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Cécile Fabio

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The neural basis of tactile localization through tools

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Abstract

Touch is of primary importance when interacting with our environment. When we come in contact with an object, our brain receives a wealth of information from touch alone (e.g. texture, form, ...) that are combined to create a consistent perception of that object. In order to interact with it, our brain also needs to process the exact location of that object that can guide motor behavior. Localizing touch on the body involves the use of reference frames, which is reflected in the oscillatory activity of the alpha and beta-band: alpha activity reflects the mapping of touch in an external reference frame, whereas beta activity reflects the mapping of touch in an anatomical reference frame. Additionally, touch is not restricted to the body but can also extend to external objects. When we use a hand-held tool to contact an object, we feel the touch on the tool and not in the hand holding the tool. The ability to perceive touch on a tool actually extends along its entire surface, allowing us to accurately localize where it is touched, similarly as we would on our own body. While the neural mechanisms underlying the ability to localize touch on the body have been largely investigated, those underlying tactile localization on a tool have been mostly unexplored. Thus the aim of this thesis is to investigate the neural correlates of tactile localization on a hand-held tool.

In a first study, we combined behaviour, electrophysiology and neuronal modelling to characterize how the human brain localize touch on a hand-held tool. Participants performed a match-to-sample tactile task with stimuli applied on the tool, and in a second session on their arm. As with the body, participants localized touches on a hand-held tool with near-perfect accuracy. Using electroencephalography (EEG), we found that where a hand-held tool was touched was immediately coded in the neural dynamics of primary somatosensory and posterior parietal cortices. Moreover, touches on the tool and arm surfaces were localized by similar stages of cortical processing. Multivariate decoding algorithms and cortical source reconstruction provided further evidence that early limb-based processes were repurposed to map touch on a tool, as we notably found similar regions involved for localizing on each surface.

In a second study, we investigated the oscillatory correlates of tool-extended tactile localization. We performed time-frequency decomposition on the EEG dataset of the first study and found that alpha activity was solely modulated by the location of tactile stimuli applied on a hand-held rod, while beta power was insignificantly affected by it. Source reconstruction suggested that this alpha power modulation was localized in a network of fronto-parietal regions previously implicated in higher-order tactile and spatial processing.

In a third study, we aimed at comparing the reference frame-based neural processing—as reflected in alpha- and beta-band oscillatory activity—during body-based and tool-extended tactile localization. We used EEG to record oscillatory activity while participants performed a cued tactile localization task where contact was applied to either hands or the tips of hand-held rods. Posture of the hands/tool-tips was uncrossed or crossed at participants' body midline, which allowed us to disentangle brain responses related to these different coordinate systems. We found that the scalp distributions of alpha and beta modulation were nearly identical when touch was on the body or on a tool. Only alpha oscillations were modulated by posture, suggesting that they are related to processing of touch in external spatial coordinates. Interestingly, this modulation was identical for mapping touch on the hand or on a tool. Furthermore, source reconstruction of this space-related alpha modulation revealed a similar bilateral network of parieto-occipital regions involved in mapping touch on tools and on hands.

Our findings revealed similar neural mechanisms for mapping touch on a hand-held tool and on the body. This supports the idea that neural processes devoted to body-related information are being repurposed for tool-use. Furthermore, alpha-band modulation followed the position of touch into external space. This is thus the first neural evidence that tactile localization on a hand-held tool involves the use of external spatial coordinates. Our work opens perspectives to develop tools used as extended sensors, like prosthetic device or cane, so that they can be more adapted to their users.

Résumé

Notre sens du toucher est primordial pour interagir avec notre environnement. Lorsqu'un élément extérieur nous touche, notre cerveau reçoit une multitude d'informations tactiles (ex : texture, forme, ...) qu'il combine afin de créer une image cohérente de cet élément. Pour interagir avec lui, notre cerveau doit également localiser la position exacte de cet élément afin d'exécuter un mouvement. D'un point de vue cérébrale, la localisation d'un contact sur le corps implique l'utilisation de système de référence qui sont reflétés dans l'activité oscillatoire des rythmes alpha et bêta : le rythme alpha reflète l'encodage du toucher dans un système de référence externe, tandis que le rythme bêta reflète l'encodage du toucher dans un système de référence anatomique. Toutefois, le toucher ne se limite pas au corps, mais peut également s'étendre aux objets extérieurs. Lorsque nous utilisons un outil pour toucher un objet, le contact est ressenti sur l'outil et non dans la main qui le tient. Nous pouvons en fait percevoir un contact sur toute la surface d'un outil, et ainsi localiser précisément où il a été touché, comme cela est possible sur la peau. Alors que les mécanismes neuronaux sous-tendant la capacité de localiser le toucher sur le corps ont été largement étudiés, ceux à la base de la localisation tactile sur un outil ont pour l'instant été sous-explorés. L'objectif de cette thèse est donc d'étudier les corrélats neuronaux de la localisation tactile sur un outil.

