COVER PAGE

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Somatosensory EEG

TITLE PAGE

i. Title

Electroencephalography of Touch

ii. Summary/abstract (1-2 paragraphs)

Electroencephalography (EEG) is one of the major tools to non-invasively investigate cortical activations from somatosensation in humans. EEG is useful for delineating influences on the processing pathways of tactile stimulation and to map the dynamics between the cortical areas involved in and linked to tactile perception. This chapter focuses on the process of recording somatosensory EEG from mechanical tactile stimulation, including affective touch, and their related cortical activations. Practical and participant-specific challenges are detailed, and best practices are shared. In addition, the main areas of research in tactile perception using EEG are discussed. These include perception, attention, multisensory perception, as well as emotional and self-other processing. We discuss the major considerations when conducting these types of research.

iii. Keywords (5-10 keywords)

tactile, somatosensory, electroencephalography, EEG, ERPs, SEPs, multisensory, attention, affect

1. INTRODUCTION

Somatosensory stimulation has been combined with electrophysiological recordings since the birth of electroencephalography (EEG) in the late-nineteenth century [1]. Studies on somatosensory EEG have developed along with the EEG technique. While earlier studies used single electrodes with poor signal quality, current EEG systems apply critical adaptations such as shielding, real-time-filtering, dense-arrays and post processing to produce much improved signals. EEG, with its sub-millisecond temporal resolution, is important for understanding the timeline of cortical processes, the dynamics of the regions involved, and cognitive influences linked to tactile signals.

EEG measures electrical activity from postsynaptic potentials from populations of aligned pyramidal cells in the cortex. The cortex is folded, and it is mainly the pyramidal cells perpendicular to the scalp that contribute to the signal, while activation from sulci and deeper tissue do not. For these reasons, EEG activity stems from specific regions of the cortex, which needs to be taken into account when interpreting EEG data. For somatosensory stimulation, this means that signal strength and morphology can vary depending on which body surface is stimulated. This, along with the fact that the electrical signals propagate from their neural source(s), makes localization of the neural generator(s) inexact and contributes to EEG's relatively poor spatial resolution.

EEG generates a large amount of data, which can benefit from one of several powerful analytic approaches to extract more useful information from the data. One such approach is event-related potentials (ERPs), which uses averaging of the cortical responses to many time-locked stimulus presentations to improve the signal to noise ratio. For early (<100ms) somatosensory evoked or event-related potentials (SEPs) it is not uncommon to have

repetitions of over 1000 events. Usually, ERPs later in processing (>100ms) average at least 60 events per condition, but oftentimes more.

SEPs from mechanical or electrical stimulation of the median nerve commonly elicit a set of characteristic positive and negative components from traditionally somatosensory as well as orienting and decision-related areas of the cortex. SEPs before 20 ms stem from peripheral nerves and subcortical activations and are followed by cortical SEPs. The cortical SEPs generally include the N25, P45, N80, P1/P100, N1/N140, P2/P200 and the N2 (about 250 ms after touch onset) and P3 components. Earlier component names reflect the timing of the component peak from the touch onset, while later ones such as P300 actually occur later at 350-500 ms [2-4]. Standards exist for reporting SEPs [5], but unfortunately there are still many reporting inconsistencies. Similarly, guidelines for preregistration of ERP studies and analyses have been developed, but not yet universally adopted [6].

[Fig 1 near here]

SEP components reflect a hierarchical processing stream from thalamus to primary somatosensory (S1) to higher somatosensory areas [7], with early cortical SEP components (P45 and N80) generated in the contralateral S1 [e.g., 8,9]. The observed polarity reversal for these components over ipsilateral and contralateral cortex (and sometimes over more frontal or motor areas) suggests that there is a focal contralateral dipole location (Figure 1). Activation in S1 and secondary somatosensory cortex (S2) is represented based on the area of stimulation according to the somatosensory homunculus and is proportional to innervation. The morphology of SEP waveforms from stimulation at different regions of the body are similar but can show slight differences (Figure 2). After about 100 ms, S2, posterior parietal and frontal regions activate, with the P100 generated in bilateral S2 [e.g., 8,10-13] and the N1, P2, N2 and P3 bilaterally in increasingly frontal areas [4,14,15].

[Fig. 2 near here]

1.1. Attention and SEPs

Selective attention allows us to focus our capacity-limited perceptual systems on currently relevant or salient information. While attention effects have been studied extensively in the visual domain, there is now also a good body of work documenting its influences on somatosensory processing [see 16 for a recent review], showing that selective attention can modulate even early stages of somatosensory processing [17]. Somatosensory ERP studies have shown that spatial attention can enhance amplitudes at early SEP components, from the P45 [9,18] and most commonly the P100 and N140 [19-22], and to a later prolonged processing negativity, which has been linked to in-depth stimulus processing [23]. Most of these studies have investigated the effects of attention when it is directed to one location on the body, usually to one of the fingers. Recently, an effective somatosensory target selection mechanism, the N140 central-contralateral (N140cc) component has been described when participants select a tactile target among concurrent distractors or non-targets. In addition to investigating the neural modulation of touch processing by attention, some studies have shown that the orienting of attention to a body location modifies somatosensory activity in the expectation of touch [i.e., the late somatosensory negativity component; 24,25], and this is modulated in somatic symptom disorder [26].

