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Tool use modulates somatosensory cortical processing in humans

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Running title: Tool use modulates somatosensory processing

Abstract

Tool use leads to plastic changes in sensorimotor body representations underlying tactile perception. The neural correlates of this tool-induced plasticity in humans have not been adequately characterized. The present study used event-related brain potentials to investigate the stage of sensory processing modulated by tool use. Somatosensory evoked potentials, elicited by median nerve stimulation, were recorded before and after two forms of object-interaction: tool use and hand use. Compared to baseline, tool use—but not use of the hand alone—modulated the amplitude of the P100. The P100 is a mid-latency component that indexes the construction of multisensory models of the body and has generators in secondary somatosensory and posterior parietal cortices. These results mark one of the first demonstrations of the neural correlates of tool-induced plasticity in humans and suggest that tool use modulates relatively late stages of somatosensory processing outside of primary somatosensory cortex. This finding is consistent with what has been observed in tool-trained monkeys and suggests that the mechanisms underlying tool-induced plasticity have been preserved across primate evolution.

Keywords: body representation, electroencephalography, embodiment, event-related potentials, touch

The primate sensorimotor system is highly sensitive to how the body is used to act on the world (Buonomano and Merzenich 1998). For example, body representations in primary somatosensory (SI) and motor (MI) cortices are shaped by long-term behavioral use (Jenkins et al. 1990; Elbert et al. 1995) and can change when learning a new sensorimotor skill (Pascual-Leone and Torres 1993; Gindrat et al. 2015). On the other hand, successfully completing many daily activities requires quick adjustments be made to sensorimotor models of the body. For example, primates often use tools to extend what they can reach (Lacquaniti et al. 1982) and sense (Miller et al. 2018). Doing so, however, means that the sensorimotor system must compensate for how the tool changes the physical and geometric properties of the arm and hand (Imamizu 2003), making tool use a good case study for investigating mechanisms of short-term sensorimotor plasticity.

Several decades of research have found that sensorimotor models of the body adjust their parameters to account for the extended reach of the limb-tool system (for reviews, see Maravita and Iriki 2004; Martel et al. 2016). This leads to lasting and measurable changes in how the user controls their limb (Kluzik et al. 2008; Cardinali et al. 2009; Baccarini et al. 2014; Cardinali, Brozzoli, Finos, et al. 2016; Day et al. 2017), perceives tactile stimuli impinging on its surface (Cardinali et al. 2011; Canzoneri et al. 2013; Miller et al. 2014; Miller, Cawley-Bennett, et al. 2017), and judges its spatial extent (Sposito et al. 2012; Garbarini et al. 2015). These modulations are often taken as evidence that tool use has modulated the represented size of the limb (Martel et al. 2016). Both visual (Miller, Longo, et al. 2017; Guerraz et al. 2018) and proprioceptive (Sengül et al. 2013; Cardinali, Brozzoli, Luauté, et al. 2016; Martel et al. 2019) feedback during tool use appear to play a critical role in the tool-induced plasticity of sensorimotor body representations.

At the neural level, studies with macaques have identified significant functional and structural changes in somatosensory regions following tool use learning, specifically in the secondary somatosensory cortex (SII; Quallo et al. 2009) and the anterolateral portion of area 5V (aIPS; Iriki et al. 1996; Hihara et al. 2006). It remains unclear, however, how these findings map onto the aforementioned behavioral changes in humans, as the neural correlates of tool-induced sensorimotor plasticity have received little attention in humans.

To our knowledge, only a single study has measured how using a tool modulates somatosensory processing in the human brain. Schaefer and colleagues (2004) used magnetoencephalography (MEG) to record primary somatosensory responses to puffs of air applied to the fingers during tool use, hand use, and rest. They found that tool use (but not hand use) increased the distance between the representations of D1 and D5 in primary somatosensory cortex, as measured from the dipoles of the M60 evoked-field. However, since these measurements were made *during* tool use, it is unclear how they relate to the lasting recalibration of sensorimotor models observed in the aforementioned behavioral experiments. We aimed to begin filling this gap in the literature.

In the present study, we used event-related brain potentials (ERPs) to identify the stage(s) of somatosensory processing modulated by tool use in humans. ERPs are an ideal method for this research question given their good temporal resolution. Further, the cortical generators of several somatosensory evoked potentials (SEP) in humans have been mapped using intracranial recordings (Allison et al. 1991) and MEG (Kakigi 1994). Short-latency SEPs (e.g., P45, N60) are thought to reflect activity in primary somatosensory cortex (SI; Allison et al. 1992), whereas mid-latency SEPs (e.g., P100, N140) index activity within SII, PPC, and regions of the frontal cortex (Forss et al. 1994; Mauguière et al. 1997; Barba et al. 2004).

Given the behavioral results discussed above, it is often assumed that tool use recalibrates higher-order sensorimotor models of the body outside of SI. Along these lines, we hypothesized that tool use would modulate the amplitude of mid-latency SEPs (e.g., P100, N140) that have sources which are consistent with what is found in tool-trained macaques (Iriki et al. 1996; Hihara et al. 2006; Quallo et al. 2009). However, the findings by Schaefer and colleagues (2004) leave open the possibility that even low-level stages of processing in SI may be modulated by tool use. To foreshadow our results, we found significant evidence that tool use (but not hand use) modulates the amplitude of the mid-latency P100 component, an index of multisensory models of the body (Cardini and Longo 2016).

Methods & Materials

Participants

Twenty-two healthy right-handed participants (12 females) between the ages of 19 and 39 years old (*Mean*: 29.1; *SD*: 4.2) took part in the present study. One participant was removed due to equipment failure and another was removed due to excessive eye blinks (almost every trial). Two additional participants opted to discontinue the experimental session midway through because they found the stimulation uncomfortable. The remaining eighteen participants were further analyzed. All participants had normal or corrected-to-normal vision and no history of neurological problems. Each gave informed consent before participating. The experiment was approved by the local ethics committee at Birkbeck, University of London.

Stimuli and Apparatus

Electric shocks (0.2 ms in duration) were delivered to the right median nerve at the wrist with a Digitimer DS7A constant current high-voltage stimulator (Digitimer, Welwyn Garden City, UK). Median nerve stimulation was chosen because it is known to elicit robust and well-studied SEPs (Allison et al. 1991). Each participant's median nerve was located and the stimulation intensity was set using two criteria: 1) a single electric shock produced noticeable tingling sensations in the right thumb, index, and middle fingers, but not in the two remaining digits; 2) an involuntary thumb twitch could be elicited. The stimulation intensity used throughout the experiment was set to an average of 121% (*SD*: 11) of each participant's motor threshold (*Mean*: 8.33 mA; *SD*: 2.19). The position and orientation of the stimulation electrodes was monitored throughout the experiment to ensure that they did not change.

