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Commentary

Probing the neural representations of body-related stimuli

Comment on "Revealing the body in the brain: an ERP method to examine sensorimotor activity during visual perception of the body-related information" by Alejandro Galvez-Pol, Beatriz Calvo-Merino and Bettina Forster

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In recent years there has been great interest in the representation of body-related information coming from the different senses and to what extent these contribute to form a coherent body representation (Azañón et al., 2016). In this respect, we know that there are brain areas that preferentially respond to body-related visual stimuli (Orlov, Makin, & Zohary, 2010; Peelen & Downing, 2007) as well as bodily actions (Urgesi, Candidi, Ionta, & Aglioti, 2007). Moreover, such responses can be modulated by the distance of the visual stimuli from the body (e.g., Macaluso & Maravita, 2010), affect processing of stimuli in other senses such touch (Tamè, Farnè, & Pavani, 2013), and improve integration of sensory and motor signals (Tamè, Carr, & Longo, 2017). However, it has proved challenging to study the neural bases of body representation and, in particularly, to isolate the different sensory components carrying information about the body, such as touch and vision, and their interactions with the motor system, that contributes to body perception, whether of our own or others' bodies.

In their stimulating and timely paper, Galvez-Pol, Calvo-Merino, and Forster (2020) present a novel methodological approach that can be applied to electroencephalographic (EEG) data to study how the brain processes visuallypresented body-related information. The authors point out that their approach takes advantage of the methodological strengths of EEG, such as its low cost, high temporal resolution, and well-established paradigms. At the same time, it improves the ability to distinguish between sources of neural signal generated by different brain areas. Indeed, we know that when participants are exposed to visually-presented images of bodies or actions there is considerable activity in the posterior visual cortices. As such, this neural activity spreads across the scalp and mixes with other sources of neural activity coming from other brain areas that are also involved into the processing of body/action related stimuli such as the somatosensory and motor cortices (Galvez-Pol, Calvo-Merino, Capilla, & Forster, 2018; Galvez-Pol, Forster, & Calvo-Merino, 2018; Hardwick, Caspers, Eickhoff, & Swinnen, 2018; Thompson, Bird, & Catmur, 2019), making it difficult to dissociate these various sources.

Therefore, it is important to determine the role of different brain areas in processing body-related information. The

https://doi.org/10.1016/j.cortex.2020.08.019

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authors propose a solution which includes an EEG paradigm in which body-related and non body-related stimuli are visually presented to participants in half of the trials in isolation and in the other half while a tactile stimulus is delivered to the finger. Then, they dissociate neural activity coming from the sensorimotor areas versus from the visual areas by subtracting the neural activity generated by the two different stimulation conditions, namely trials containing only visual stimuli and the ones containing visual and sensorimotor stimuli. As a result, they propose that this approach is able to isolate visually-driven neural activity in non-visual brain areas.

This is an interesting approach that provides a novel angle on an old problem. We believe that this method has great promise for understanding neural representations of bodyrelated information, as has already been shown by the authors' existing studies (Arslanova, Galvez-Pol, Calvo-Merino, & Forster, 2019; Galvez-Pol, Calvo-Merino, et al., 2018; Galvez-Pol, Forster, et al., 2018; Sel, Forster, & Calvo-Merino, 2014). In this commentary, we will discuss some issues that remain uncertain, specifically: (1) whether there is a natural border between body-related stimuli and other categories of stimuli; (2) whether neural signals coming from different sources (e.g., sensory modalities and motor response) are sufficiently distinguishable to support the subtractive logic employed; and (3) whether the method can be generalized to other semantic domains.

A central goal of the method Galvez-Pol and colleagues proposed is to assess the perception of "body-related" stimuli and information. This, however, raises the difficulty of defining a clear border between body-related and non-bodyrelated stimuli. Typically, in the psychological literature a body-related stimulus is considered to consist of a picture of the body or a specific body part (e.g., Brown, Poliakoff, & Kirkman, 2007; Iachini, Ruggiero, Bartolo, Rapuano, & Ruotolo, 2019). Other studies also consider as body-related more abstract stimuli, such as body-related words (Albery et al., 2016). Moreover, there are many non-body objects that are nevertheless directly related to the body. Galvez-Pol and colleagues mention the case of tools, for which there is a vast neuroscience literature about their effects on body perception (e.g., Holmes, 2012) and representation (e.g., Maravita & Iriki, 2004; Martel, Cardinali, Roy, & Farnè, 2016; Miller, Longo, & Saygin, 2014). However, given the ubiquity of our bodies in everyday activities, nearly anything can be thought of as body-related. For example, there is evidence for sensorimotor activity related to the visual perception of everyday objects such as coffee mugs and pans which may not fit the ordinary conception of tools (Tucker & Ellis, 1998), as well as graspable natural objects such as apples or strawberries (Gentilucci, Benuzzi, Gangitano, & Grimaldi, 2001). There are obvious senses in which still further categories of stimuli could be considered body-related, such as articles of clothing or pieces of furniture. In the light of this, it is critical to be aware that the distinction between a body-related and non-body related stimuli may be subtle and not always obvious, as several types of information forming a visual stimulus may include aspects that are more or less strongly body-related.

