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Revealing the body in the brain: an ERP method to examine sensorimotor activity during visual perception of body-related information

Special issue: Understanding others

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Abstract

Examining the processing of others' body-related information in the perceivers' brain across the neurotypical and clinical population is a key topic in the domain of cognitive neurosciences. We argue that beyond classical neuroimaging techniques and frequency analyses, methods that can be easily adapted to capture the fast processing of body-related information in the brain are needed. Here we introduce a novel method that allows this by measuring event-related potentials recorded with electroencephalography (ERPs-EEG). This method possesses known EEG advantages (low cost, high temporal resolution, established paradigms) plus an improvement of its main limitation; i.e., spatiotemporally smoothed resolution due to mixed neural sources. This occurs when participants are presented and process images of bodies/actions that recruit posterior visual cortices. Such stimulus-evoked activity may spread and contaminate the recording of simultaneous activity arising from sensorimotor brain areas, which also process body-related information. Therefore, it is difficult to dissociate the contributing role of different brain regions. To overcome this, we propose eliciting a combination of somatosensory, motor, and visual-evoked potentials during processing of body-related information (*vs.* non-body-related). Next, brain activity from sensorimotor and visual systems can be dissociated by subtracting activity from trials containing only visual-evoked potentials to those trials containing either a mixture of visual and somatosensory or visual and motor-cortical potentials. This allows isolating visually driven neural activity in areas other than visual. To introduce this method, we revise recent work using this method, consider the processing of body-related stimuli in the brain, as well as outline key methodological aspects to-be-considered. This work provides a clear guideline to researchers interested or transitioning from behavioural to ERPs studies, offering the possibility to adapt well-established paradigms in the EEG realm to study others' body-related processing in the perceiver's own cortical body representation (e.g., examining classical EEG components in the social and embodiment frameworks).

Keywords: EEG method, Body perception, Embodiment, Sensorimotor, Somatosensory cortex

1. Introduction

Examining the processing of others' body-related information in the perceiver's brain across the neurotypical and clinical population is one of the central topics in the domain of cognitive neurosciences; a simple search of 'body perception' in Google Scholar reveals a steady and growing number of hits (4.7mill. in 2000-2009, ~5mill. 2010-2019). Here we argue that beyond current neuroimaging techniques, new methods that are able to capture the fast processing of others' bodies in the brain are needed. Accordingly, here we introduce a novel method that allows examining this via event-related potentials and electroencephalography (ERPs-EEG). This method possesses the advantages of EEG measurement (i.e., low cost, high temporal resolution, non-invasive, well-established paradigms) plus an improvement of its main caveats, namely, spatiotemporally smoothed resolution due to mixed neural sources. The latter occur, for example, when participants in an EEG experiment are presented with images of bodies. Such stimuli will firstly recruit posterior visual areas of the brain. Following this, visual activity may spread and mask simultaneous activations in somatosensory and motor brain areas (also recruited during perception of bodies/actions; Hardwick et al., 2018; Thompson et al., 2019). Therefore, it might be difficult to tease apart the contribution of different brain regions to the processing of body-related stimuli.

To introduce such a method, we first contextualise it within the overall EEG technique. Second, we consider how present EEG paradigms need to consider the processing of body-related stimuli as a particular type of neural processing. Third, we propose eliciting a combination of somatosensory, motor and visual-evoked potentials that allows revealing independent temporally rapid contributions of these cortices to the processing of visually perceived bodies. To this aim, we revise recent work from our lab (i.e., Sel et al., 2014; Galvez-Pol et al., 2018a, 2018b; Arslanova et al., 2019). Then, we formalise this into a reviewed method that outlines methodological aspects that need to be considered, providing a guideline to researchers interested or transitioning from behavioural-only studies to the use of ERPs in embodied and social cognition. Altogether, we foster the development of new approaches exploiting well-known EEG paradigms to investigate with high temporal resolution the processing of bodily-related stimuli in the brain.

Footnote 1. The search in Google Scholar included the following keywords: action observation, action perception, embodied perception, mirror neurons, and body perception; not including patents and citations in the searching engine.

2. A very short introduction to EEG

2.1 Measuring EEG activity

Electroencephalography (EEG) is the non-invasive recording of the brain's electric fields. The release of a given neurotransmitter from the presynaptic terminal causes the flow of ions, eliciting a change in the voltage of the extracellular space. Then, the voltage flows throughout the neuron and create a small dipole. Depending on the properties of the tissue and alignment of the neurons (Murakami et al., 2002, 2003; Murakami and Okada, 2006), the summation of many dipoles from pyramidal cells approximates a single equivalent current dipole. If the dipole runs along the surface of the scalp, it can be recorded with scalp electrodes. The distribution of voltage recorded by these electrodes is modulated by the orientation and disposition of concurrent dipoles. Thus, extracellular field recordings measured via EEG are the result of superimposed electric fields that originate in from those electric currents generated by active neurons (see Buzsáki, Anastassiou, & Koch, 2012; Luck, 2014).

2.2 Extracting meaningful information from EEG data

After recording EEG data, segments of brain activity that are time-locked to an event of interested are usually extracted from the global signal (i.e., ERPs). Next, ERPs including both task and non-task-related brain activity are averaged. This averages out the latter (unsystematic/random) activity while isolating consistent task-related neural responses (Glaser and Ruchkin, 1976; Luck, 2014). The observed ERP activity will change according to the underlying neural (and cognitive) generators; quantitatively measuring changes in ERPs equals to measure changes in the underpinning brain network. Because ERPs are structured in time and space (latency and topography), they have been well-documented in more or less canonical patterns of brain activity (ERP components) that are linked to and offer meaningful information about the timing of specific cognitive process and candidate brain areas (Luck, 2014; Biasiucci et al., 2019).