Dans une première étude, nous avons combiné étude comportementale, électrophysiologie et modélisation neuronale afin de caractériser comment le cerveau humain localise le toucher sur un outil tenu à la main. Les participants ont effectué une tâche tactile de type " match-to-sample " avec des stimuli appliqués sur l'outil, et dans une seconde session sur leur bras. Les résultats comportementaux ont révélé que les participants ont localisé les contacts sur le corps et sur un outil manuel avec une précision quasi parfaite. L'électroencéphalographie (EEG) nous a permis d'observer que la position d'un contact sur l'outil était immédiatement codée par la dynamique neuronale des cortex somatosensoriel primaire et pariétal postérieur. De plus, les contacts reçus sur l'outil et sur le bras étaient localisés par des étapes similaires de traitement cortical. Les algorithmes de décodage multivariés et la reconstruction de source ont également indiqué que les processus dédiés aux membres du corps sont réutilisés afin de localiser un toucher sur un outil. Nous avons effectivement trouvé des régions cérébrales impliquées dans la localisation du toucher en commun entre l'outil et le corps.

Dans une deuxième étude, nous avons examiné les corrélats oscillatoires de la localisation tactile sur un outil. Nous avons effectué une décomposition temps-fréquence des données EEG de la première

étude et avons observé que seul le rythme alpha était modulé par l'emplacement des stimuli tactiles appliqués sur l'outil, tandis que le rythme bêta étant quant à lui non affecté. La reconstruction de source a montré que cette modulation du rythme alpha était localisée dans un réseau de régions fronto-pariétales qui ont déjà été impliquées dans le traitement de haut niveau des informations tactiles et spatiales.

Dans une troisième étude, nous avons comparé l'encodage du toucher dans les systèmes de référence - tels que reflété dans l'activité oscillatoire des rythmes alpha et bêta - lors de la localisation du toucher sur le corps et sur l'outil. Grâce à l'EEG, nous avons enregistré l'activité oscillatoire de participants effectuant une tâche de localisation tactile guidée où les stimuli étaient appliqués soit sur les mains, soit sur les extrémités de bâtons tenu en main. Les mains ainsi que les bâtons étaient alternativement en position décroisée ou croisée par rapport à la ligne médiane du corps. Cela nous a permis de distinguer les réponses cérébrales liées aux différents systèmes de coordonnées. Nous avons constaté que les topographies de scalp des rythmes alpha et bêta suivant le stimulus tactile étaient presque identiques entre la main et l'outil. Seul le rythme alpha était affecté par le changement de posture, ce qui suggère son implication dans l'encodage du toucher avec un système de référence externe. On peut également noter que la modulation d'alpha était identique lors de la localisation du toucher sur la main ou sur l'outil. De plus, la reconstruction de la source de cette modulation a révélé un réseau bilatéral similaire de régions pariéto-occipitales impliquées dans la localisation du toucher sur l'outil et sur la main.

Les résultats de nos études démontrent la similarité des mécanismes neuronaux pour localiser le toucher sur un outil tenu en main et sur le corps. Cela soutient l'idée que les processus neuronaux qui traitent les informations liées au corps sont réutilisés lors de l'utilisation d'un outil. En outre, le rythme alpha a été modulé en fonction de la position du toucher dans l'espace externe. Il s'agit ainsi de la première preuve, au niveau neuronal, que la localisation tactile sur un outil tenu en main implique l'utilisation de coordonnées spatiales externes. Nos travaux ouvrent des perspectives pour le développement et l'amélioration d'outils utilisés pour obtenir des informations sensorielles, comme les prothèses ou la canne blanche.

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It is said that a PhD resembles a marathon, I'll argue that it is actually an obstacle course. This was a long journey, with its hard part but also the good ones, and I am glad I arrived at the other end. I wouldn't have made it without you, so I would like to thank you all, in no particular order.

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Introduction

Swapping a fly that came to bother you by landing on your arm, or petting the cat that just rubbed on your leg, are daily activities that we think of as effortless. Yet acting on our environment, meaning in the space occupied by our body, represents a challenge for our brain. It needs to integrate signals coming from multiple senses in order, not only to construct a coherent percept of the world, but also to prepare and execute the appropriate action. The sense of touch is of primary importance in these processes. When we come in contact with an object, our brain receives a wealth of information from touch alone: texture, form, size, weight, ... that are combined to create a consistent perception of that object. In order to interact with it, our brain also faces the challenge of processing the exact location of that object that can guide motor behavior. Imagine that a fly lands on the back of your hand. If you want to swap it, you need to know where it is exactly, not just on your skin, but also in the space occupied by your body. The tactile information about skin location on your hand is indeed not enough to localize the origin of the tactile event in the external, three-dimensional space, because your hand could be in a lot of different positions around your body, for example, in front of your body or behind your back. Thus, to successfully localize the fly, the brain needs to integrate somatosensory skin-based information and body-related information, such as the size, shape and spatial configuration of the stimulated body part, as well as integrating these information across different parts and sides of the body. This PhD work will hence be centered on the spatial perception of tactile stimuli, and more specifically, the mechanisms at play when the brain localizes such stimuli on the body, as well as on tools held by the body.