Experimental Procedure

The experiment consisted of two main blocks, one for each object-interaction task (tool use and hand use; Fig. 1a). Each block was further subdivided into three sub-blocks (see below):

a baseline EEG block, an object interaction block, and a post-interaction EEG block. The two main blocks were separated by an eight-minute break.

During each EEG recording block, participants sat in a dimly lit room with both arms resting comfortably on a table and covered with a black smock. They were asked to maintain their gaze to the location of their right hand, which was completely hidden from view. Participants performed a somatosensory target-detection task (Sambo and Forster 2009), a common task that forces participants to continually monitor the sensory state of their hand as well as maintain attention and vigilance. On each trial, the participant's job was to distinguish between a non-target single shock (90% probability) and infrequent target double shocks (two shocks separated by 50 ms; 10% probability), randomized across trials. Non-targets were ignored and required no overt response. When a target was detected, participants responded by lifting their left foot off of a foot pedal as quickly as possible within a set time window of 1600 ms. This long time-window was chosen to minimize the probability that the proceeding trial would be contaminated by residual motor activity. The inter-trial interval was randomly chosen from a uniform distribution between 400 to 600 ms. Each of the four EEG blocks (two per object-interaction block) consisted of 800 trials, 720 non-targets and 80 targets, for a total of 3200 trials for the entire experiment.

Object-interaction Procedure

The experiment was composed of two object-interaction conditions: *tool* use and *hand* use (order counterbalanced across participants). The participant's task was to pick a balloon up to eye-level and place it back down on a table. They were instructed to comfortably perform the action self-paced for a total of 8 minutes. This task was identical in both object-interaction conditions, differing only in the means by which the balloons were picked up.

In the *tool* use condition, participants used a hand-shaped exoskeleton (Fig. 1a). This tool was used in the present study because it has been previously shown to reliably modulate tactile perception on the user's hand (Miller et al. 2014), an important methodological consideration since we are stimulating the median nerve. More conventional tools (e.g., a mechanical grabber), in contrast, instead modulate tactile perception on the arm but not the hand (Cardinali et al. 2009; Miller et al. 2014). Each finger of the tool was composed of three plastic “bones” connected via fully adjustable rubber “joints”. The tool was strapped to the participant’s forearm with Velcro and their fingers rested in leather straps attached to the tool’s fingers, allowing for their individual control; movement of each strap led to a concurrent movement of the corresponding finger of the tool. This ensured that the functionality of the user’s own fingers and the fingers of the tool were comparable. The tool was approximately 21 cm wide, as measured from the base of the index finger to the base of the little finger, and 45 cm long, as measured from the base of the tool to the tip of the middle finger. The *hand* use condition served as a control for general modulations of SEPs by sustained object interaction. This condition does not lead to changes in tactile perception (Miller, Longo, et al. 2017) and is a common control in the literature (Anelli et al. 2015; Guterstam et al. 2018). Participants used their own fingers to grasp the balloon and lift it to eye-level in a similar manner as the tool use condition.

EEG Recording and Preprocessing

EEG Recording

Electroencephalography was recorded with a BioSemi ActiveTwo EEG system (Biosemi B.V., Amsterdam, The Netherlands) that had 64 active electrodes whose layout followed the international 10/10 system. Horizontal and vertical electrooculograms (EOG) were used to measure and detect horizontal eye movements and eye blinks, respectively. During data acquisition, EEG and EOG signals were amplified and digitized at 2048 Hz, and low-pass filtered at 100 Hz.

EEG Preprocessing

All data was pre-processed with EEGLAB (Delorme and Makeig 2004). The electric shock creates a large ~2 ms artifact in the EEG and EOG signal. This artifact was removed from each trial in every channel by linearly interpolating the signal from 0 to 6 ms following the shock (Cardini et al. 2011). The data was then re-referenced to the average of the left and right mastoids, band-pass filtered between 0.1 and 40 Hz, and down sampled to 500 Hz. EEG and EOG signals were epoched into periods of 450 ms, starting 150 ms before and ending 300 ms after each non-target shock. We removed target trials from the analysis as well as any non-target trials containing a response.

Data cleaning had two steps: First, we removed large artifacts—eye movements, eye blinks, and muscle activity—using independent components analysis (Makeig et al. 1996). Before performing ICA, we first combined every condition into a single continuous dataset in order to prevent any possibility of bias when removing components; next we removed stretches of time that contained disruptive events (i.e., amplifier saturation) as they are known to affect the decomposition. After ICA, independent components relating to the aforementioned artifacts were identified by visual inspection and removed. Following this procedure, trials with activity still exceeding ±80 µV (relative to baseline) were discarded (*Mean*: 62.8 trials; *Range*: 4–124 trials). A 2 (time: pre, post) x 2 (effector: tool, hand) repeated measures ANOVA demonstrated that the experimental conditions did not differ in the number of trials removed during this procedure (all *Fs* < 0.6, all *Ps* > .5)

Data Analysis

Behavioral Analysis

All statistical analysis were conducted using JASP version 0.8.5 (JASP Team 2018). To determine whether either object-interaction condition modulated behavioral performance we performed 2 (time: pre, post) x 2 (effector: tool, hand) repeated measures ANOVAs on both the accuracy and reaction times in the somatosensory target-detection task (see above). The main statistic of interest is the interaction between the two factors, as this would indicate that the two object-interaction conditions had unequal effects on target detection.

ERP Analyses

We took two approaches to analyze our EEG data: First, we performed a traditional component-dependent ERP analysis where distinct SEPs were identified by their time windows and scalp distributions. Second, we performed a component-independent cluster-based analysis in order to ensure that any effects observed in the first analysis were not due to our choices for identifying SEPs (Maris and Oostenveld 2007).

Component-dependent analysis: As the main aim of our study was to investigate how tool use modulates somatosensory processing, we focused on electrode sites over and close to somatosensory areas contralateral to stimulation (Fz, F1, F3, F5, F7, FCz, FC1, FC3, FC5, FT7, Cz, C1, C3, C5, T7, CP1, CP3, CP5, TP7, P1, P3, P5, P7; Fig. 1b). It is often not possible to know the time-windows and scalp distributions of ERP components *a priori*. We therefore identified this information *post-hoc* using visual inspection on a *collapsed localizer* (Luck and Gaspelin 2017), where the data from all participants and experimental conditions was averaged into a single waveform. Statistical analysis of each SEP component was restricted to electrodes where the magnitude of its signed amplitude in the waveform was largest. As this approach hides any differences between conditions, since they are all averaged together, it is an ideal approach for choosing electrodes-of-interest when they are not known before collecting the data. Importantly, it is typically free of experimenter bias when the data is collected using a within-subjects design (Luck and Gaspelin 2017).