2.3 Limitations to-be-considered in ERPs-EEG

ERP components recorded on the scalp via EEG (ERPs-EEG) reflect the sum of different superimposing components that are generated from different neural sources (Figure 1). Therefore, the corresponding latency and topography observed in the subsequent ERP components (timing and amplitude of the observed components) reflect the sum of several and distinct neural sources. The mixture of components reduces the temporal and spatial estimation of where in the brain the observed brain activity arises; extracellular field recordings are spatiotemporally smoothed (Luck, 2005, 2014; Niedermayer and Lopes da Silva, 2005; Buzsáki et al., 2012; Cohen, 2014). Moreover, as many neural generators are simultaneously active, these might cancel each other. This cancellation decreases the overall task-relevant activity of ERPs-EEG averaged against task-unrelated activity. Also, voltage propagation from different brain regions varies depending on the tissue across electrode positions (Ahlfors et al., 2010; Irimia et al., 2012; Tenke and Kayser, 2012).

Yet, EEG is low cost, possesses high temporal resolution (in the order of milliseconds), it is non-invasive, and there are numerous well-established paradigms that can be adapted to the study of body perception and social cognition. Moreover, problems regarding the superimposition of components can be somewhat overcome by examining how the waveforms unfold in time across various electrodes over the scalp (Kappenman and Luck, 2012). Overall, the flexibility and accessibility of the EEG technique, in combination with advances in signal processing and paradigms, allow the development of innovations that maximise its use not only as an electrophysiological tool but also as a neuroimaging technique (Biasiucci et al., 2019).

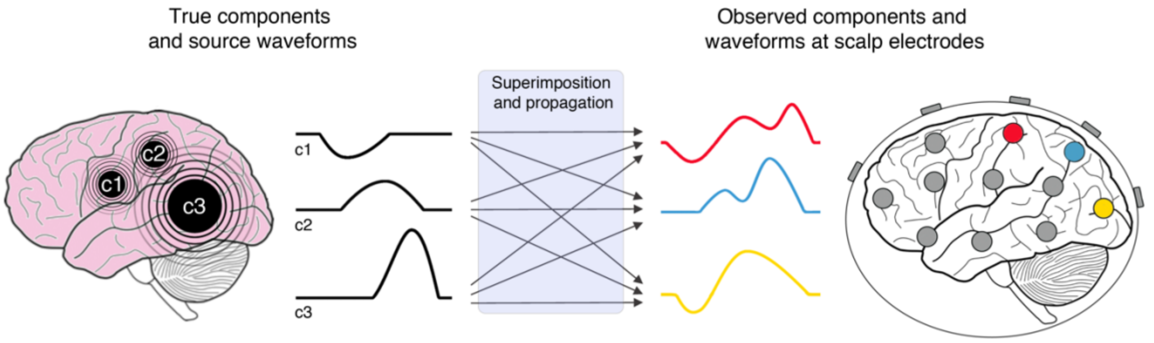

Figure 1. Schematic of the relation between true components and observed components at the scalp. From left to right, three different neural generators elicit three different components, each unfolding a source waveform. Depending on different factors such as the location, orientation, and underlying tissue, the signal propagates, superimposes, and might cancel out concurrent activity. Subsequently, in an EEG experiment, the observed components (i.e., observed modulations in activity along the waveforms of each electrode) are equal to the summation of each component, multiplied by a weighting factor reflecting the unfolding relation between each concurrent component and the electrode sites.

3. Adapting EEG to examine somatosensory and motor activity during perception of body-related stimuli

3.1 Considering the design of body-related stimuli

Many studies in the perception framework of cognitive neuroscience examine processing of arbitrary stimuli. However, body-related stimuli such as images of bodies and actions do have intrinsic and particular features that are different from arbitrary stimuli; these are as follow:

i) When perceiving body stimuli, there is a shared bodily frame between the subject (the person perceiving a body) and the stimulus (the body having something done to it). Having a common frame underpins statistical regularities between one and others' bodies. ii) This coupling supports inferences about the use of our own body by perceiving and interacting with others' bodies. This factor seems to drive sensory signals about bodily percepts onto our own body representation in the brain (Niedenthal, 2007; Rizzolatti and Sinigaglia, 2010; De Vignemont, 2011). iii) Particularly, the sight of a body does not only elicit recruitment of 'input-sensory areas' such as visual regions, but also our own cortical representation of the body in somatosensory and motor regions (Keysers et al., 2004, 2010; Gazzola and Keysers, 2009; Caspers et al., 2010; Molenberghs et al., 2012; Hardwick et al., 2018). iv) The involvement of these brain areas/systems is modulated by the degree of bodily elicitation encountered in the stimuli. Factors such as the participants' experience with the stimuli or the attended features play a crucial role (e.g., body expertise and familiarity, paying attention to body posture or body colour; see Calvo-Merino et al., 2005, 2006; Jackson et al., 2005; Bruzzo et al., 2008; Arslanova et al., 2019). v) Compared to non-body-related stimuli, body stimuli involve either arbitrary and intransitive patterns or well-defined configurations of movements. In the case of stimuli depicting actions, these are usually encoded in serial order with transitions between movements in a discrete hierarchically-organized and goal directed manner (i.e., defined by the goal of the action conveyed in the visual percept; Endress and Wood, 2011). For instance, hand movements to spatial targets can be done with more than one effector whereas other movements such as an arabesque in ballet require specific body configurations (Smyth and Pendleton, 1989). vi) Therefore, bodily stimuli can be encoded at very different levels of abstraction (e.g., kinematics, goal, actor/agent), as well as those that could be usually found within the action understanding framework (i.e., identification, goal, and intention of the action; Thompson et al., 2019). v) The above points might apply also to body-related stimuli, which involve those that even when not depicting directly the body, have a close relationship to it. For instance, body-related stimulus such as images of tools might elicit motor programs in the perceiver (e.g., Mecklinger et al., 2004; Proverbio et al., 2011).