Touch is indeed not restricted to the body surface, but can extend to hand-held tools. The most compelling example that comes to mind is of a blind person walking with a blind cane. By swapping the cane on the floor, the blind person can extract information about their surroundings. But tools are actually omnipresent in our daily life: we use them to write, to eat, to communicate... and to sense, just like a blind person with a cane. When cutting with a knife for example, we receive tactile information from the whole length of the blade, not just the tip and the handle. This phenomenon has only recently been demonstrated, and the neural mechanisms at play behind it are unknown.

The aim of thesis was therefore to investigate the neural correlates of tactile localization on a hand-held tool. This general introduction will be composed of several section. In a first section, I will bring out the importance of space in tactile perception by first, reviewing the spatial organization of the somatosensory system, and second, broaching the subject of body representation and their role in tactile localization.

The second section will touch on the impact tool use has on body and space representation. Behavioral and electrophysiological evidence of this phenomenon in human and non-human primate will be presented.

The third section will describe in details the mechanisms involved in the localization of tactile stimuli on the body, notably on the use of frames of reference.

The fourth section will focus on the neural correlates of tactile localization on the body, with an emphasis on electrophysiological studies.

The fifth and final chapter of the general introduction will review the few studies having examined tactile perception through tools, with a focus on tactile localization.

The general introduction will be followed by the experimental part of this thesis. This section will be comprised of three studies investigating the neural correlates of tactile localization through tools. The first study aimed at characterizing the cortical dynamics implicated in the spatial encoding of touch received on a hand-held tool. The second study investigated the oscillatory activity involved in this phenomenon. The third and last study addressed the question of the spatial codes used for encoding touch on the tool by manipulating the reference frames of touch received on the tool.

In a general discussion, the main findings of the experimental part will be presented, before being interpreted and integrated with the existing literature. Potential limitations of our studies will be discussed, and perspective for future research will be proposed. I will finish by concluding remarks.

1. Space is a crucial aspect of touch

1.1. The organization of the somatosensory system

Touch is the ability to understand the world through physical contact. It activates specialized sensory receptors embedded in the skin, muscles and joints of our body, giving our brain a wealth of information about the environment. The whole network of structures involved in the perception of touch is known as the somatosensory system.

There are four main types of receptors at the peripheral level of the somatosensory system:

- thermoreceptors, which code for temperature variations (Hensel, 1973).
- nociceptors, that respond to high intensity and potentially noxious stimuli (Belmonte and Viana, 2008).
- cutaneous mechanoreceptors, located in the skin, that respond to physical stimuli, such as mechanical pressure and vibration (Johnson, 2001).
- and finally proprioceptors, located within muscles, tendons, and joints, which detect distinct kinematic parameters (e.g. joint position or muscle length) and thus encode information about the position of the different parts of the body in relation to each other and the surrounding environment (Rothwell, 1987; Tuthill and Azim, 2018).

Since the topic of this dissertation is not concerned about thermoception nor nociception, only the last two types of receptors mentioned are relevant here. Mechanoreceptors, though primarily conceived to convey tactile information, also contribute to proprioception. Three types of proprioceptors actually mediate human proprioception: muscle spindles, which are embedded in skeletal muscles, Golgi tendon organs, which lie at the interface of muscles and tendons, and joint receptors, which are low-threshold mechanoreceptors embedded in joint capsules (Rothwell, 1987; Tuthill and Azim, 2018).

Mechanoreceptors of the skin can be categorized by the type of stimulation they respond to, by their receptive field features, as well as by their rate of adaptation (Johnson, 2001). The receptive fields of these mechanoreceptors are regions of the skin where stimulation will elicit a neuronal response. Once stimulated, the neuron will start to fire at an elevated frequency (the stronger the stimulus, the higher the frequency). If the stimulation persists, it will then adapt (i.e., reduce) its firing rate (Mendelson and Loewenstein, 1964). If you drag your finger across a textured surface, the skin of your finger will vibrate. Such low frequency vibrations are sensed by Merkel corpuscle end-organ (also known as Merkel discs), which have small receptive fields (Merkell, 1875). They elicit slowly adapting type I responses to enable tactile discrimination of an object's shape, curvature, texture, and other physical properties (Roland S. Johansson and Flanagan, 2009; Johnson, 2001). When you use a tool, for