The time window of each component was also determined using the aforementioned collapsed localizer. For each SEP, we drew a temporally symmetric window around its peak amplitude. The temporal boundaries of the components were chosen to be consistent with what has been used in the literature previously (Allison et al. 1992).

Based on previous studies investigating electrophysiological signatures of somatosensory processing, we focused our analysis on five main components of interest: the P45, N60, P100, N140, and P200. The short-latency P45 component was calculated as the mean amplitude at C3, C5, CP3, and CP5 between 34 and 54 ms post-shock. The short-latency N60 component was calculated as the mean amplitude at F1, F3, FC1, and FC3 between 54 and 70 ms post-shock. Both the P45 and N60 reflect stages of sensory processing in SI (Allison et al. 1992). The mid-latency P100 component was calculated as the mean amplitude at CP1, CP3, P1, and P3 between 70 and 110 ms post-shock. The P100 is the earliest component to index visual-tactile integration (Sambo) and reflects the maintenance of a multisensory model of the body (Cardini and Longo 2016). It has known generators in SII and PPC (Forss et al. 1994; Barba et al. 2004). The long-latency N140 component was calculated as the mean amplitude at C5, T7, CP5, and TP7, between 110 and 170 ms post-shock. Modulations of the N140 are the most common index of the effects of early tactile spatial attention (Garcia-Larrea et al. 1995; Macaluso and Driver 2001). Lastly, the vertex P200 was calculated as the mean amplitude at Cz, FCz, and Fz between 170 and 260 ms post-shock. The P200 is a common index of perceptual saliency across all sensory modalities (Mouraux and Iannetti 2009).

All statistical analysis were conducted using JASP version 0.8.5 (JASP Team 2018). To determine whether either object-interaction condition modulated somatosensory cortical processing, we performed a 2 (time: pre, post) x 2 (effector: tool, hand) repeated measures ANOVA on the mean amplitude of each component. The main statistic of interest is the interaction between the two factors, as this would indicate that the two object-interaction conditions modulated the specific component differently. To account for the five interaction tests, we set our alpha level to .01 (i.e., Bonferroni correction). Significant interactions were followed up with paired *t*-tests.

The inferences one can draw from frequentist statistics are limited by the fact that *p*-values quantify the probability of your data given the null hypothesis. However, scientists often wish to know the opposite—the likelihood of a hypothesis given the data—in order to derive stronger inferences about what the data might mean. The likelihood of a hypothesis given the data can be quantified using Bayesian statistical approaches. Therefore, to further quantify the effect of object interaction on each evoked potential, we compared the pre and post amplitudes for both tool and hand using an analogous Bayesian repeated measures ANOVA. As with our frequentist analysis, the interaction between time and effector was the main statistic of interest. The Cauchy prior width was set to 0.707, the default prior in JASP.

Component-independent analysis: The high-dimensional nature of EEG data means that it suffers from a multiple comparisons problem (Kilner 2013). In our case, this could amount to 14,440 comparisons (64 channels x 225 timepoints). The previous analysis goes some way towards alleviating this problem, but does so at the expense of potentially introducing biases and circularity into the analysis. We therefore performed a data-driven component-independent analysis to verify that results from the prior analysis were independent of our chosen electrodes and timepoints. Specifically, we used a non-parametric permutation test (10,000 permutations) with cluster-based correction (Maris and Oostenveld 2007) as implemented by the Mass Univariate Toolbox (Groppe et al. 2011). To isolate the interaction (our main statistic of interest), we performed the cluster-based analysis on the difference waves between pre- and post-conditions for tool use and hand use. The analysis included all electrodes and targeted all timepoints between 30 and 230 ms, ensuring that we captured the peaks of all components of interest in every participant's dataset. Importantly, the clusters returned by the analysis are component-independent and merely reflect spatio-temporal regions of elevated significance.

Cluster-based tests use soft-correction to control for Type-II error rates (Groppe et al. 2011). It is therefore a known problem that time points at the edge of a cluster have an elevated false-positive rate and therefore these regions should be treated with caution (Sassenhagen and Draschkow 2019). We took two extra steps to ensure that time points in the clusters reflected robust results: First, we re-ran the permutation test using the component-specific time windows that matched the timespan of any observed cluster. For example, if we observed a cluster spanning 62 to 100 milliseconds, we would re-run the permutation test on two time-windows: 54 to 70 (N60) and 70 to 110 (P100) milliseconds. Second, we re-ran the permutation test with the more conservative alpha level used in the component-based analysis (i.e., .01).

Results

Neither tool use or hand use influenced target detection

All participants performed a target detection task that required them to keep their spatial attention constant throughout each block. Their task was to detect infrequent targets (double shocks separated by 50 ms) among frequent non-targets (single shocks). When targets were detected, participants responded by lifting their left foot off of a foot pedal as quickly as possible. Table 1 shows the results for each experimental condition for two dependent measures of behavioral performance: accuracy and reaction time. We did not find any statistical evidence that target detection accuracy (all $Fs < 0.7$, $Ps > .4$) or reaction time (all $Fs < 1$, $Ps > .3$) varied across blocks. This suggests that the ability to maintain spatial attention to the location of the electric shocks was not affected by our experimental manipulations. Therefore, any modulation we see in SEP components are not likely due to effects of spatial attention.

Tool use modulates the amplitude of the P100

Median nerve stimulation leads to several well-defined somatosensory evoked potentials (Allison et al. 1991). Consistent with previous studies, we observed five prominent components within the first 300 ms post-shock in all experimental conditions: P45, N60, P100, N140, and P200. Figure 2 shows the grand average collapsed across conditions for the electrode site C3 as well as the scalp topography of each component. The time course and scalp topography of each component is consistent with prior studies.

Only the P100 showed a significant change in its mean amplitude following tool use (Table 2; Fig. 3). We observed a significant interaction between time (pre, post) and type of object interaction ($F_{1,17} = 12.62$, $P = .002$, $\eta^2_p = .43$). Follow-up *t*-tests revealed that tool use led to a significant increase in P100 amplitude in electrodes over the contralateral sensorimotor cortex ($0.82\ \mu v \pm 0.15$; paired *t*-test: $t_{17} = 5.06$, $P < .001$, $d_z = 1.19$; Fig. 3a). An increase in P100 amplitude was observed, to some extent, in the majority of our participants (15 out of 18; Fig. 3b). In contrast, and as expected, we did not observe a significant modulation in P100 amplitude following hand use ($-0.01\ \mu v \pm 0.12$; $t_{17} = -0.05$, $P = .96$, $d_z = 0.01$).