Since the number of trials needed to isolate ERP components from the background noise is larger than those needed for behavioural measures (e.g., accuracy), it is not possible to manipulate extensively the parameters of body-related stimuli across trials; additional caution needs to be taken when designing stimuli for EEG experiments (Picton et al., 2000). If a researcher aims to examine concomitant processes related to visual perception of bodies, it is important to display unambiguous information. For instance, brain activity associated to encoding of hand images resembling objects or conveying semantic information (i.e., specific hand signs and gestures) might elicit a variable range of cognitive/neural mechanisms across subjects. Gao and colleagues (2014) showed that instructing participants to verbally encode biological motion shown in points of light display portraying different bodily actions abolished mu suppression (a neural index of embodiment) compared to when participants were not prompted to explicitly use verbal codes; i.e., abolishing a neural correlate reflecting our ability to process body-related percepts and other stimuli at the sensory, motor, and/or affective levels in the same ways as one's own body (De Vignemont, 2011; Gallese and Sinigaglia, 2011; Makin et al., 2017).

3.2 Considering brain activity elicited by body-related stimuli

Any EEG experiment will face a number of challenges that will obscure data interpretations, namely, signal propagation, its decay and cancelation, the presence of multiple and active neural generators, and the superimposition of observed ERP components. Moreover, experiments examining body-related visual processing possess an additional challenge: measuring ERP waveforms beyond those electrodes positioned over input-stimulated cortices, that is, measuring brain activity arising from cortex other than visual (e.g., central cortices such as somatosensory or more anterior as motor).

Visual perception of stimuli elicits visual-evoked potential (VEP) that can be recorded over posterior/occipital electrode sites. This allows good measuring of activity directly linked to computations of the visual system. EEG studies examining the processing of visual features such as colours and shapes report subsequent VEPs over posterior electrodes sites; the location on the scalp where activity from the visual system usually arises (e.g., Norcia et al., 2015). Neuroimaging studies have also reported regions in the visual cortex that seem dedicated to process human bodies and body parts (fusiform and extrastriate body areas, respectively; Peelen and Downing, 2007; Urgesi et al., 2007). These regions seem to hold strong connections with more anterior parieto-frontal areas of the brain dedicated to bodily computations involved in processing posture and action (Zimmermann et al., 2018). In addition to the visual cortex, the sight of body-related stimuli, including stimuli such as images of hands, bodies, and points of light display depicting biological motion, recruits somatosensory, motor, and other anterior brain regions across a distributed complex known as the action observation network (see e.g., Calvo-Merino et al., 2006; Cross et al., 2006; Molenberghs et al., 2012; Hardwick et al., 2017; Vingerhoets, 2008). The visually acquired body is rapidly recoded over one’s body-related cortices, which play a fundamental role in extracting, predicting, and performing computations related to others’ bodies and actions, as well as one’s sense of body. However, in EEG studies the initial sight of body stimuli elicits the aforementioned VEPs that spread from posterior/visual to more anterior and body-related cortices, masking thenceforth the brain responses that are also responsible for the processing of body-related information. This is different from fMRI studies whereby distributed voxels can be independently examined. Therefore, brain responses reflecting cognitive processes related to the transformation of bodily information onto our own cortical body representation (i.e., somatosensory and motor) are difficult to tease apart from the original VEPs delivering the visual percept. Measuring VEPs over posterior/occipital electrode sites allows good measuring of activity directly linked to visual processing but it does not facilitate direct inspection of the state of somatosensory and motor cortices. Consequently, neural processes within areas representing the body are difficult to dissociate from on-going visual processing.

3.3 Dissociating body-related activity from visual coexisting activity in EEG

Residual effects of concurrent visual ERPs in brain regions such as somatosensory cortex may obscure data interpretation. As warned by Adler and Gillmeister (2019), this is more likely beyond early ERP components. For instance, later components (e.g., N80, P100, N140) concur with visual C1 (75 ms), P1 (100 ms), and N1 (135-150 ms) ERP components to visual images. How can we dissociate visual and body-related cortical activity in the brain via EEG? To illustrate the subsequent method, we based our observations in four studies that have already used it (Arslanova et al., 2019; Galvez-Pol et al., 2018a; Galvez-Pol et al., 2018b; Sel et al., 2014). These studies were developed under the overall framework of sensorimotor recruitments models (D'Esposito and Postle, 2015), which postulate the resemblance between perceptual, attentional, and mnemonic computations in the brain (e.g., brain areas processing action/body stimuli as neural candidates to underpin a wider range of cognitive processes). We outline their background (Table 1) to exemplify how well-known EEG paradigms can implement the succeeding method, as well as detail the experimental setting of such studies in Table 1 of the Supplementary materials.