Thus, it is important to consider, when designing an experiment, whether the stimuli of interest as well as the ones used as a control can unambiguously fall into one of the two categorises (i.e., body vs non-body related). Examples of nonbody stimuli might be natural or artificial objects on which we cannot directly act, use to perform an action, and which are not closely linked semantically to the body. The farthest category we can think of might be large natural objects such as the sky, a planet, the sea, or artificial objects such as a dam or a bridge. Of course, we have to be aware that any object/category to some extent can have some sort of at least intrinsic body-association. A clear differentiation between stimulus categories is particularly relevant when using a method such as the one developed by Galvez-Pol and colleagues that aims to study the neural correlates of body perception. Indeed, we know that viewing the body can influence the perception of somatosensory stimuli by modulating areas of the premotor and parietal cortices (Macaluso & Maravita, 2010). These same brain areas are thought to be the regions where multisensory input interact modulating also unisensory visual and somatosensory cortices (Macaluso & Maravita, 2010). Moreover, it should be considered that people in their everyday life interact most often with dynamic rather than static objects. Recently, using functional magnetic resonance imaging it has been shown that dynamic body stimuli activate brain areas not only of body selectivity but also of biological movement (Ross, de Gelder, Crabbe, & Grosbras, 2020). It would be interesting to explore the effects of dynamic information about bodies in future research.

Another important issue concerns the rational of the subtractive methodology that forms the core of the authors' approach. They express this logic using the following equation:

(VEPs & SEPs) - VEPs = SEPs only

where the visual event-related potentials (VEPs) were subtracted from the sum of the somatosensory event-related potentials (SEPs) and the VEPs, resulting in SEPs only. There are complications relating to potential over- or underadditivity of multi-modal compared to uni-modal stimuli (Stein & Meredith, 1993), which the authors discussed. We wish to consider another issue which is not discussed. Taken at face value, the subtractive logic only holds if the uni-modal visual and somatosensory evoked-potentials are completely independent and do not share any common component. Recent studies, however, have shown that this is far from the case. For example, Mouraux & Iannetti (2009) measured evoked-potentials elicited by unimodal visual, auditory, tactile, and nociceptive stimuli, finding remarkably similar patterns across the scalp from stimuli in each modality. Indeed, quantifying neural activity as global field power, Mouraux and Iannetti found that the majority of evokedresponses reflected activity common to all modalities. This similarity between uni-modal VEPs and SEPs complicates any simple subtractive logic. For example, Mouraux and Iannetti find that common activations across modalities are maximal around the times of the N2 and P2 ERP components, which had peaks at around 250 msec and 330 msec post-stimulus, respectively. This is very similar to the time window of 200-300 msec in which Galvez-Pol and colleagues report body-related effects. Certainly, the "SEPs only" on the righthand side of the equation above cannot be thought of as identical to an SEP elicited by a uni-modal tactile stimulus.

Therefore, we believe that it is important to consider that the neural activity generated by a stimulus in one sensory modality may not uniquely represent processing of that sensory modality, but also other processing related for instance to spatial and/or attentional aspects. Thus, it would be important in future study to optimise such an approach to minimise any possible confound that may limit its application.

Another interesting point refers to the generalizability of this approach. While Galvez-Pol and colleagues developed this approach in the context of the body and discussed the subtraction method with respect to the motor and somatosensory systems, it is conceivably applicable to any semantic domain about which information arrives from multiple sensory modalities. For example, similar logic could be applied to speech perception using auditory and visual stimuli, or to situations in which audio-tactile interaction occurs. For instance, when we are playing an instrument (e.g., piano or guitar) and the tactile component is directly linked with the sounds produced by the movement of our fingers on the instrument. Thus, it is interesting to consider whether the present method is applicable to a much broader range of topics than just body-related representations.

As we have seen, the work of Galvez-Pol and colleagues is a very interesting and timely contribution to the important topic of the neural basis of body-related information. Together, the issues that we have discussed show the importance of developing effective methodological approaches to better understand the neural bases of body perception and representation. This approach has the advantage of being widely applicable to different domains. Understanding the mechanisms that govern the perception of body-related information across different sensory modalities and how such information is processed by our brain to serve motor behaviour is a pressing research goal. We hope that this method will be applied beyond the study of healthy individuals to clinical contexts where patients may suffer from deficits related to body perception/representation.

Credit author statement

Luigi Tamè: Conceptualization, writing - original draft, writing - review & editing.

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Acknowledgments

LT was supported by the UK Experimental Psychology Society. We would like to thank three anonymous Reviewers for their constructive comments on an early version of the present manuscript.

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Received 20 May 2020 Reviewed 29 June 2020 Revised 16 July 2020 Accepted 7 August 2020 Published online 10 September 2020