1.2. Multisensory attention and SEPs

Attention can enhance behavioral performance within as well as between sensory modalities. Multisensory attention involves presenting stimuli from different sensory modalities in spatial and/or temporal proximity to each other. Just like for unisensory spatial attention, attention across modalities can speed up reaction times (RTs), increase accuracy and modulate perception of temporal order for stimuli in another sensory modality presented

at the same location [27]. There are reciprocal interactions in the cortex between all the senses. We have learned from functional magnetic resonance imaging (fMRI) and invasive recordings in monkeys that the senses' cortical pathways connect first, or strongest, to their primary sensory areas and then proceed throughout the cortex. Traditionally, the early sensory areas for vision, audition, and somatosensation (V1, A1, S1) were thought to be unimodal, but this view has changed [see e.g., 28]. Interactions between the senses have been observed as early as the primary sensory cortices under specific conditions.

Spatial coincidence of multisensory stimuli leads to enhanced evoked potentials. Behavioral studies have shown that the better multisensory stimuli coincide spatially, the stronger the attentional effects are between them [29]. This carries over to ERPs too. Both visual and spatial attention to the locations of multisensory stimuli can enhance their evoked potentials [30], while a mismatch of the exact spatial locations can reduce this effect. Hence, it is important to ensure that tactile stimuli coincide spatially with auditory and visual stimulation.

Another important consideration when comparing multisensory ERP activation is the chosen method of subtraction when comparing unisensory visual (V) and tactile (T) conditions to multisensory visual-tactile (VT) conditions. Many studies have used a subtraction of the multisensory activation to the two activations from the unisensory stimuli (e.g., VT - (V+T)) to evaluate the multisensory specific activation, but this may not be optimal [see 31 for discussion], as two activations are subtracted from one. This leads to inequities in the areas that are compared between sensory and non-sensory activation. An alternative comparison is to balance the equation by comparing two activations with two activations, according to the formula (VT+T) - (V+T).

Multisensory spatial attention involving touch might present a slightly different case than between other sensory modality pairings. Touch and vision, for example, are of special interest as tactile information is represented somatotopically in the post-central gyrus, while visual input is organized retinotopically in the occipital cortex. This means that the coordinate systems for touch and vision sometimes have to be dynamically remapped into a coherent representation of the world. This has been applied to understand cortical organization by varying the body posture and looking at visual and tactile interactions [32-34]. Results suggest that it is not the initial hemispheric projection, but external coincidence of visual and tactile stimulation that guides multisensory spatial attention, and that this attentional cueing can be remapped dynamically based on posture changes.

1.3. Affective Touch

Although it has been proposed that in glabrous skin touch comprises four mechanical (SA1, FA1, SA2, FA2) and a number of different thermoreceptors, including C-cold, cool A-delta, C-warm, C-nociceptor (hot), hot A-delta [see, e.g., 35], virtually any somatosensory stimulus evokes SEPs. In hairy skin it looks slightly different which does not have FA1s, but also has hair and field afferents. C-tactile afferents also exist in hairy skin and possibly a sparse number in glabrous skin [36]. However, there is one major distinction that is particularly important for SEPs: between the speed of the fiber, i.e., fast A-beta and A-delta vs. slow C-fiber; however, most somatosensory stimuli produce mixed input, but this can, in principle, be separated in the brain responses by the speed of transmission. [37].

The physiology and basis of C-Tactile (CT) afferents is discussed in detail in Chapter 6. To summarize, these are thin, unmyelinated nerve afferents that predominantly respond to slow gentle stroking, but also very well to simple pressure. In essence, they are slowly-conducting mechanoreceptors. It is hypothesized, therefore, that these are responsible for signaling the

rewarding quality of social or interpersonal touch. Though they respond to all touch, the afferents are show preference for certain types of stimulation, particularly slow (1-10cm/s), gentle (0.3N) touches at skin temperature (32℃). Taken together, these criteria match those of prosocial human interactions such as a gentle caress [38]. However, the physiology of these slow-conducting, unmyelinated afferents means that the process for measuring the temporal response of them is widely under researched.

FMRI has been used extensively to measure the cortical responses to stimulation of these nerve fibers, but to date few studies have incorporated electrophysiological methods. Predominantly, interest in this domain came from Ackerley, Eriksson and Wessberg [39], who reported activation including an ultra-late potential (ULP) recorded for CT-targeted stimulation, later replicated by Haggarty et al [40]. Similarly, a late positive potential is recorded in response to unmyelinated pain afferent (C-nociceptor) stimulation in response to laser heat stimuli [41,42]. Both potentials are recorded in the frontal lobe late in the typical time frame for ERP epochs (>1000ms). This has made the process of finding specific cortical responses difficult. It is not yet clear what the source of this activity is, but it is hypothesized that the activity is from evaluative processes, determining the affective valuation of the stimuli. Despite the latency of these evoked responses, Ackerley et al. [39] showed not only an evoked response late into the ERP epoch, but also that this response changed the time course of its peak based on minor changes (+- 1cm/s) in the velocity of the stroking touch. This reveals the link between the ULP and this specific type of touch input, and further suggests that this response is linked to the offset and subsequent evaluation of the stimuli (Figure 3).