Table 1

Framework, component examined, main findings and studies dissociating visual from sensorimotor brain activity during processing of body-related stimuli

Framework	Component	Main findings
Simulationist models of face-based emotion recognition	N170	Somatosensory engagement during facial discrimination of emotions beyond on-going visual activity (Sel et al., 2014)

Sensorimotor recruitment: mnemonic and attentional computations occurring in those brain areas also involved in the perception of the stimuli.	CDA	Memory load for body-related images *vs.* non-bodily images modulated somatosensory activity (Galvez-Pol et al., 2018a)
	RP	Memory load for body-related images *vs.* non-bodily images modulated motor-cortical activity (Galvez-Pol et al., 2018b)
	N2pc	Recruitment of somatosensory cortex when attending to body features *vs.* non-bodily of same stimuli (Arslanova et al., 2019)

Note. Brain activity examined was based on classical components but described in sensorimotor brain areas. N170 known to reflect neural processing of faces (Rossion et al., 1999). Contralateral delay activity (CDA), known as neural signature of memory capacity (Vogel and Machizawa, 2004). Readiness potential (RP) known as neural marker of motor processing (Deecke et al., 1976). N2pc known as a component of selective attention (Eimer, 1996). A detailed list of the experimental parameters used in the above studies dissociating visual from sensorimotor activity via ERPs-EEG is provided in Table 1 Supplementary materials

In the above-mentioned studies we propose a solution to probe the state of body-related cortices (somatosensory and motor cortex) during visual perception of body stimuli in ERP-EEG experiments. This involves four elements: i) the use of stimuli or instructions triggering different degree of bodily elicitation (e.g., attending to body postures *vs.* attending to their colour). ii) On half of the trials, measuring those VEPs elicited at the sight of stimuli (VEPs-only trials). iii) On the other half of the trials, measuring the same VEPs, as well as simultaneously eliciting task-irrelevant ERPs arising in those cortices known to process body stimuli. iv) Subtracting brain activity from previous steps: this involves subtracting visual activity from VEPs-only trials to the compound of visual and task-irrelevant ERPs arising from body-related cortices across multiple electrode sites and conditions. The idea behind this method is to isolate specific ERP components by means of difference waveforms (see e.g., Luck, 2014). Specifically, computing differential activity by subtracting ERP waveforms elicited by one condition from the ERP waveforms elicited by another condition. These conditions refer here to the type of stimulation delivered, each reflecting activity due to the single or combined elicitation of ERPs during the processing of body stimuli.

In three of the aforementioned studies to dissociate somatosensory activity from concomitant visual activations elicited when seeing body-related images, the authors elicited simultaneously ERPs in visual and somatosensory areas. Visual ERPs (VEPs) were automatically elicited at the onset of the visual stimuli depicting bodies. The somatosensory ERPs (SEPs) were obtained by delivering brief cutaneous stimulation through small mechanical taps. This tactile stimulation evokes SEPs that can be observed in the contralateral primary and secondary somatosensory cortices (S1, SII). SEPs are a practical and non-invasive mean to assess/probe the state of the somatosensory system and its underlying processing. If these brain areas are processing the visually perceived body stimuli, changes in the succeeding component waveforms are observed. SEPs were elicited by brief task-irrelevant tactile stimulation delivered at the index fingers of both hands. Painless tactile stimulation was applied during the processing of visual images of bodies by delivering a brief single tactile tap using two 12 V solenoids (5mm in diameter, 2ms duration). When a current passed through the solenoids, an attached metal rod with a blunt conical tip contacted the participants' skin. Both solenoids were attached with microporous tape to the tip of the index fingers, one for each hand (and also on the face in Set et al., 2014). The experimenters ensured that participants felt the touch during the practise trials preceding the main experiments. However, the mechanical tactile taps were task irrelevant, and participants could easily ignore these during the main experimental task. Participants reported no attentiveness to it after a short period of habituation time in the experiment. The only purpose of these task-irrelevant tactile taps is to reveal the state of somatosensory cortices during visual processing of body-related stimuli.

The signal of the task-irrelevant SEPs can be almost conceptualised as the initial 'ping' of a sonar, whereby the impulse travels across a brain structure revealing changes in its function by means of echoed activity. This design allows measuring source waveforms (i.e., those reflecting original somatosensory processing; SEPs free of VEPs) by subtracting brain activity from trials containing only VEPs to those VisualTactile trials containing a mixture of both VEPs and SEPs. By conducting the subsequent subtraction (VEPs & SEPs) – VEPs, it is possible to exhibit novel evidence of pure somatosensory processing modulated by the nature of the underlying bodily computation with high temporal resolution.