example digging with a shovel, contact between the ground and the shovel will produce deep pressure and high-frequency vibration picked up by Pacinian (or Lamellar) corpuscles in the hand (Brisben et al., 1999). These corpuscles have large receptive fields and are considered rapidly adapting type II mechanoreceptors (Bell et al., 1994; Loewenstein and Mendelson, 1965). While digging, the handle of the shovel might often slightly slip in your hand: such light touch is transduced by the encapsulated endings known as tactile or Meissner corpuscles. These are rapidly adapting type I mechanoreceptors with small receptive fields that provide feedback signals for grip control (Johansson and Westling, 1984; Macefield et al., 1996). Stretching of the skin is transduced by stretch receptors known as bulbous corpuscles or Ruffini corpuscles, which have large receptive fields and are slowly adapting type II mechanoreceptors (Vallbo and Johansson, 1984). Furthermore, hair follicles are also wrapped in a plexus of nerve endings known as the hair follicle plexus. These nerve endings detect the movement of hair at the surface of the skin, such as when an insect may be walking along the skin. Free nerve endings can also be found in the skin, detecting touch, pressure, stretching, as well as the tickle and itch sensations.

Tactile perception begins with the activation of these afferents, for example a distortion of the skin will activate cutaneous mechanoreceptors that transduce mechanical deformation information into an electrical signal to the spinal cord. The degree of myelination of their axon can vary, ranging them from heavily myelinated A β afferents, lightly myelinated A δ afferents, and unmyelinated C-fibers. A β neurons have the fastest conduction velocity and the largest axonal diameter. A δ fibers have a slightly smaller diameter than A β fibers and a slower conduction velocity due to thinner myelination. C-fibers are the slowest and smallest diameter class of somatosensory neurons and account for the majority of neurons innervating the skin. Afferent somatosensory axons penetrate the spinal cord in a somatotopic, columnar manner, and forms synapses upon second order neurons in the spinal cord dorsal horn (see Figure 1). Each spinal nerve innervates a specific area of skin called a dermatome. These somatotopically arranged columns are thought to be an important step in the integration and processing of somatosensory information (Li et al., 2011). The next step of subcortical tactile processing occurs in the dorsal column nuclei (DCN), where second order neurons connects with third order neurons (Jörntell et al., 2014a; Loutit et al., 2021). The gracile nucleus of the DCN receives inputs from the lower half of the body (lower torso and lower limbs) whereas the cuneate nucleus receives inputs from the upper half of the body (upper body and upper limbs). Projections from these neurons in the DCN then cross the midline at the medulla before continuing through the midbrain. At this point, the first functional map of the body arises in the superior colliculus (Groh and Sparks, 1996). Signal arrives at the thalamus, where thalamic relays represent another level of tactile processing (Vazquez et al., 2013), before tactile inputs are transmitted to the primary (SI) and secondary (SII) somatosensory

cortices (Hsiao and Yau, 2008). The whole body is not only topologically represented in SI (Penfield and Boldrey, 1937), similarly to how the retina provides a map of visual space, but other topological representations have also been reported in second-order associative areas of the brain (Orlov et al., 2010; Zeharia et al., 2012).

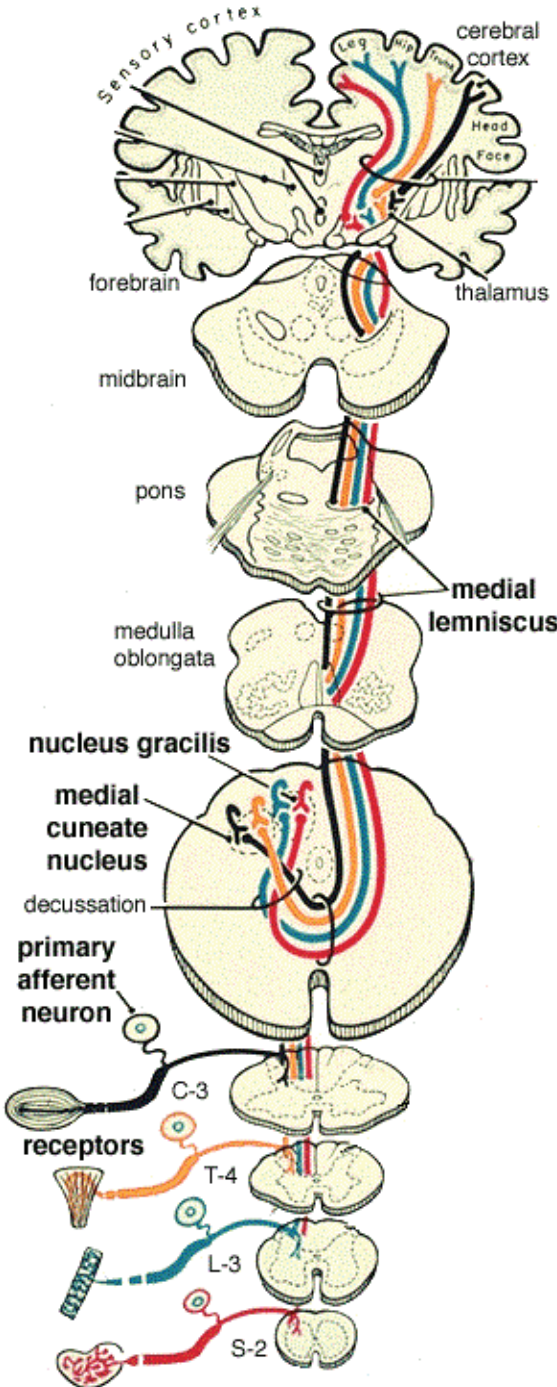


Figure 1. Illustration of the afferent pathways and neuro-anatomical projections of tactile inputs. Tactile information is transduced by skin-embedded mechanoreceptors (primary afferent neurons) to the dorsal