[Fig. 3 near here]

1.4. Emotions and SEPs

Current models of emotion understanding propose that initial visual processing is followed by activation of sensorimotor and somatosensory areas that are key to the experience of the emotion. Among these areas, the motor and sensory cortices including the somatosensory cortices S1 and S2, are critical areas for action representation and they are highly interconnected to the limbic system [43-45].

Ample evidence supports the contribution of the somatosensory cortex to emotion understanding. A novel body of work has allowed for investigation of the selective involvement of the right S1 and S2 cortices in visual emotional processing [46,47]. The core principle of this approach relies on the ERP subtraction method to isolate somatosensory responses from visual processing. Specifically, this method comprises the presentation of an emotional facial expression in two experimental conditions. In one condition, the visual emotional expression is presented alone and EEG activity is recorded from the visual cortex with scalp electrodes (visual-only condition); in another, the visual emotional expression is followed shortly after by tactile stimulation on a body part such as the right finger, while EEG activity is recorded from both somatosensory and visual regions (visual-tactile condition, Figure 4). This experimental setup allows the researcher to subsequently isolate the responses of S1 and S2 over and above the effects induced by other processing regions. It is therefore possible to subtract purely visually-evoked potentials (VEPs; visual-only condition) from tactually-evoked SEPs (visual-tactile condition) during facial processing, obtaining “VEP-free SEPs”.

[Fig. 4 near here]

The efficacy of the ERP subtraction method to isolate somatosensory from visual responses has not only been proven effective in emotion understanding, but also in other domains such as visual perception and memory of bodies and actions [48-51; for an extensive review of the ERP subtraction method, see 50]. The ERP subtraction method can be readily applied to study the involvement of somatosensory cortices in emotional processing in other domains such as music or emotional sounds, as well as for body-related information in both healthy and clinical populations.

1.5. Self-other processing and SEPs

Human touch in the real world is frequently a multisensory experience, which is felt more than merely through the receptors in our skin. Somatosensation, like other bodily senses, thus provides one critical basis for our ability to distinguish experiences that pertain to the self from other sensory impressions in the environment. [for reviews see 52-54; see also 55].

This section showcases the use of SEPs in somatosensory resonance paradigms (also known as visual remapping of touch, VRT, or mirror touch paradigms) to investigate the neural basis of embodiment of one's self and its distinction from the embodiment of others within the wider somatosensory system. Like the emotional paradigms mentioned in the previous section, somatosensory resonance paradigms exploit the propensity of the somatosensory system to activate vicariously. Critically, such activations reflect the self-relatedness of the observed stimuli at different ERP components, which researchers may exploit to investigate the bodily self and its socio-cognitive basis across the lifespan, as well as in clinical disorders. In most variants of this paradigm, observers receive tactile stimuli on their own body, which is hidden from view, while viewing a body being touched or not touched at the same time on a computer screen. Touches are, typically, a brief tap or stroke

with a finger, pencil, cotton bud or brush, shown via video or a series of still images. In behavioural studies, participants are then asked to report on the presence, location or intensity of the touch on their own body. In ERP versions of the paradigm, SEPs are obtained from tactile stimuli in each trial.

[Fig. 5 near here]

SEP studies have shown that resonance effects are stronger and/or occur earlier in cortical processing for more self-related stimuli, such as for touch on human hands compared to rubber objects [56], for touch on one's own face compared to that of another person [57], and for touch on hands shown in first-person compared to third-person perspective [58]. Furthermore, clinical conditions marked by detachment from one's bodily self (e.g., depersonalization or derealization disorder) are also marked by alterations in somatosensory resonance for tactile events on one's own body [57; see also 59].

2. MATERIALS

2.1. Tactile stimulators

Most of the devices used to produce mechanical tactile stimulation for behavioral studies can be applied in the EEG environment, though solenoid, electrical or piezo-electric stimulators are most common (see also Chapters X, X, X). Solenoids can have a mechanical delay, and electrical buzzers have a minimum duration, which need to be taken into consideration, if relevant for the paradigm (**Note 4.3**). EEG recordings will quickly show if any of the stimulators produce artefacts, which then need to be addressed.

For affective touch, a rotary tactile stimulator (RTS) is commonly used, which will send a signal once it starts to move. Force records can be used to deduce the moment the skin is

touched, to time lock the onset of the stimulus. This is more difficult with manual stroking, however, so the equipment needs to be capable of delivering accurate recordings for the beginning of a stimulus. For example, in Haggarty et al. [40] the breaking of a laser beam over the participant's arm signals the beginning of the stroking protocol (**Figure 6a**). Furthermore, Hauser and colleagues [60] used a series of sensory and infrared measurements (**Figure 6b**) to determine the location of the stroking hand in relation to the stroked surface.