As can be seen in Figure 3a, we observed a qualitative difference in the P100's baseline (i.e., 'pre' condition) for tool use and hand use. One potential explanation for this is that effects of tool use last longer than the eight-minute break that separated each block. We would therefore expect that when tool use was performed first, the baseline amplitude in the 'hand use' block would not have returned fully to the baseline amplitude in the 'tool use' block. To test this assertion, we performed an exploratory 2 (order: hand-first; tool-first) x 2 (block number: one; two) mixed-ANOVA with 'order' as a between-subjects factor and 'block number' as a within-subjects factor (Figure 4). We observed a significant interaction between factors ($F_{1,16} = 6.56$, $P = .02$, $\eta^2_p = .21$) but no other main effects (all *Fs* < 1.7, all *Ps* > .21). As expected, when participants performed tool use first, the baseline of the hand-use block (2.65 μv ± 0.52) remained significantly elevated relative to the baseline of the tool-use block (2.06 μv ± 0.44; $t_8 = 3.33$, $P = .01$, $d_z = 1.11$). This pattern was not observed for participants who performed hand use first (pre-hand vs. pre-tool: 1.77 μv ± 0.49 vs. 1.42 μv ± 0.25; $t_8 = 1.09$, $P = .31$, $d_z = 0.36$); if anything, we observed a numerical decrease in the amplitude of the pre-tool use baseline.

Furthermore, repeating the original ANOVA with 'order' as a between-subjects factor found the same time x effector interaction but no additional effects including the factor 'order'. Tool use led to an increase in the amplitude of the P100, regardless of whether the first block was for tool use (Figure 4a) or hand use (Figure 4b). Therefore, the magnitude of the observed P100 effect did not depend on the order of the object-interaction tasks, even if there were minor differences in baselines.

No effects of tool use or hand use were observed in any of the other four components (Fig. 5). We did not find a significant interaction for either early SEPs: P45 ($F_{1,17} = 1.37$, $P = .26$, $\eta^2_p = .07$); N60 ($F_{1,17} = 2.48$, $P = .13$, $\eta^2_p = .13$). We also did not find a significant interaction for the later SEPs: N140 ($F_{1,17} = 0.22$, $P = .65$, $\eta^2_p = .01$); P200 ($F_{1,17} = 0.05$, $P = .83$, $\eta^2_p < .01$). The full statistical details for each component can be seen in Table 2. As with the P100, these results did not change when we performed an exploratory ANOVA that included the between-subjects factor ‘order’ (all *Fs* < 3, all *Ps* > .1, for all components).

Our Bayesian analyses converged to a similar picture. We found strong evidence for an interaction between effector and time in the P100 component. Namely, the interaction results were BF_{10} = 136.57 times more likely to be explained by the experimental hypothesis than the null hypothesis. In contrast, evidence for or against the null hypothesis was ambiguous for the P45 (BF_{01} = 1.54) and N60 (BF_{01} = 1.22). We did, however, find weak evidence in favor of the null hypothesis for the N140 (BF_{01} = 3.03) and the P200 (BF_{01} = 3.14).

A data-driven analysis reveals the robustness of the P100 modulation

We next performed a data-driven cluster-based analysis that did not depend on the *a priori* spatio-temporal selection of SEP components. This analysis compared the pre-post difference waves for each condition and is equivalent to the above interaction. As with the prior analyses, we found a significant difference between the effect of tool use and hand use (all *Ps* < .05). These clusters spanned the time period of 58 to 128 ms post-shock and covered the centro-posterior portions of the scalp bilaterally (Figure 6). Noticeably different from our prior analysis, this cluster included the majority of the time window for the N60. However, the significant effects were in channels over the positive portion of its dipole (see the scalp topography in Figure 2).

We followed up these findings with two additional approaches: First, we performed cluster-based analysis on the component-specific time windows of the N60 and P100. If the significant effect in either component reflects a real difference and not a false positive, the same results should be observed in an analysis targeting their time window. As expected, we observed significant clusters in the P100 time window (all *Ps* < .05). In contrast, no significant clusters were found in the N60 time window. Second, we lowered the alpha level to .01, as was used in our component-dependent analysis. This revealed a significant cluster from 76 to 118 ms post-shock covering the centro-posterior portions of the scalp bilaterally. Noticeably absent were time points in the time window of the N60.

Discussion

In the present study, we used ERPs to investigate how using a tool modulates somatosensory cortical processing. SEPs were measured before and after two object-interaction conditions—tool use and hand use—in which participants picked up balloons for 8 minutes. To successfully use a tool, sensorimotor models of the body must adapt to its weight and geometry, a recalibration that is not necessary when only the hand is being used. As expected, sustained use of the hands to pick up the balloons did not modulate the amplitude of any SEP. Using a tool, conversely, led to a bilateral modulation of the amplitude of the P100 at posterior recording sites around sensorimotor areas. This modulation was observed in both our component-dependent and component-independent analyses. Our component-independent analysis also found a significant modulation within the time window of the N60, though the evidence for this effect was weak. The implications of these findings are discussed in more detail below.

Effects of tool use on somatosensory evoked potentials

The effect of tool use on somatosensory perception is well-documented. Brief training with a tool has been found to modulate the perceived locations of touches in space (Cardinali et al. 2011), the space between two tactile points (Canzoneri et al. 2013; Miller et al. 2014; Miller, Cawley-Bennett, et al. 2017; Miller, Longo, et al. 2017), and where user's judge the midpoint of their arm (Sposito et al. 2012; Garbarini et al. 2015; Romano et al. 2019). These results have been taken as evidence that tool use affects the represented size of body parts by the sensorimotor system. However, it has been unclear whether this reflects a change in early or late stages of somatosensory processing. This was our main motivation for using ERPs to measure tool-induced somatosensory plasticity.

We found strong evidence that tool use modulated the P100, an SEP that has been implicated in mapping somatosensory inputs within a sensorimotor coordinate system (Heed and Röder 2010) and aligning tactile and visual maps of space (Sambo and Forster 2009;

Cardini and Longo 2016). For example, a recent study by Cardini and Longo (2016) found that incongruent visual and tactile feedback disrupted intracortical inhibition within the time window of the P100. Specifically, incongruent multisensory stimulation led to a "blurring" between finger representations. In this context, our finding suggests that tool use modulated a stage of processing where touch is mapped within a coherent model of the body.

The present results can provide some insight as where tool-induced sensorimotor plasticity happens in the human brain. Studies using intracranial recordings and MEG have identified generators of the P100 in SII (Barba et al. 2004) and PPC (Forss et al. 1994; Mauguière et al. 1997). Further, monkey neurophysiology (Avillac et al. 2007) and human transcranial magnetic stimulation (Konen and Haggard 2012) studies demonstrate that multisensory parietal regions are activated within the time window of the P100 used in the present study. The generators of the P100 are also consistent with two decades of work that has implicated the parietal lobe in several important functions for tool use (Johnson-Frey 2004; Maravita and Romano 2018), such as planning tool use actions (Johnson-Frey et al. 2005) and performing visuo-motor transformations (Stark and Zohary 2008). Many of these regions also have overlapping tool and hand representations (Peeters et al. 2009; Gallivan et al. 2013). Taken at face value, these studies suggest that using a tool modulates sensory processing in SII and/or PPC in humans, consistent with previous findings in macaques (Iriki et al. 1996; Hihara et al. 2006; Quallo et al. 2009). The mechanisms underlying the influence of tools on sensorimotor models of the body may have been preserved across primate evolution.