horn of the spinal cord. Second order neurons of the spinal cord project to the Dorsal Column Nuclei (DCN): the medial cuneate nucleus and the nucleus gracilis. Decussation, i.e. the crossing of sensory fiber over the midline, occurs in the medulla, before the signal is projected through the medial lemniscus to the contralateral sensory thalamus. Thalamic projection neurons sends axons to the somesthetic area of the cerebral cortex. From <http://vanat.cvm.umn.edu/neurLab2/pages/TouchKinesthesiaTract.html>, illustration by T.F. Fletcher.

1.2. Body representations underlying somatosensory information processing

1.2.1. Tactile localization relies on body representations

SI (as well as the motor cortex) contains a spatially organized representation of the sensory receptors of the skin referred to as the Homunculus, representing the whole cutaneous surface of the body. The Homunculus is a highly deformed representation of the body surface, as it is based on the proportion ratio between the amount of skin receptors and the size of the receptive fields of each body part (see Figure 2; Penfield and Boldrey, 1937; Penfield and Rasmussen, 1950; Sur et al., 1980). However, our everyday experience is not consistent with having a distorted body - that is, our fingers do not feel larger even though they have a larger cortical representation than our back. Therefore, perceiving the exact location of touch on our body cannot be achieved only by mapping its position onto the skin surface: information from the “distorted” representation in SI needs to be mapped to an accurate representation of the skin surface.

Head & Holmes (1911) study on patients with cerebral lesions was the first to suggest multiple integrated representations of the human body (Head and Holmes, 1911). It has since been widely accepted that there are multiple, higher-order, representations of the body that serve to link output from SI to a representation of locations on the skin surface. (Berlucchi and Aglioti, 2010; de Vignemont, 2010; Mancini et al., 2011; Schwoebel and Coslett, 2005). One way to examine the relationship between tactile localization and higher-order representations is, for example, to manipulate perceived body size. The Pinocchio illusion provides a key piece of evidence supporting the existence of these representations (Lackner, 1988). In this illusion the participant holds their nose with one hand. The biceps muscles of that arm are vibrated; this is known to engage muscle receptors, creating the illusion that the arm is extending forward. Given that the hand is touching the nose, and that the hand is perceived as moving away from the body, participants tend to experience that their nose is growing longer. This can be explained by the brain’s need to reconcile conflicting information (i.e. the arm is moving forward, and the hand is touching the nose): a higher-order representation of body size and shape is thought to change, resulting in perceived elongation of the nose. This leaves us wondering

how tactile localization is affected when these higher-order representations of body size and shape can change: if someone perceives a body part to be longer/shorter, do they perceive concomitant changes in perceived touch? Or are the changes in perceived body size and shape separate from changes in tactile localization?

De Vignemont and colleagues (2015) used a variant of the Pinocchio illusion, in which when one finger is grasped by the other hand, vibration of the elbow flexors of the other arm can be used to create the illusion that the finger is extended. Participants were asked to judge the distance between two tactile stimuli presented on either the forehead or the finger during the illusion. Tactile distances were perceived to be longer on the finger, providing evidence that changes in perceived body size lead to changes in the perception of tactile distances (de Vignemont et al., 2005). Distortion of higher-order body representations caused by visual information can also influence touch perception, as evidenced by Taylor-Clarke and colleagues (2004). In their experiment, participants viewed their hand as reduced and their forearm as magnified for one hour, after which touch perception was tested. Perceived distance was reduced on the finger and increased on the forearm (Taylor-Clarke et al., 2004). In conjunction with the results from de Vignemont’s study, this observation may demonstrate that changes in perceived body size lead to changes in perceived extent on the skin.