[Fig. 6 near here]

2.2. EEG acquisition systems

Commercial systems that record EEG come from a number of companies, including BrainSystems, GTec, Biosemi, Compumedics Neuroscan, Brain Products and Magstim EGI. EEG is very sensitive to timing so it is important that the stimulators are reliable and instant. All of these products can have accurate timing, but it is important to verify your set-up. The systems have different set-up times with gel-free systems being the fastest.

The EEG commonly relies on a trigger to indicate when a stimulus was presented, and it is important that this trigger occurs simultaneously (or reliably with) with the tactile stimulus. Most modern presentation software (e.g., Presentation, MatLab, ePrime, PsychoPy) have accurate timing [61], though this should always be evaluated for each system *in situ*, especially for multisensory presentations **(Note 4.2)**.

3. METHODS

Methods for recording SEPs are mostly similar to those for recording VEPs and auditory evoked potentials (AEPs) and have been detailed elsewhere [e.g., 62]. Here we focus on those aspects of recording and analysis that are specific to SEPs.

3.1. Timing of SEPs

The timings of the characteristic potentials are approximate and vary slightly depending on the experimental paradigm, although they remain quite stable between individuals. In addition, the density and type of mechanoreceptor found in a specific skin site can influence the responses found and their timing. (**Figure 2**). Signal strength and latency can also vary based on factors such as the age, gender, height, skin temperature, sleepiness, drugs/medication and attentional state of the participant [63]. It is worth noting that, especially with mechanical stimulation, the delay between the electrical signal for the mechanical parts to move and the activation of the touch receptors can be several milliseconds, which needs to be considered in study design and also the placing of triggers in the continuous EEG. Information on mechanical delay, force and other stimulus parameters is normally provided by the device manufacturer. Skin contact from mechanical tappers (solenoids) relative to other stimuli and triggers may also be measured accurately via acoustic sensors (e.g. Cedrus StimTracker) with tappers attached to a resonant surface (e.g. table top) or a force sensor in line with the actuator. When comparing multisensory interactions, it is important to keep in mind the different processing times of the constituent stimuli. Vibell et al. [14] found that touch had to lead vision by 38 ms for them to be perceived as simultaneous, but that this could increase to 94 ms depending on how attention was directed. These findings are consistent with those of behavioral studies of the visuotactile and audiovisual prior-entry effects [e.g., 27,64]. Therefore, it is important to calibrate stimulus presentation times between the senses, and to know if the study requires objective or subjective (perceived) simultaneity.

3.2. Vision of the body and SEPs

Non-informative vision of the body can increase tactile acuity [65] and enhance early SEPs [66]. Similarly, attentional modulations of SEPs are usually enhanced when viewing the body parts [67,68], except when selecting between different fingers of the same hand [69,70]. At least on a behavioral level, such effects of vision on tactile perception have been found even when location was task-irrelevant [71], suggesting that simply viewing the body profoundly changes tactile perception, which is also reflected in enhancements of SEPs.

3.3. Multisensory temporal and spatial proximity

The response times to different sensory stimuli can differ significantly within and between participants, and a decision will have to be made on how best to equate these, particularly since non-simultaneous stimuli can have a distracting effect. Some examples of setting the presentation timing of stimuli from different sensory modalities include no adjustment, individual adjustment and staircase procedures [72]. Spatial attention effects between modalities depend on the spatial coincidence of stimuli, and if stimuli are moved further apart it can reduce attentional distraction [73]. In addition, the somatotopic reference frame for touch allows researchers to create conflicting stimulus lateralizations when the arms are crossed. This means that a stimulus presented on the left side and viewed in left visual space can be presented to the right arm. The contralateral projection to the brain results in the multisensory stimulus activating the right hemisphere visual (and auditory), but the left hemisphere somatosensory cortices.

3.4. Body posture, spatial congruency and SEPs

Body posture can have a profound effect on tactile processing, as shown in delayed and less accurate behavioral responses when the hands are crossed compared to uncrossed [74; see 75 for review]. This has been attributed to a rapid recoding of tactile stimuli from a somatotopic to an external reference frame [76]. The influence of body posture has also been documented on SEPs. In particular, attentional modulations are stronger when the hands are close together [77,78], and even within-hand posture effects have been reported [69]. Therefore, the relative location of tactile stimuli to each other in both somatotopic and external space need to be considered in experimental designs [75]. The spatial congruency between the body parts that are seen and felt to be touched may also play a role in somatosensory resonance paradigms.

3.5. Temporal window of emotion SEPs

Hierarchical models of visual processing propose that emotional face processing and other types of face processing require a series of interactions between brain areas, starting from the visual cortex (occipital face area, fusiform face area, and superior temporal sulcus), that feed-forward to central and frontal regions [79,80]. In this vein, Pitcher [81] demonstrated that facial emotion recognition comprises a hierarchical cascade of activations starting in the visual cortex from about 60 - 100ms after face onset, followed by activation in the somatosensory cortex between 100 - 170ms after face onset. Therefore, it is crucial that we probe the state of S1 and S2 with tactile stimulation at the time that somatosensory cortices are maximally involved – that is, between 100 and 170ms after the onset of the emotional visual stimulus. Given that tactile information transduced by sensory fibers in the periphery takes around <20ms to reach S1, an ideal tactile stimulation onset lies between 100 and 140ms after the emotional visual stimulus onset.