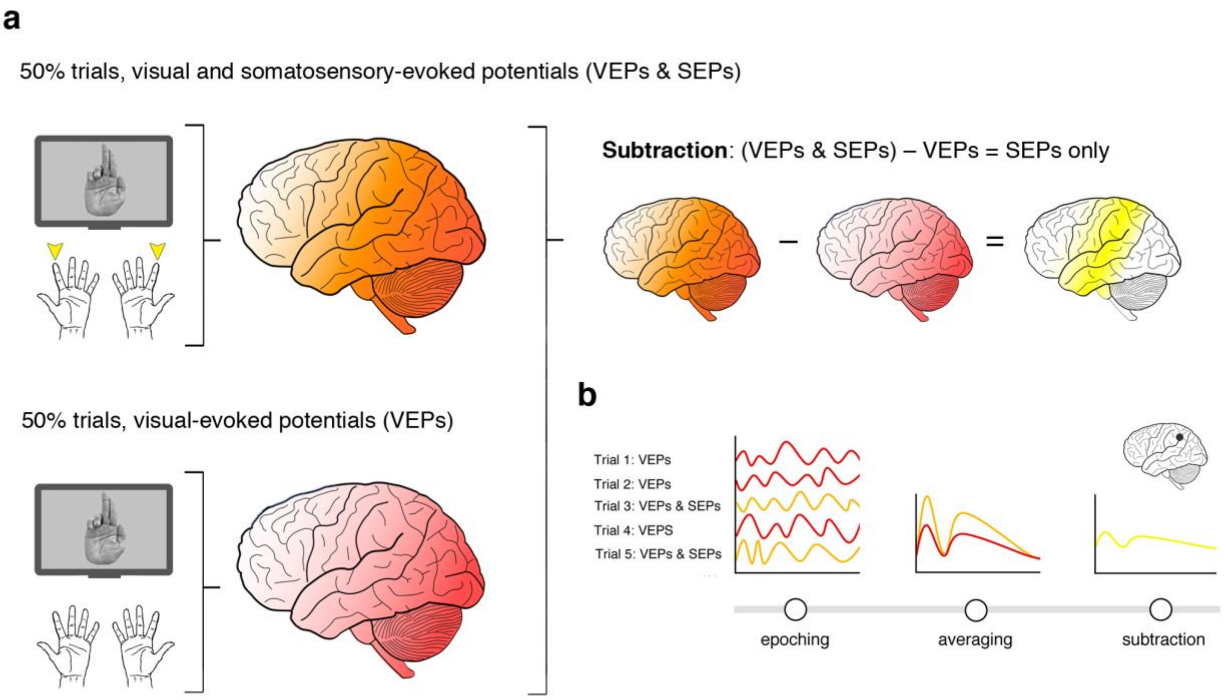

Figure 2. Schematic illustration of subtractive methodology using SEPs and VEPs. **a** from left to right, perceiving bodily stimuli elicits visual-evoked potentials that conceal possible and concurrent processing in other regions such as somatosensory cortices. Next, 50% of trials include visual perception of body-related stimuli, which elicits VEPs (central-bottom part). The remaining 50% of trials include similar VEPs and somatosensory-evoked potentials (SEPs) elicited by task-irrelevant tactile stimulation (central-upper part). The latter allows probing the state of the somatosensory cortices by examining SEPs free of VEPs [(VEPs & SEPs) – (VEPs-only)]. **b** After pre-processing the data, trials containing VEPs & SEPs and those containing only VEPs are epoched. Then, they are averaged separately, and the subsequent grand average waveforms are subtracted from each other. The same operation is computed for the control and experimental condition. Modulation of SEPs free of VEPs should be observed in the condition involving body-related processing of information.

In brief, perceiving bodies elicits VEPs and allows inspection of visual processing at posterior electrode sites. Perceiving bodies and simultaneously producing SEPs results in compound activity from which SEPs free of VEPs can be obtained by subtracting activity from trials containing only VEPs. By subtracting VEPs it is possible to isolate neural processes that are differently exposed across stimulation conditions while reducing brain activity equally present in both conditions. The same procedure should be applied in a control condition whereby the stimuli or the instructions do not involve body-related processing of the stimuli. The subtraction should reflect modulations of SEPs free of VEPs in the experimental body-related condition. The four studies in which we based our observations used polygonal shapes matching the outline of hand images or different instructions (attending to actors' gender and the colour of hand images). This approach diminishes the amount of spatiotemporal smoothness caused by concurrent neural generators.

The idea behind the current method can be easily adapted to study further sensorimotor areas (i.e., motor brain regions). In one of the four above-mentioned studies (Galvez-Pol et al., 2018b) we developed a working memory paradigm in which participants were asked to remember body and control non-body-related images. On half of the trials, visual-evoked activity that was time-locked to the sight of the stimuli allowed us to examine VEPs. On the other half of the trials we additionally elicited a task-irrelevant key pressing during the consolidation interval of the stimuli in working memory. This manipulation elicited motor-cortical potentials (MCPs; a cued version of the volitional readiness potential) concomitant to visual processing (visual-motor trials). Somewhat similar to the depiction in Figure 2, this design allowed us to dissociate motor activity revealed in the MCPs from concurrent visual processing by subtracting activity from the visual-only trials to the compound activity of visual-motor trials. MCPs free of VEPs showed that the number of body-related images to-be-remembered modulated this activity; see further details in Table 1 of the Supplementary materials.

3.3.1 Considering the subtraction of brain activity in EEG

Subtractive methodologies vary in their scope and design. In some experiments, participants perform complementary tasks with increasing cognitive demands. Subtracting the output of these tasks (e.g., reaction time) informs about the added cognitive costs; each task is thought to reflect a part of a major cognitive process (much like those differences in the mental operations of Donders' experiments; Donders, 1868). Nevertheless, current postulates criticize this linear approach because it seems to neglect interactions between cognitive/neural processes (Friston et al., 1996; Jennings et al., 1997; Price and Friston, 1997; Vidal et al., 2011).

A subtraction closer to the one proposed here is that one found in studies examining multisensory integration whereby different stimuli are presented through one, two or more sensory modalities in a de/synchronised manner. By subtracting brain responses from unimodal to multimodal conditions, it is possible to dissociate waveforms that likely reflect sensory integration (Dell'Acqua et al., 2003; Talsma and Woldorff, 2005; Talsma et al., 2010; Mahoney et al., 2015). However, there are at least two differences between this type of subtraction and the one introduced here. For instance, many studies of audiovisual integration examine brain activity containing waveforms elicited by either visual stimulation, auditory, or both simultaneously. Audiovisual integration is assessed by computing difference waveforms between the audiovisual condition and the sum of unimodal auditory and visual conditions (Audiovisual – (Audio + Visual). This is different from the subtraction proposed in the current paper (Visual & Tactile – Visual). First, these two subtractions diverge in the number of operations; only one is used in the latter. Second, in our method SEPs *per se* do not provide any information about the visual input. SEPs elicited by task-irrelevant tactile taps can hardly convey any valuable information about the characteristics of the body stimuli. Somatosensory responses to visually perceived body-related information probably reflect sensory associations that summon processing resources (Meyer et al., 2011; Sun et al., 2016).