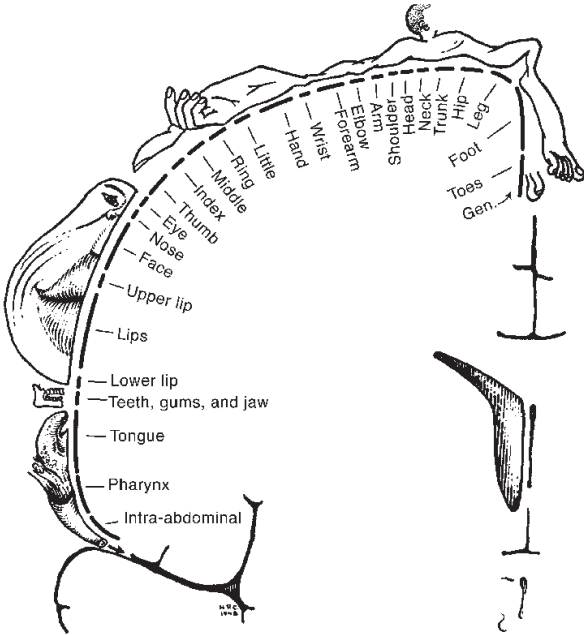


Figure 2. Sensory homunculus. Cortical representation of various body parts as mapped in the primary somatosensory cortex (SI). Adapted from Penfield & Rasmussen (1950).

1.2.2. Higher-order body representations involved in tactile processing

Multiple definitions of these higher-order body representations have been proposed, and authors still have not seemed to reach a consensus on them at the moment (de Vignemont, 2010). The following list is therefore a tentative description of the body representations involved in tactile processing, based on the combination of several authors' work (Head and Holmes, 1911; Longo et al., 2010; Medina and Coslett, 2010; Serino and Haggard, 2010). It is important to note that each of those representations are not sufficient for tactile localization alone, as tactile inputs needs to be integrated with all of them in order to obtain the precise location of touch on the body that can guide motor behavior.

- *a representation of the skin surface*: Penfield and colleagues have originally demonstrated that the whole cutaneous surface of the human body is represented in SI proportionally to the amount of skin receptors and the size of the receptive fields of each body part (Penfield and Boldrey, 1937; Penfield and Rasmussen, 1950). Single-cell recording studies in mammals have since shown that this somatotopic organization can change dynamically due to peripheral modifications such as amputation (Rasmusson and Turnbull, 1983) or deafferentation (Merzenich et al., 1983) or following brain lesion (Jenkins and Merzenich, 1987). This representation of the body surface has been labeled by some as “the superficial schema” (Head and Holmes, 1911; Longo et al., 2010).
- *a representation of the size and shape of the skin surface*: Each body part has different levels of tactile acuity which is reflected on the size on their cortical representation in SI (Weinstein, 1968). The fingertip, for example, has a much larger cortical representation than does the lower back. Yet we still have a coherent experience of the size of our own body and also of objects in contact with it. This require information from primary somatosensory representations to be rescaled in order to be used by a second representation which contains information on the perceived size and shape of body parts (Longo et al., 2010; Taylor-Clarke et al., 2004). This secondary representation of size and shape of the skin surface can be referred as a *body form representation* (Medina and Coslett, 2010).
- *postural representations of the body*: Localizing touch on the body surface is not by itself sufficient to interact with the environment. When writing for example, we need to know about the configuration and spatial position of the hand holding the pen. Thus information such as proprioceptive, vestibular and visual inputs needs to be combined into a dynamic representation of the current postural configuration of the limbs. Interaction requires the integration of skin-based information with these informations about the spatial configuration of the body. The term “postural schema” can sometimes be used to regroup these representations (Head and Holmes, 1911; Longo et al., 2010).

These body representations affect integration of tactile information as well as guide motor behavior, they are therefore required to process the localization of touch. Another way of referring to the position of touch on the body is through the concept of reference frames (see section 3).

Importantly, touch is not restricted to processing events on the body surface: for example, a blind person can use a white cane to extract information about their immediate surroundings. Even in the sighted, when a person touches an object with the tip of a handheld tool, the object is perceived to be at the tip rather than at the hand that holds the tool (Vaught et al., 1968). Humans can indeed sense several of an object's properties with a tool, such as its surface texture (Klatzky and Lederman, 1999; Yoshioka et al., 2007), softness (LaMotte, 2000), length (Peck et al., 1996), and position in space (Carello et al., 1992; Giudice et al., 2013). The next chapter will thus focalize on tool use and its impact on body and space representation.

2. Tool use induces spatial representational plasticity

Tools are ubiquitous in our daily life. From knife and pencil to smartphones, humankind has mastered the use of tools. The widely-accepted definition of tool use from Beck (1980, updated in 2011) describe it as: "The external employment of an unattached or manipulable attached environmental object to alter [...] the form, position, or condition of another object, another organism, or the user itself when the user holds and directly manipulates or carries the tool during or just prior to use" (Shumaker et al., 2011). Tool use is not exclusive to humans though, and has been observed in many species, in the wild as well as in captivity (Seed and Byrne, 2010; Shumaker et al., 2011). But only humans have reached such a high level of sophistication in the making and using of tools.