3.6. Emotion and self-other SEPs, lateralization and correspondence between stimuli

The majority of studies demonstrate that the somatosensory involvement in emotion processing is lateralized to the right hemisphere [47,81,82]. Similarly, self-related processing is more strongly lateralized to the right hemisphere across wider cortical networks [83]. Therefore, locations on the left side of the body (e.g., the left finger) are likely to be good candidates to study somatosensory processing related to visual emotions and self-other processes, especially if the duration of an experiment necessitates a choice between stimulation or left or right sides. In addition, a recent study [84] has demonstrated that right S1 and S2 do not exhibit a general excitatory response to emotional stimuli, but they do contribute in a discrete somatotopic fashion to specific emotions. As an example, activations in the finger S1 and S2 recorded during the processing of angry faces show a significantly different pattern of response than the finger S1 and S2 activity recorded in response to sad face processing. Relatedly, the experiential match between seen and felt touch may amplify resonant responses in S1, which also encodes the sensory qualities of touch [84]. Rigato et al. [58] recently argued that vicarious enhancement of the P45 component may be opposite in direction, depending on whether the seen and felt sensory qualities were more or less similar in different SEP studies (e.g., soft touch or brushes, pointed taps, vibrations). Researchers may therefore wish to maximize, or purposefully manipulate, visual and tactile matches.

3.7. Vicarious touch parameters

There are two further critical aspects of somatosensory resonance paradigms. One is that the viewed no-touch stimulus should contain similar visual information as the touch stimulus (e.g., similar motion paths but without the final contact) in order to avoid SEP enhancements being confounded by stronger activation of the visual system or by greater attention in more visually exciting viewed touch trials. The other is to ensure participants' attention to the visual stimulation (specifically, the touch event), which may be necessary to obtain an optimal

resonant response from the primary somatosensory system. An fMRI study by Chan & Baker [85], where participants responded to infrequent visual events unrelated to observed touch, found that vicarious activations were restricted to posterior parietal cortex and absent from S1 and S2. To increase the relevance of seen touch events in SEP studies, participants could silently count and eventually report infrequently seen 'double taps' [57].

3.8. Affective touch parameters

It is important to consider previous psychophysical studies when designing an affective touch study, but it is especially important to take into account the 'gold-standard' microneurography studies (Chapter XX), which show the kind of stimuli that these nerve afferents respond to optimally. Studies may use "affective touch" as a descriptor for their stimuli, but this is not always the case. Two important points to consider are first, that stroking touch delivered at 3cm/s is optimal for CTs, and that this is not greatly affected by the manner of stroking (i.e., RTS, brush, hand, or glove), so this should be considered the basis of affective touch probing. However, if you stroke a rough surface over the skin, it is not at all pleasant, but CTs would still respond similarly. This is the difference between (positive) affective touch and CTs. CTs are just encoding the touch and the A-beta afferents would be very much involved in the conscious pleasantness perception too (even if it is not directly encoded in their firing). Second, the onset of the touch should be controlled to ensure that the epoch is precisely time locked, which requires the use of creative methods to ensure the beginning of the stroking is accurate. A- and C-type fibers have very different conduction velocities, so these need to be considered during the planning of the study and extraction of epochs (**Note 4.1**).

4. NOTES

4.1. Peripheral conduction velocity

When comparing the cortical responses to affective touch, the conduction velocity of CTs means that the signal does not reach the cortex as quickly as other sensory modalities. For example, Aβ touch afferents have a conduction velocity of around 50m/s, while CTs conduct at a velocity of less than 1m/s, therefore reaching the cortex much later. In Ackerley et al. [39] and Haggarty et al. [40] this was overcome by being aware that a 700ms delay was added to the epochs to account for the approximate distance from the stroked surface to the cortex and the conduction velocity of these afferents. Furthermore, this distinction between conduction velocities has been considered in facial electromyography research, allowing for conduction velocity to account for delays in affective arousal (Ree, Mayo, Leknes & Sailer, 2019).

4.2. Acoustic interference

Tactile stimulators typically make a noise that is perceivable by participants and that can confound the processing of tactile stimulation. To mask sounds made by the tactile stimulators, it is recommended to play white noise (~65 dB, measured from the participants' head) with loudspeakers at a distance of about 90 cm from the participants' head. Headphones (e.g., in-ear) may also be used to play white noise, but care must be taken to avoid interference with EEG recording. If earlobe (reference) electrodes are used with in-ear headphones, it can help to place these at the back rather than the front of the earlobe.

4.3. Tactile interference in EEG recording

The driving pulse for the tactile stimulators from the computer is commonly a square wave, consisting of all frequencies, which may introduce electrical noise in the EEG recording. The electrical discharge from the tactile stimulators can sometimes be detected in the EEG trace and should be eliminated through, for example, grounding of the device. A sinusoidal pulse with a gradual incline and decline usually stimulates equally well, but without potential noise.