Another EEG study has used task-irrelevant ERPs to examine brain activity that otherwise is concealed. Wolff et al., (2015) used task-irrelevant visual stimulus during the maintenance of visual stimuli in working memory. These latter stimuli functioned as task-irrelevant impulses that aided to reveal hidden EEG activations. We have showed that applying task-irrelevant SEPs while encoding body-related information elicits ERP components arising from body-related cortical regions that otherwise are also concealed. Once SEPs are elicited, these act like impulses that reveal processing of body-related information. Importantly, in this context, tactile stimulation *per se* have little cognitive relevance and their only purpose is to elicit neural impulses that allow subtracting concomitant ERPs arising from different neural generators.

The current method and subsequent paradigms minimize differences between stimulation conditions by maximizing top-down processing. Namely, tactile taps were task-irrelevant, the stimuli (body *vs.* non-body-related) were matched in difficulty, or the stimuli remained the same and only the instructions changed (attending to posture *vs.* attending to colour). This is congruent to other ERP experiments studying visual and somatosensory processing, which have maximised similarities between stimulation conditions by using attention-direction cues (see e.g., Gillmeister, 2014; Adler et al., 2016; Rigato et al., 2019). Nevertheless, it is important to note the possibility of distinctive visual processing across stimulation conditions; differing unisensory visual contributions cannot be utterly eliminated (see later discussion).

3.3.2 Considering data analysis and inspection

After subtracting activity from visual-only trials (VEPs) from visual-tactile trials' activity (VEPs & SEPs), it is important to calculate if the number of trials in each stimulation condition is similar. Otherwise the signal-to-noise ratio (e.g., impact of visual activity) may differ and the results could reflect somewhat arbitrary effects. Comparing the number of accepted trials across all conditions and testing whether or not these are significantly different is a quick but effective method to rule out this possibility.

Next, it is critical to inspect the difference waveforms across regions of interest and conditions. Somatosensory and motor processing should be observed at central/postcentral electrode sites (~C3/C4/CP3/4/5/6 of the 10/20 arrangement of scalp electrodes). A first step here is to inspect the presence of a well-known component (a positive peak ~45ms after tactile stimulation; Hämäläinen et al., 1990; Eimer and Forster, 2003) elicited by the tactile tap used to evoke the task-irrelevant SEPs (Figure 3a). Secondly, if the current method has been effective in subtracting components present in both stimulation conditions (visual-only and visual-tactile), the modulation of the resulting waveforms should be observed over the above-mentioned electrodes. Conversely, little or no modulation should be found over additional sites. Here we recommend testing waveforms at other electrode sites against zero (no differences), as well as directly examining their modulation in posterior electrodes whereby visual processing is usually observed.

3.4 Considering the lateralised disposition of the body in the brain

One's body representation in the brain is both organised in a contralateral manner (Penfield and Rasmussen, 1950; Roux et al., 2018) and coordinated/represented in an ipsilateral manner; i.e., bilaterally. This is different from the classical notion that unilateral tactile processing is represented only in the contralateral somatosensory cortex (Tame et al., 2019). Under certain conditions, tactile and proprioceptive afferent information from the left and right parts of the body seem to interact at early stages of the processing via transcallosal communication. This would allow coordination between the two hemispheres, a critical aspect of goal-directed bimanual tasks (see Rusconi et al., 2014; Tame and Longo, 2015; Tame et al., 2016). In the context of the current work, it is important to highlight that we mostly applied tactile stimulation in the form of task-irrelevant SEPs on the index fingers (but see Sel et al., 2014). The site of stimulation matches the target visual stimuli; i.e., tactile stimulation on hands and visually processing of hand images. Also, we aimed to evoke a clear SEP in a lateralised manner. Given the cortical representation of the body in the brain, tactile stimulation on the feet elicits a different and less lateralised response. Further work should examine the current ERP-EEG method under different stimulation locations (e.g., fingers, face, torso).

Others' body representation in the perceiver's brain seem to be somewhat remapped in our own cortical body representation a contralateral manner (Buccino et al., 2001; Shmuelof and Zohary, 2006; Perry and Bentin, 2009; Goslin et al., 2012). Yet, this effect depends on posture and perspective. For instance, observing right hand actions seem to elicit in the perceiver the same brain activity responsible for the execution of those actions -as if those were actually performed. Conversely this effect seems reduced when observing left hand actions (Alaerts et al., 2009). Overall, the laterality embedded in the stimuli and where in the hemispace these are displayed are factors to-be-considered. For instance, videos showing right hand actions displayed on the right side of the screen (congruent) are likely to evoke greater bodily elicitation in the contralateral hemisphere than left hand actions in the right side of the screen (incongruent matching).

During inspection of SEPs and MCPs modulated by perception of body-related stimuli, if considered and well controlled, the factor hemisphere (contralateral/ipsilateral) can be included in our experimental design as an additional source of information. To include the factor hemisphere in our analyses, there are at least two different approaches. The first approach is to conduct a two-way analysis of variance ANOVA after subtraction of VEPS on the grand average waveforms. The resulting SEPs are compared between hemispheres and any other conditions of interest (i.e., Hemisphere (ispi-contralateral) x Condition (body and non-body-related perceptual task; see e.g., Galvez-Pol et al., 2018). A second approach is to subtract activity between both hemispheres and compare activity between the remaining conditions by using a t-test. The ANOVA and t-test will lead to similar *p* values, but the analysis and display of the data will differ. Last, since interhemispheric differences are regional differences that need to be supported by appropriate tests, if two conditions or groups are different in a region of interest but not in another one, an interaction of group/condition by region of interest is recommended to show this difference (Kappenman and Luck, 2012, 2016; Keil et al., 2014). Alternatively, it is also reasonable to report these effects by showing that one condition differs from zero whereas the second condition does not (no differences).