Crucially, tools allow us to interact with our environment by extending our physical body, therefore amplifying our sensory-motor capabilities. Doing so, however, means that sensorimotor representations of the body must adapt for how the tool changes the physical and geometric properties of the arm and hand (Imamizu et al., 2003). It was originally proposed over one century ago that tools become incorporated into a plastic neural representation of our body (Head and Holmes, 1911). In the next section, we will review the change induced by tool use on body and space representation. Body representations remain conceptually and functionally difficult to disentangle; hence we choose here to keep the umbrella term "body representation" when reviewing the impact of tool-use on body-related processes.

2.1. Behavioral evidence of tool use effects

2.1.1. *Patients' studies*

The behavioral and neural implications of tool use in humans have been highlighted by studies on brain-damaged patients, particularly those patients who exhibit unilateral spatial neglect or extinction. Both phenomenon can be observed following brain damage to one cortical hemisphere, most often the right one. Neglect patients fail to report, respond or orient to stimuli contralateral to the side of their brain damage (Bisiach and Vallar, 2000; Heilman and Valenstein, 1979). Patients with extinction are unable to report a stimulus delivered to the side contralateral to the damaged hemisphere when it is concomitantly presented with a stimulus on the ipsilesional side, whereas it is normally well perceived when presented alone (Bender, 1952; di Pellegrino et al., 1997; Làdavas et al., 1994).

Neglect

Berti & Frassinetti (2000) examined the effect of tool-use in a patient exhibiting a specific type of neglect selective to the space close to their body (near space). Using a line bisection task, which is typically used to reveal neglect, they asked the patients to mark the center of a drawn line with a pen. Neglect patients usually shift their mark towards one side from the objective midpoint, the same side as their cerebral lesion. The study's patient exhibited the same type of bias in this condition. However, when using a laser pointer on lines presented out of hand's reach (far space), their bisections were faultless. By contrast, when a long stick was used for to perform bisection in the far space, the patient showed a rightward bias again, which was as severe as in the near space (Berti and Frassinetti, 2000). The authors concluded that the use of a tool that extended the space accessible by the patient affected the representation of different sectors of space. Similar results were found by Ackroyd and colleagues (2002) with a patient exhibiting severe left and far space neglect. Their ability to detect visual targets in left and far space was improved, however, when they held a tool, suggesting a remapping of space induced by the hand-held tool (Ackroyd et al., 2002).

Differing from these studies, Pegna and colleagues (2001) observed a different pattern of results with their patient suffering from left neglect. No bias was observed when the patient bisected the lines with a light projection pen whether the task was carried out in near or in far space. By contrast, the use of the pencil and stick produced a rightward bias, whatever the distance. The explanation offered by the authors is that the representation of space may be modified depending on the action to be carried out (Pegna et al., 2001). In line with this explanation, it was also found that the mere

observation of tool-use while holding the same tool induced a remapping of far space into near space for a neglect patient as well as neurotypical participants (Costantini et al., 2014).

Cross-modal extinction

Extinction following brain damage can occur in one sensory modality (e.g. tactile extinction), but it can also be influenced by the concurrent activation of another modality. Patients suffering from cross-modal, visual-tactile extinction, fail to report tactile stimuli on the contralesional hand when presented together with competing visual stimuli near the ipsilesional hand (Figure 3.a). Crucially, extinction is reduced when the competing visual stimuli is presented in the far space (Figure 3.b). Tool use in such patients has been shown to modulate their degree of extinction. In Farnè & Làvadas (2000) study, cross-modal extinction was assessed in right-brain damage patients holding a tool in their ipsilesional hand, with the competing visual stimulus always presented in the ipsilesional far space (Figure 3.c). Cross-modal extinction was more severe after patients used the tool, here a rake, to retrieve distant objects with respect to a condition in which the rake was not used. These results showed that the tool transiently expanded the space near the hand, as this effect disappeared a few minutes after tool use (Farnè and Làvadas, 2000). Similar results were obtained when patients wielded a stick in each hand: cross-modal extinction from the far visual stimulus increased, but not if the sticks were laying passively without being connected to the patient's hands (Figure 3.d) (Maravita et al., 2001). This suggest that the remapping of space by the tool is dependent on the active use of that tool, an idea that was further supported by another study of Farnè and colleagues (2005) who investigated the impact of various tool use as well as different tool-length on cross-modal extinction. When their patient was passively holding a rake, the degree of extinction was similar to that obtained when the tool was absent. As expected, extinction increased after a period of retrieving objects with the rake. Additionally, when using another, shorter rake, with the visual stimulus still being presented at the same distance as previous conditions, cross-modal extinction was also more severe than without the tool. Hence, both the longer and smaller rake modulated the space near the hand, supposedly in a linear relationship between tool-length and the amount of space extension around the hand (Farnè et al., 2005).

Interestingly, when trained to use a tool with their contralesional hand in order to manipulate visual objects in the ipsilesional hemispace, so with the tool in a crossed position (Figure 3.e), cross-modal extinction of the patient was actually reduced (Maravita, 2002). Authors hypothesized that such training with the tool linked the left hand and right visual hemispace within a common, integrated visual-tactile space representation. This theory was validated by Farnè and colleagues in 2007, by measuring extinction with various distance between the visual stimulus and the hand after tool use. Whether the visual stimulus was presented at the distal edge of the tool, or midway through its length,

the worsening of cross-modal extinction was similar, clearly supporting the notion that tool use induces a real extension of space around the hand holding the tool (Farnè et al., 2007).