Any stimulator-related noise usually happens before SEPs and can be removed during offline processing if needed.

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FIGURE CAPTIONS

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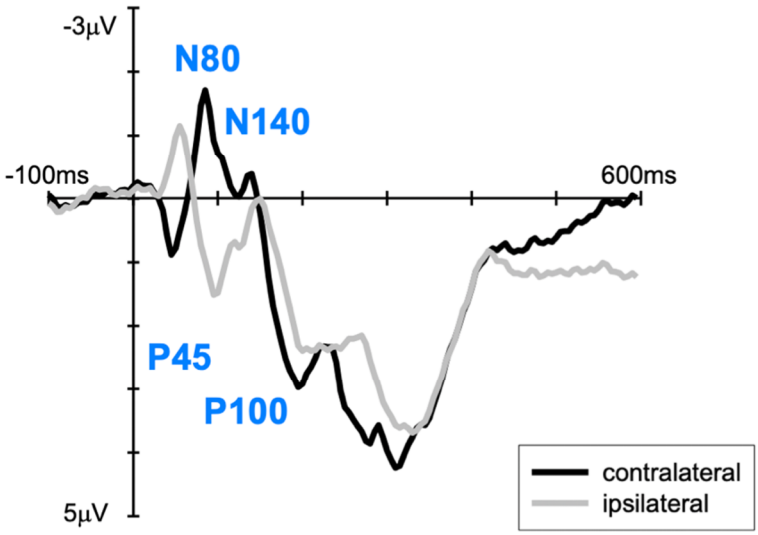
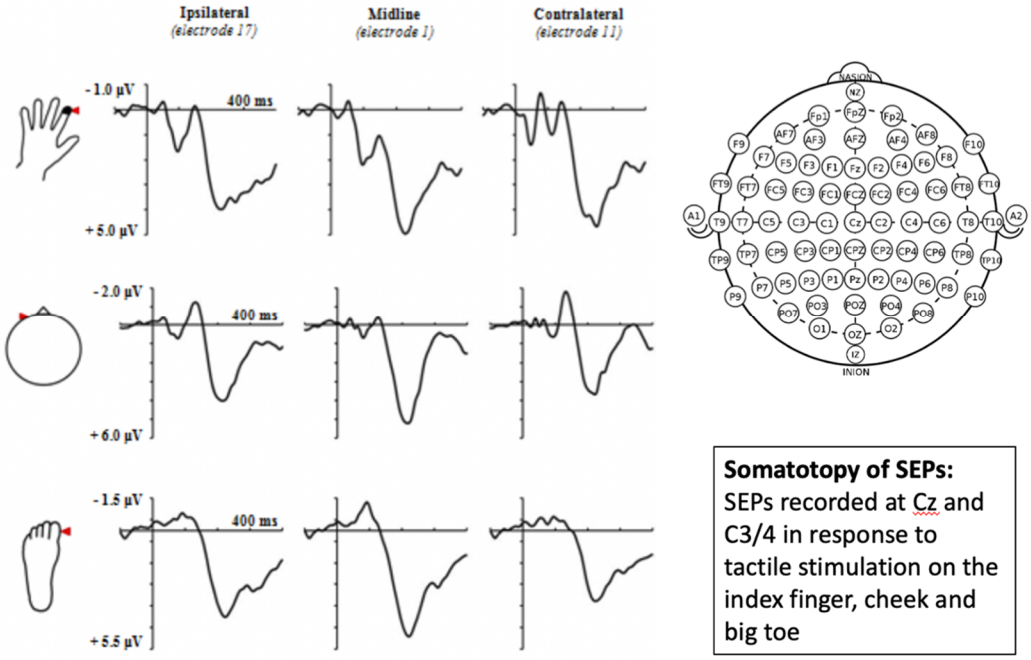
FIGURES



Polarity reversal for early SEP components over ipsilateral and contralateral cortex suggesting single contralateral dipole location. SEPs recorded at C3/4 in response to tactile stimulation on the index finger

Figure 1. SEPs recorded at C3/4 in response to tactile stimulation on the index finger. Polarity reversal for early SEP components over ipsilateral and contralateral cortex suggesting a single contralateral dipole location.