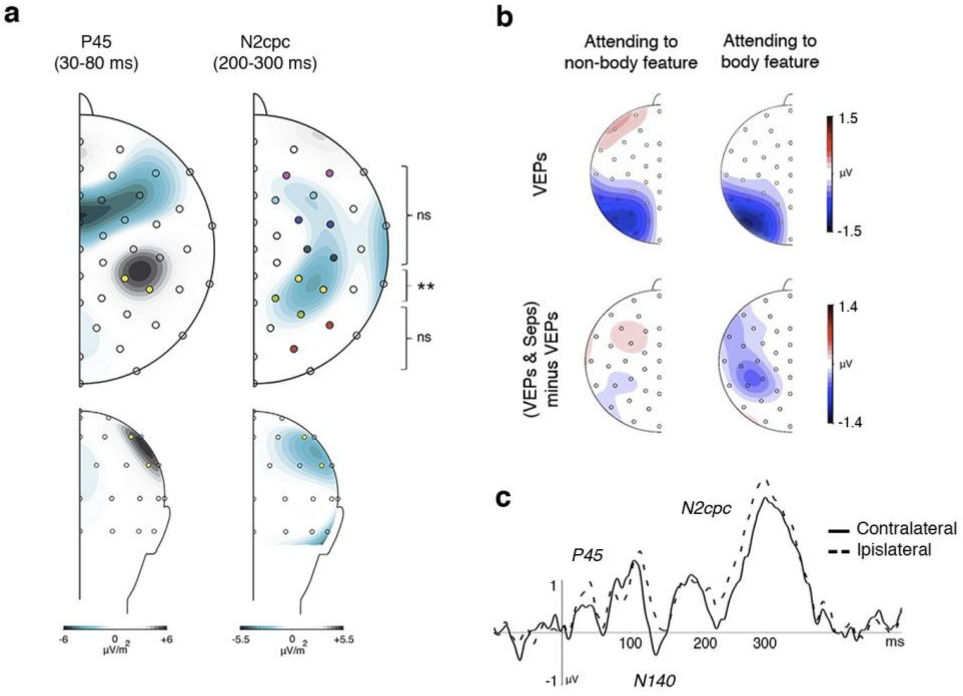

Figure 3. Topography and waveforms of VEPs and VEPs & SEPS after subtracting VEPs; participants attended to images of hands. **a** Tactile tap elicits an early positivity over expected spatiotemporal coordinates (~45ms after over central electrodes). Next, attention to body-related images elicited a significant negativity over these electrodes. The timing of this effect was congruent with previous literature in selective attention (~200-300ms). **b** Upper panel depicts visual processing of body and non-body visual features of the same stimuli. Lower panel depicts SEPs (free of VEPs), showing somatosensory recruitment only when attending to body features. **c** Hemispheric waveforms after subtracting VEPs showing that attention to body features elicits a significant negativity at 200-300ms (alike results of panel and study **a**). Statistical differences were only found over parietal electrode sites (~CP3/CP4 and CP5/CP6 electrodes) in the time range 200-300ms. No significant differences were

found over more anterior and posterior scalp regions. Results adapted from Galvez-Pol et al., (2018a) and Arslanova et al., (2019); positive plotted upwards.

4. Assumptions of the current method

Despite the utility of difference waveforms, the data obtained after subtractions will be always noisier compared to the original waveforms (Luck, 2014). Also, what is actually subtracted needs to be carefully inspected in each individual experiment. For instance, Teder-Sälejärvi et al., (2002) described how some interactions in multisensory integration could be actually accounted by a double subtraction of an anticipatory ERP that was equally present in all experimental conditions (i.e., auditory, visual, audiovisual). Therefore, when computing multisensory integration in 'Audiovisual – (Auditory + Visual) waveforms' the anticipatory activity might be subtracted twice, creating the impression of an early interaction due to cross-modal interaction (see a follow up of this issue in Talsma and Woldorff, 2005). Parameters such as the participants' expectation and the timing in which the evoked activity is elicited need to be carefully contemplated in subtractive methods.

In the body-related literature, multisensory integration in the form of crossmodal congruency between what it is felt via somatosensory processing and what is seen has been associated to changes in visuo-proprioceptive estimates of one's body. Yet, we believe that the current method does not elicit this process. In our case, we conceptualise the signal of the task-irrelevant SEPs as the initial 'ping' of a sonar, whereby the impulse travels across a brain areas revealing changes in its function by means of echoed activity. Another issue concerns the use of different sensory stimulations during encoding of body-related information and its effects on later subtractions. Isolating SEPs by the subtraction '(VEPs & SEPs) – VEPs' assumes that visual effects are equally distributed across conditions and that once the subtraction is conducted only modulations of SEPs free VEPs would be observed. Nevertheless, as stated above, interactions of brain activity modulated by multisensory integration and other processes (e.g., attentional mechanisms) would particularly affect early ERP components (Busse et al., 2005). In a similar vein, we assume that habituation to visual and somatosensory stimulation unfolds in a similar manner. Studies on different sensory modalities (e.g., visual and tactile) using the paradigm of repetition suppression have shown decreasing neural responses when stimuli are presented more than once (e.g., Barron et al., 2016; Tame et al., 2016). Here, it is conceivable that neural signals reflecting bodily *vs.* non-bodily computations of the visual percept could decrease in a different order of magnitude across cortical regions; this is a matter to be further examined.