It is unclear from the present results whether tool use modulates early stages of processing linked to activity in primary somatosensory cortex (Allison et al. 1992). Our Bayesian analysis found that the evidence was ambiguous as to whether tool use modulated the amplitudes of the P45 and N60. Our data-driven analysis, on the other hand, did find some evidence that tool use modulated the N60. At first glance, this finding appears consistent with Schaefer and colleagues (2004), who found that tool use changes the dipoles of the M60 (the evoked-field equivalent of the N60). However, the evidence for a modulation of the N60 in our dataset was rather weak, given that the effect was absent in two follow-up analyses. It is therefore still an open question as to whether tool use has lasting effects on activity in primary somatosensory cortex.

Factors constraining tool-induced somatosensory plasticity

The factors contributing to tool-induced somatosensory plasticity are an important topic of research that has recently begun receiving substantial attention. Changing the spatial aspects of (multi)sensory feedback modulates tactile perception in a similar manner as has been shown following tool use (Taylor-Clarke et al. 2004; De Vignemont et al. 2005; Tajadura-Jiménez et al. 2012). For this reason, several authors have hypothesized that changes in sensory feedback during tool use are a primary driver of its effects on body representations (Miller et al. 2014; Serino et al. 2015). For example, we have previously shown that a visual illusion of tool use can modulate tactile distance perception on an arm that is stationary (Miller, Longo, et al. 2017). Furthermore, the hand-shaped exoskeleton used by participants in the current study specifically modulates tactile perception on the hand but leaves tactile perception on the arm unaffected (Miller et al. 2014). Congruency between the shape of a body part and the tool may constrain where plasticity takes place. In all, these findings suggest that tool-induced plasticity is a multisensory process, consistent with the functional profile of the P100 component (Sambo and Forster 2009; Cardini and Longo 2016).

It is well-established that tool-induced plasticity requires the user to actively wield the tool (Maravita et al. 2002; Witt et al. 2005), though how much tool use is needed likely depends on how the tool is being used. Several studies have found the wielding a tool modulates sensorimotor processing almost immediately (Holmes et al. 2007) or within minutes (Cardinali et al. 2009; Miller, Cawley-Bennett, et al. 2017; Miller, Longo, et al. 2017). The rapid effects of tool use are even found with unfamiliar tools (Baugh et al. 2012), such as in the present study. However, a recent study that did not require active lifting during tool use only found effects after several weeks of training (Marini et al. 2014). In this study, participants were trained to grasp objects using a functional robotic hand that was controlled via the participant's own electromyographic signals. The necessary length of training suggests that proprioceptive feedback during active tool use is a critical driver of sensorimotor plasticity on a short timescale (Martel et al. 2019). Proprioception conveys information about the physical characteristics of the tool, such as its inertial properties (Turvey and Carello 2011). Taking these properties into account is necessary for accurately using tool and is likely a main reason why tool use leads to sensorimotor plasticity in the first place.

Germane to the present discussion is whether or not the exoskeleton used in the present study is indeed a "tool". According to a popular set of criteria for distinguishing between tools and non-tool objects (Holmes and Spence 2006), a "tool" must be unattached from its user, held/carried in the hand, and have the possibility of being oriented independently of the body. Though it was not permanently attached to the user, use of the exoskeleton in our task required it to be strapped to user's forearm. Furthermore, its orientation in space was strongly coupled with the arm and hand. One could therefore argue that the exoskeleton failed to meet the criteria of a "tool". However, by this definition, the exoskeleton qualifies as a tool if it is wielded in hand but stops being a tool the moment it is strapped to the arm, even if it is used in the same goal-directed manner. It is likely in both cases that similar plasticity is required to perform the task. We therefore believe that the aforementioned criteria may be too restrictive. Perhaps a more informative approach to addressing this question is determining whether the brain would treat the exoskeleton any differently than a tool that fulfilled the above criteria.

Along similar lines, the exoskeleton used in the present study is considerably different than tools typically used to study tool-induced plasticity (e.g., rakes, mechanical grabbers), which often extend the user's reaching space. Several studies have reported that short tools (e.g., 20 cm in length) do not lead to significant plasticity in the represented length of arm (Sposito et al. 2012; Patané et al. 2017). However, the representation of the hand can indeed be updated by tools whose functions and shape are more 'hand-like', such as pliers (Umiltà et al. 2008; Cardinali, Brozzoli, Finos, et al. 2016) or the exoskeleton used in the present study (Miller et al. 2014). Nevertheless, it raises that important question as to whether the observed modulation in the P100 would be found in other tools and in other tasks. Addressing this question is beyond the scope of the current study.

The relationship between tool-induced plasticity and motor learning

It is currently a matter of debate as to whether tool-induced plasticity reflects the effects of general sensorimotor learning mechanisms (Franklin and Wolpert 2011) or mechanisms specific to tool use (Martel et al. 2016). How the sensorimotor system recalibrates its model of the arm during tool use appears to be dependent on what is necessary to complete the goal of a task. In a recent study, Romano and colleagues (2019) found that reach-to-grasp movements led to a distalization of the perceived midpoint of the arm whereas swing-to-hit movements led to a proximalization. Furthermore, several studies have found that force-field adaptation—like tool use—leads to lasting effects on the perceived position of the arm (Ostry et al. 2010) and movement kinematics (Ohashi et al. 2019). These studies suggest that the effects of tool use reflect general mechanisms of motor learning. However, whether force-field adaptation—or other classic motor learning paradigms—modulates the represented size of body parts has to our knowledge not been addressed. Thus, the link between motor learning and sensorimotor plasticity following tool use is at present incomplete.

It is possible that the modulation we observed in the P100 was driven by general motor learning and not mechanisms specific to tool use. We may therefore have expected to see a P100 modulation in our hand use condition had it been more difficult. Relevant to this possibility, a recent study by Nasir and colleagues measured SEPs before and after force-field adaptation (Nasir et al. 2013). They observed a significant change in the amplitude of a positive-going SEP within the time window of 70 to 90 ms that was significantly correlated with the magnitude of the adaptation. However, given that it was the earliest component observed in their dataset, it is unclear whether this activity reflects an early P100 or a late P50. Regardless, the direction of their modulation was in the opposite direction as ours (i.e., a decrease in amplitude), making it unlikely that it was driven by similar underlying mechanisms as our tool use effect. That being said, the specificity of our P100 effect to tool use is unclear from the results of our study. Whether motor learning mechanisms underlie tool-induced plasticity requires more attention in future research.