Somatotopy of SEPs: SEPs recorded at Cz and C3/4 in response to tactile stimulation on the index finger, cheek and big toe

Figure 2. Somatotopy of SEPs: SEPs recorded at Cz and C3/4 in response to tactile stimulation on the index finger, cheek and big toe

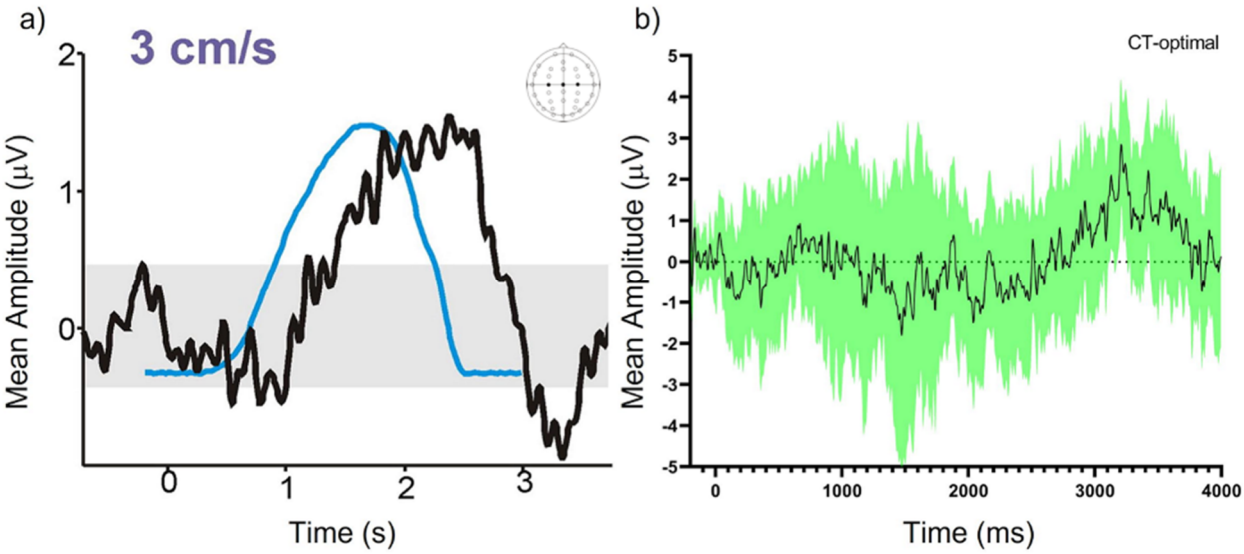


Figure 3. The typical time course of an ULP is atypical, considering past research studies. The black line is the ERP response and the blue line is the force measured by the RTS (stroking robot). The afferents transmitting responses to affect touch are slow conducting, and so do not reach the cortex until a time when most sensory stimuli typically have already been processed, particularly the earliest stages of primary sensory processing. a) shows the ULP measured by Ackerley et al. [39] and b) that measured by Haggarty et al. [40]. Reproduced with permission from Elsevier and Wiley.

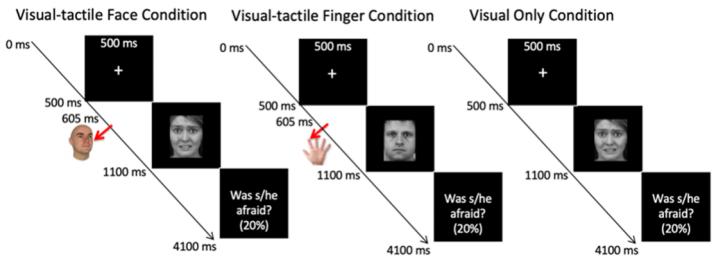


Figure 4: Typical experimental setup comprising two visual-tactile conditions, visual-tactile face condition (VTFAC) and visual-tactile finger condition (VTFIC), and visual only condition (VOC) in an emotion task. In VTFAC and VTFIC, tactile probes were delivered 105ms after the face onset to the face and the finger, respectively. Participants were instructed to observe the emotions, and in 20% of trials they were asked to indicate the emotional content of the stimulus after presentation of the face (Reproduced from Sel, Forster, and Calvo-Merino, 2014 under Creative Commons license)