Generally, it is possible to minimise confounds in the ERP subtraction of the current method by considering the features of the visual and tactile stimulations. Regarding the former, visual properties should be similar in the visual-only and visual-tactile conditions. If consistency is not feasible (e.g., when comparing body *vs.* non-body-related stimuli), the stimuli should be well controlled through counterbalancing and the matching of parameters such as size, difficulty, and brightness. Regarding the tactile stimulation, it is important to highlight that this stimulation should be task-irrelevant, so, other unexpected computations are not mistakenly measured. Also, it is important to note that studies probing the state of the somatosensory cortex (Table 1) elicited SEPs at consistent time points; i.e., with no jittering. The rationale behind is that our method intends to examine ERP components over sensorimotor areas by subtracting the corresponding moment-by-moment visual processing, as indexed by VEPs, to the compound activity of VEPs & SEPs. This implies subtracting activity from somatosensory and visual stimulation conditions that match the on-going processing of the visual stimuli in similar time frames. Yet, in Galvez-Pol et al., (2018b) this method was applied while using a jittered neural response, specifically, motor neural responses generated by participants' keypresses. In order to dissociate motor from on-going visual activity, a timestamp of generated keypresses in visual-motor trials was exported to EEG epochs containing visual-only trials; this allowed subtracting in a trial-by-trial basis an analogous amount of visual activity across stimulation conditions.

5. Future directions and applications

The current method can be applied to examine visual, somatosensory, and motor cortices in both neurotypical and clinical or subclinical populations. This method can contribute to contemporary research topics such as: somatosensory disturbances and bodily distortions, alexithymia and simulationist models of emotion recognition, memory for visually perceived bodies and actions, and interoceptive processing during body and touch observation. Accordingly, vision, touch, proprioception and motor efferent copies converge upon a coherent and adaptive representation of the body. Erratic processing of these systems underpins neuropsychological conditions affecting one's body processing as well as the decoding of others' body-related information (see e.g., Ihme et al., 2014; Crucianelli et al., 2016; Gillmeister et al., 2017; Romano and Maravita, 2019). Here, it is fundamental to delineate the interplay between cortical regions, which could be probed through changes in ERP components with milliseconds resolution along electrode sites when processing one's visually perceived body and/or others' bodies. Regarding the third example, numerous studies have examined the neurobehavioral mechanisms of body and action perception. However, only few studies have inspected such process beyond the perceptual stage. Namely, when lasting body representations are recalled in the absence of the original percept (a body-related memory; see review in Galvez-Pol et al., 2019). The proposed method allows to assess the fast processing of the percept to-be-remembered from the encoding and retention to its recall (see studies in Table 1). Last, the emergence of interoception, which refers to the set of physiological and cognitive processes involved in determining the physiological condition of the body (Craig, 2002; Khalsa et al., 2018), seems to provide a promising venue to apply the current method and test novel conceptualisations on how exteroceptive processing of body-related information may be modulated by the interoceptive processing of inner bodily organs (Ebisch et al., 2011; Heydrich et al., 2018).

The present work was developed to increase the spatiotemporally smoothed resolution of the EEG due to mixed neural sources. In this setting, we believe that this method could be useful to researchers interested or transitioning from behavioural to ERPs studies while benefiting of the relatively low cost of EEG. In addition, future studies may implement the current method through other alike electrophysiological techniques such as the magnetoencephalogram (MEG; Lopes da Silva, 2013).

6. Conclusions

Generating new methods and research questions in the frameworks of action observation, embodiment, and akin fields may benefit from sampling data with high temporal resolution by using techniques such as ERPs-EEG. Nevertheless, an issue here is that such approach does come with an important caveat: spatiotemporally smoothed resolution due to mixed neural sources. This is especially relevant in the above-mentioned frameworks because visually perceiving bodies or body-related stimuli elicits visual-evoked activity (VEP) that masks concurrent processes in somatosensory and motor cortices, which are brain areas well-known for playing a crucial role in processing body-related information. Therefore, it is difficult to examine brain activity in areas other than visual. Consequently, Here, we propose a novel method to dissociate visual and body-related cortical processing by the use of visual-evoked potentials (VEPs), somatosensory-evoked potentials (SEPs), and alternatively, motor-cortical potentials (MCPs). By eliciting SEPs/MCPs during encoding of visually perceived body-related stimuli it is possible to probe the state of somatosensory/motor cortices. However, the resulting activity contains a mixture of activity due to SEPs/MCPs and VEPs. For this reason, it is necessary to include a homologous condition in which the only difference is the absence of SEPs (VEPs-only condition). Then, SEPs/MCPs are isolated by computing the subtraction of mean average waveforms across conditions (i.e., VEPsSEPs – VEPs). In the present work, this method is tailored to examine body-related information because it fosters new research questions that are guided by the literature in the above research frameworks (e.g., neural candidates), while allows to i) dissociate brain activity from different neural generators and ii) examine well-known ERP components in brain areas other than visual. Overall, the current method allows examining with high temporal resolution the involvement of somatosensory and motor cortices when visually processing and encoding bodily-related information.

Ethics

Ethical approval for methods and procedures included in the current work were obtained from the City, University of London Psychology Department's Research Ethics Committee. All human subjects provided written, informed consent.

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