Limitations of the current study

The current study suffers from at least two limitations in its experimental design. First, we left a relatively short time between experimental blocks. It is currently unknown how long the effects of tool-induced somatosensory plasticity last, though some research suggests that it lasts equally as long as the tool use itself (Iriki et al. 1996). In contrast, we found significant carry-over effects from the tool use into the hand use block. Thus, eight minutes of tool use was sufficient to lead to an effect on the P100 that lasted at least twice as long. There is some evidence that a short period of motor learning can lead to changes in somatosensory perception that last for 24 hours (Ostry et al. 2010). In the context of these findings, we may have expected that the effects of tool use also last a considerable period of time. Future studies should take this into account when deciding how long to separate the tool use and control conditions. Second, we did not record any behavioral or neural measures while participants used the tool or their hands to lift the balloons. Doing so would have allowed us to characterize the observed P100 effect in more detail and is crucial for understanding what drives the sensorimotor system to update its internal models in response to the demands of tool use.

Conclusion

In sum, we found significant evidence that using a hand-shaped exoskeleton modulated a mid-latency somatosensory evoked potential called the P100. This component likely indexes the maintenance of an internal model of the body. This pattern of plasticity is therefore consistent with human behavioral studies that have implicated tool use in updating a sensorimotor representation of the body, often called the *body schema*. Furthermore, the neural generators of the P100—SII and PPC—are consistent with monkey studies that have implicated these regions in tool-use learning. Future work is need to fully characterize the neural correlates of tool-induced somatosensory plasticity.

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	Tool Use		**Hand Use**		**ANOVA**		
	Pre	Post	Pre	Post	Tests	*F*	*P*
***Accuracy* (%)**	96.4±1.23	96.5±1.12	96.5±1.23	97.2±1.08	Effector	0.69	.42
					Time	0.21	.65
					Effector * Time	0.38	.55
***Mean RT* (ms)**	420±16	427±18	433±18	420±16	Effector	0.05	.83
					Time	0.12	.73
					Effector * Time	0.97	.34

Table 1. Effect of tool use and hand use on behavior

Mean±s.e.m.

SEP	**Tool Use**		**Hand Use**		**ANOVA**		
	Pre	Post	Pre	Post	Tests	*F*	*P*
P45	1.28±0.21	1.43±0.26	1.37±0.28	1.27±0.26	Effector	0.13	.73
					Time	0.31	.59
					Effector * Time	1.37	.26
N60	-1.04±0.36	-0.85±0.44	-1.11±0.43	-1.04±0.36	Effector	0.25	.63
					Time	>0.01	.96
					Effector * Time	2.48	.13
P100	1.74±0.26	2.56±0.36	2.21±0.36	2.21±0.34	Effector	0.32	.58
					Time	22.54	<.001*
					Effector * Time	12.62	.002*
N140	-0.79±0.29	-0.68±8.33	-0.79±0.29	-0.74±0.27	Effector	0.06	.81
					Time	0.72	.41
					Effector * Time	0.22	.65
P200	1.88±0.49	1.98±0.40	1.74±0.34	1.90±0.38	Effector	0.36	.56
					Time	1.44	.25
					Effector * Time	0.05	.83

Table 2. Effect of tool use and hand use on all components

Mean±s.e.m. *significant with an alpha of .01; SEP = somatosensory evoked potential

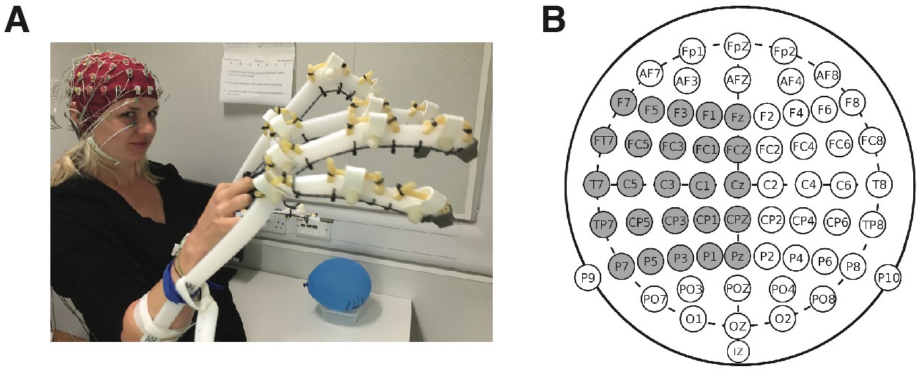

Figure 1. Experimental procedures

(a) Participants picked up balloons in two object-interaction conditions. In the ‘tool use condition’, they used a hand-shaped tool that has been previously shown to modulate tactile perception on the hand (Miller et al. 2014). In the ‘hand use condition’, participants picked up balloons with their hands; this condition served as our control. **(b)** Scalp map of the 64-channel EEG system used in the present study. Channels included in the component-dependent analysis are presented in gray. All channels were included in the component-independent analysis.

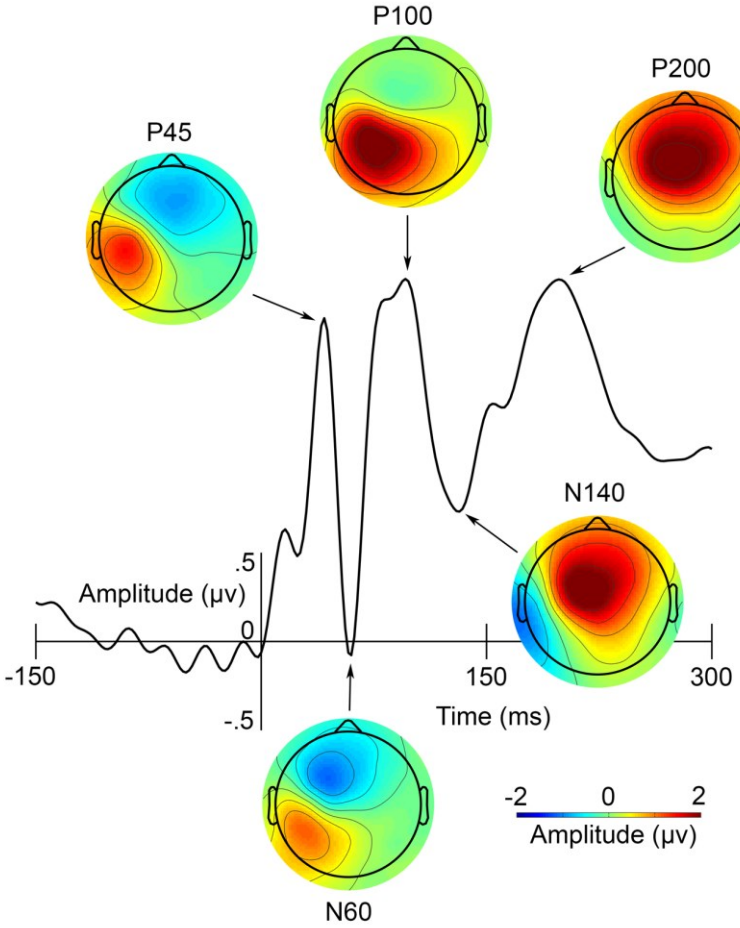

Figure 2. Scalp topography of all SEP components

The current figure illustrates the scalp topographies of each of the five SEP components included in our analyses: the P45, N60, P100, N140, and P200. These components are evident in the grand average SEP waveform for channel C3, which is presented here because it contained electrical volleys relating to all five components.