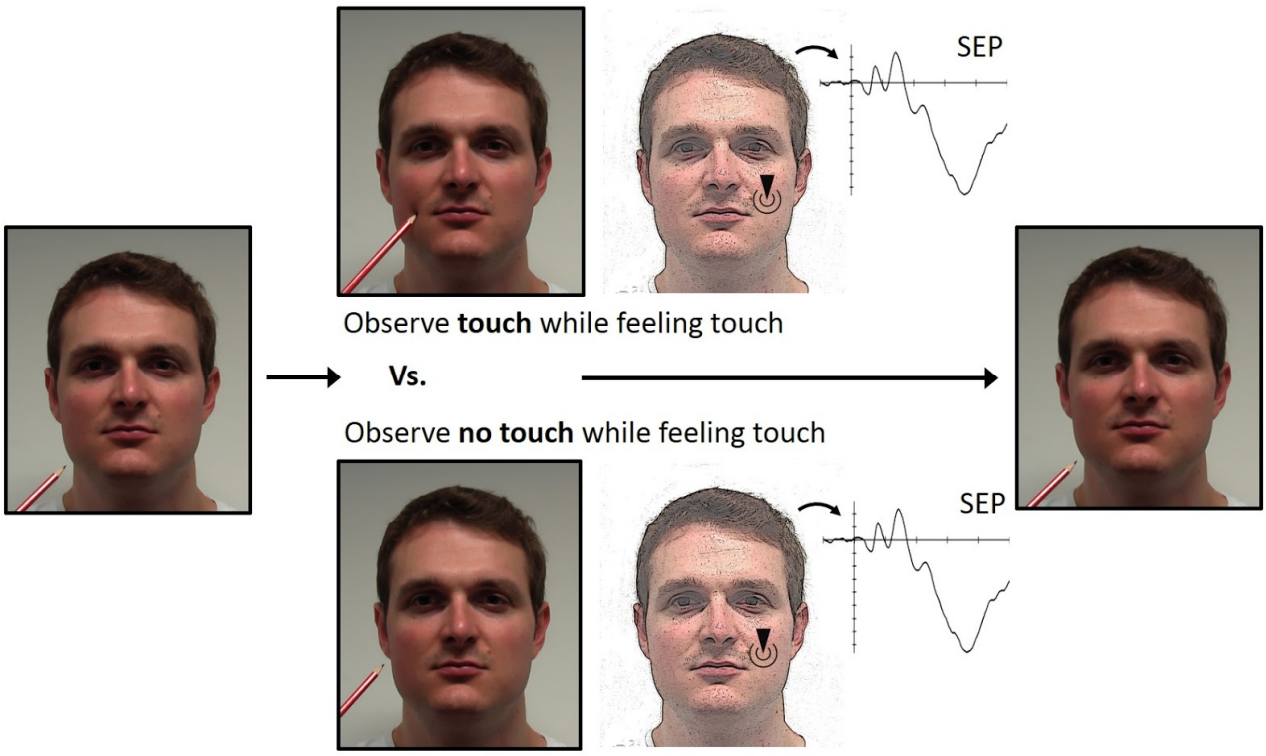


Figure 5. Example trial design for embodiment and self-other processing studies. A trial starts and ends with the visual presentation of a body and a tactile stimulation device (in this example, an image of the self-face and a pencil). This is replaced by a brief presentation of a visual touch (centre top left) or, in separate trials, of a visual no touch (centre bottom left) together with an actual tactile stimulus felt on the observer's own body (centre top and bottom right). As embodiment entails the internal simulation of observed bodily events, SEPs in touch-viewed trials should be enhanced relative to no-touch-viewed trials (somatosensory resonance).

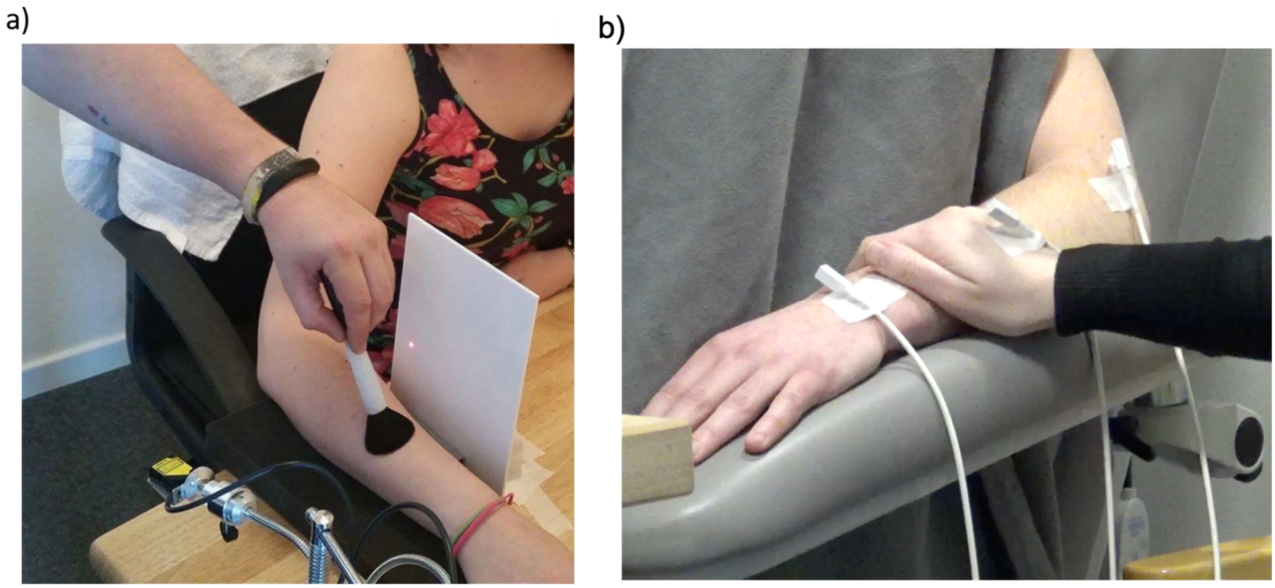


Figure 6. Time sensitive measures of touch stimulation. In a) Haggarty et al. [40] use the breaking of a laser beam over the arm to signal when the stroking has begun, this signal is sent directly to the EEG acquisition computer as a unique stimulus trigger, to distinguish time 0 from the trigger sent by the onset of trials on the

experimental computer. In b) Hauser et al. (2019) the researchers used a series of motion sensors to detect the onset and relative position of the stroking touch throughout. NB: Only Haggarty et al. [40] used EEG, but both methods are appropriate for time locking manual stroking to the onset of the stimulus.