$$\frac{M_1 BF_{10}}{M_0 BF_{10}} = \frac{.036}{.109} = .358$$

The reciprocal of this value which expresses the strength of evidence for the null model over the alternative model ($1/BF_{10} = 2.79$) was considered ‘anecdotal’ (Wetzels & Wagenmakers, 2012) or ‘not worth more than a bare mention’ (Jeffreys, 1961) support for this model.