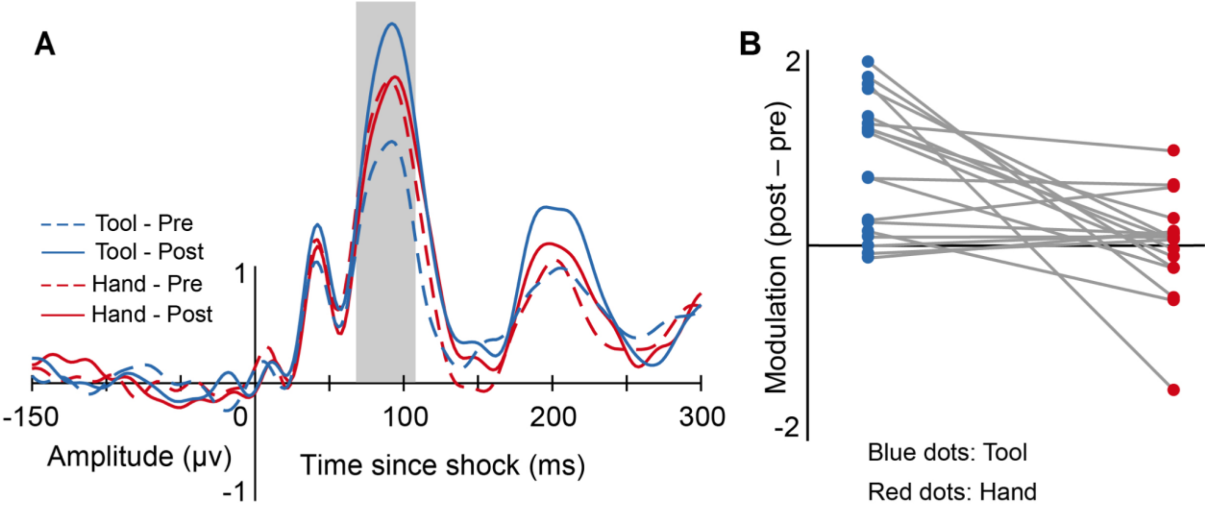

Figure 3. Component-dependent results for the P100

(a) Tool use led to a significant modulation in P100 amplitude. Grand average SEP waveforms before (solid lines) and after (dashed lines) each object-interaction condition: tool use (blue) and hand use (red). The time window of the P100 component is highlighted by the light gray rectangle. As is evident, tool use led to a large increase in the P100 amplitude. Hand use had no effect on the amplitude. **(b)** The change in the mean amplitude of the P100 following tool use (blue dots) and hand use (red dots) for each participant. The amplitude of the P100 increased following tool use in the majority of participants.

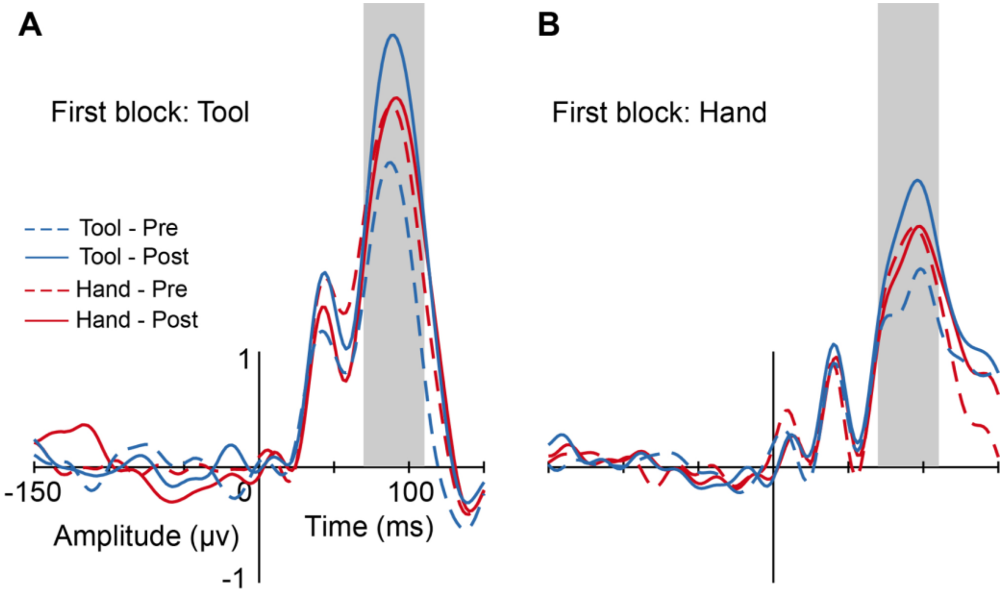

Figure 4. Effects of block order on the P100

(a) SEPs when the first block was tool use (blue lines) and the second block was hand use (red lines). As shown in Figure 3, tool use led to an increase in the amplitude of the P100 (grey rectangle). The baseline for the hand use block (dashed red line) did not return to the amplitude level of the baseline for the tool use block (dashed blue line), likely because 20 minutes was not sufficient for the tool-induced plasticity to completely wash out. **(b)** SEPs when the first block was hand use (red lines) and the second block was tool use (blue lines). Tool use led to an increase in the amplitude of the P100 (grey rectangle) whereas hand use did not. Thus, the effect of tool use on the P100 was independent of block order.

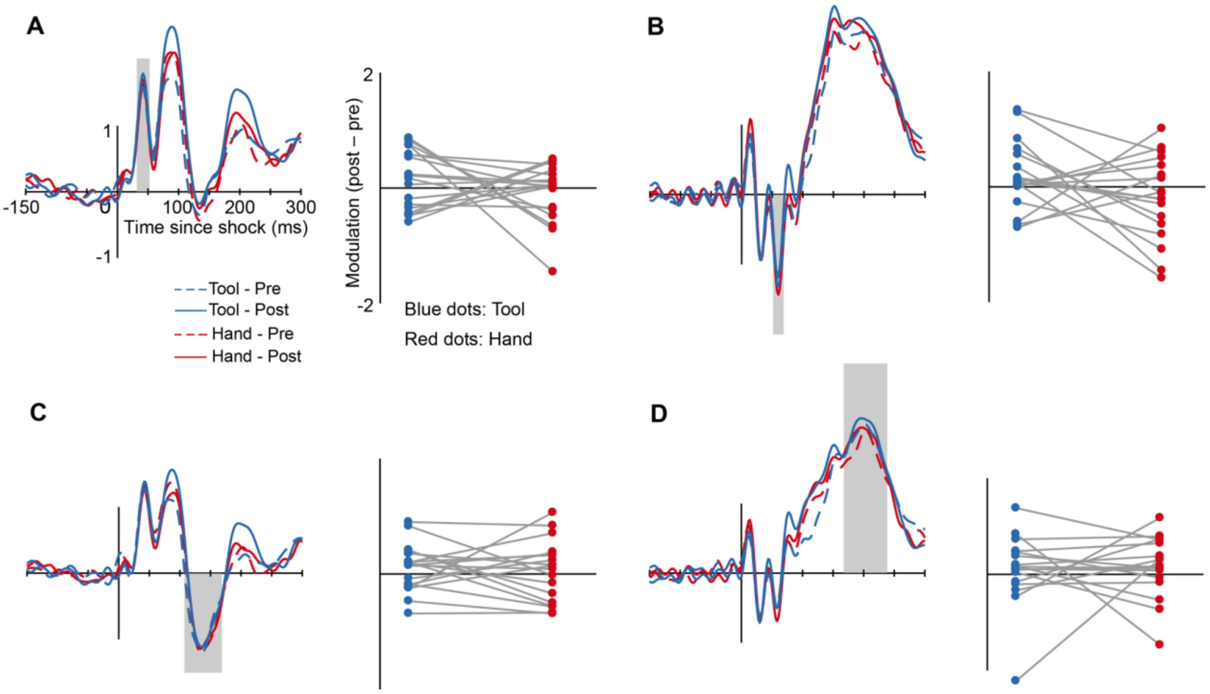

Figure 5. Component-dependent results for all other components

Results for the four remaining components: **(a)** P45; **(b)** N60; **(c)** N140; and, **(d)** P200. The grand average SEP waveforms (Left panel) for each condition; the time window used in the analysis is highlighted by a gray rectangle. No significant effects of object interaction were found for any component. This is supported by inspecting the results for each individual participant (Right panel), where the modulations following tool use (blue dots) and hand use (red dots) are centered close to zero.

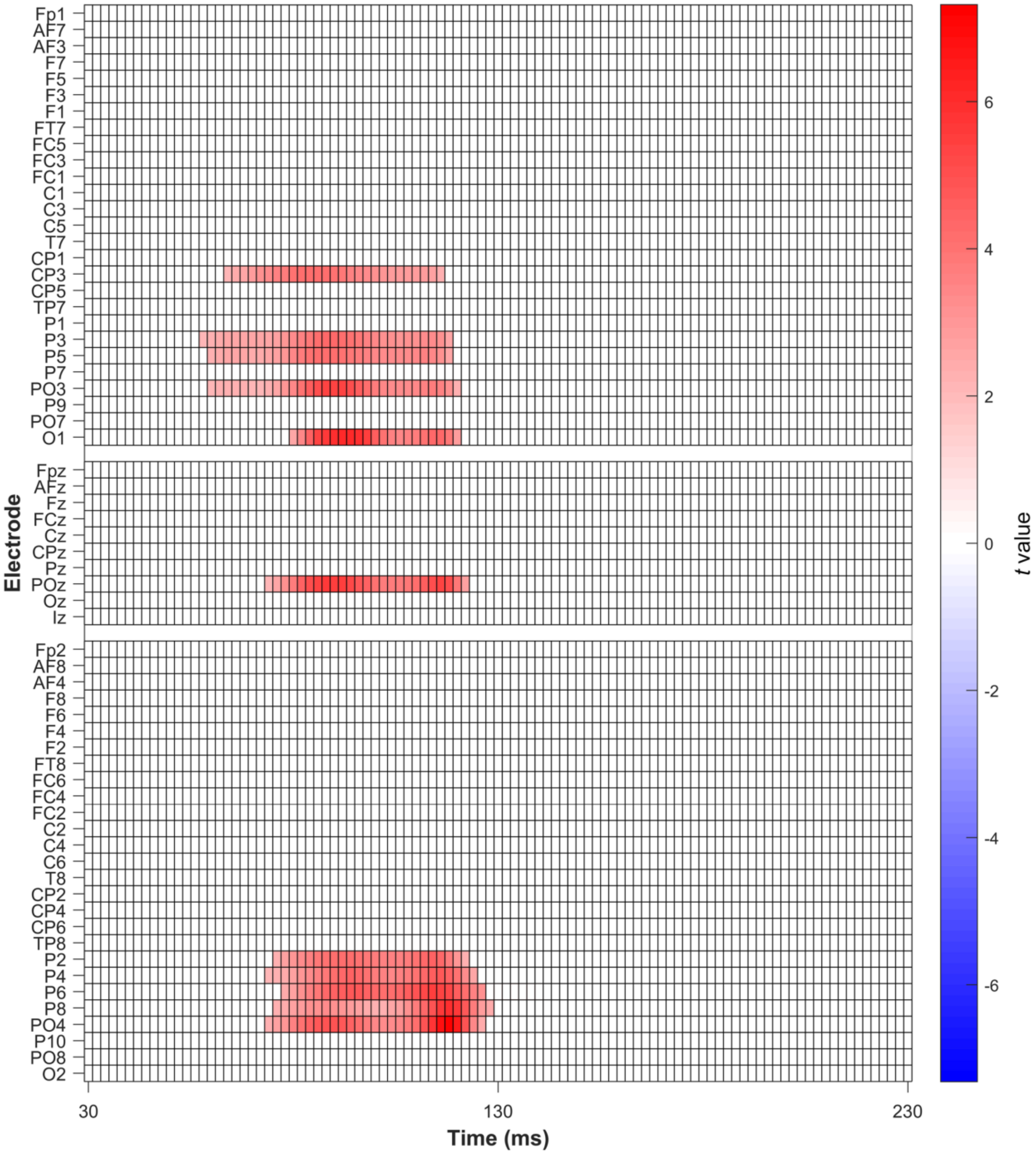

Figure 6. Cluster-based analyses replicate the P100 effect

A cluster-based non-parametric permutation test revealed a significant interaction within the time range of the N60 and P100 (56-128 ms). Significant temporal clusters (red) were found in a subset of channels over bilateral parietal regions. It should be noted that two follow-up analyses (not shown) failed to find effects within the time range of the N60, whereas the effects within the time range of the P100 were always found (see Main Text for details).