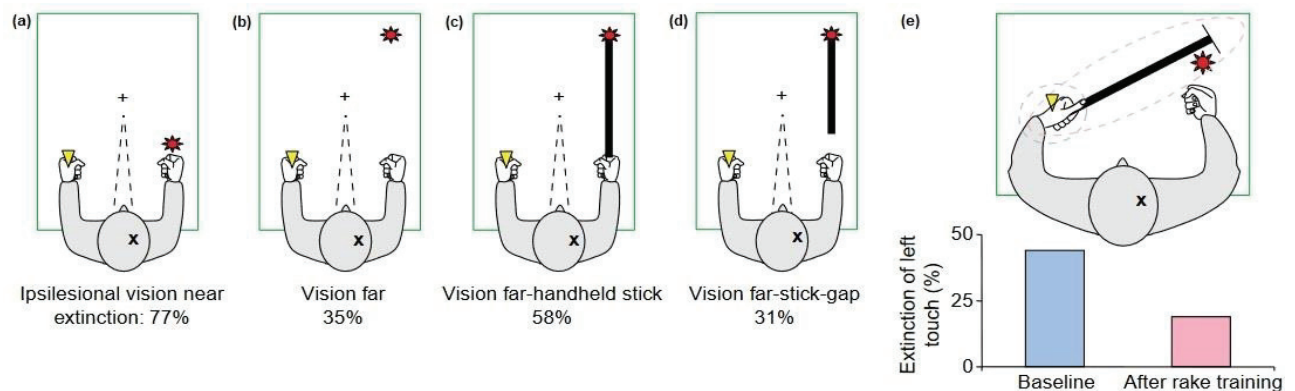


Figure 3. Tool-use effects on cross-modal extinction

(a-d) Crossmodal extinction (percentages below each panel) of left touches in the right-brain damage patient of (Maravita 2001 & 2002a). X marks the side of the lesion. Extinction decreased when simultaneous flashes near the right hand (a) were moved further away (b). Extinction increased again if the far flash was reached by a long stick (c) but not if the stick was disconnected from the hand (d). (e) After ten minutes of rake-assisted reaching with the left hand, left tactile extinction from right flashes at the tool tip decreased (pink bar) compared with the pre-training baseline level (blue bar). The pink dotted oval represents the expansion of a hand-centred somatosensory–visual space representation up to the tool-tip following tool-use. This expansion might underlie the reduced competitive extinction. From Maravita & Iriki (2004).

2.1.2. Neurotypical participants

Several non-patients' studies have also shown that tool use can modify the representation of space around body. Longo & Lourenco (2006) employed the same line bisection task used with neglect patients, but presented the lines to cross at various distance from participants. When using a laser pointer, participants exhibited a left bias in near space, that shifted to the right as the lines were moved from near to far space. However, when using a tool, a leftward bias was observed at all distances. As the authors also found the transition from near to far space was gradual, they suggested that representation of near space is not rigid, but extend with tool use and gradually transition into far space (Longo and Lourenco, 2006). Furthermore, it was shown that the state of the action performed with the tool was an important parameter in its influence on space representation (Bloesch et al., 2012; Witt et al., 2005), in accordance to the conclusion found by patients' studies (Costantini et al., 2014; Pegna et al., 2001).

Tool-use has been claimed to not just modulate the representation of space around the body, but representations of the body itself. The extension of space around the hand caused by tool use has indeed been used as an argument for the incorporation of tools into body representation (Maravita and Iriki, 2004; Martel et al., 2016a). Therefore, the next section will review studies that focused on the influence of tool use on body-related processes.

Cardinali and colleagues (2009) reported that body representation, in this case the unconscious arm representation as probed by execution of reach-to-grasp movements, was modified after using a mechanical grabber for a few minutes. Participants' free-hand movement kinematics was recorded before and after using this tool. Tool reach-and-grasp actions modified the subsequent freehand movement kinematic profile, as reflected by the observation that participants took longer to reach both velocity and deceleration peaks, resulting in a longer movement time. In addition, the amplitude of both velocity and deceleration peaks was smaller, as compared to that observed during the bare hand movements performed before tool-use. Furthermore, this effect was driven by an increase of the represented length of the arm: after tool-use, subjects localized touches delivered on the elbow and middle fingertip of their arm as if they were farther apart. These findings were taken as evidence for tool incorporation into the arm representation (Cardinali et al., 2009a). This was further supported by similar results from the same group (Cardinali et al., 2012, 2011; Martel et al., 2019), as well as by the work of Sposito and colleagues (2012) who adapted the bisection task, typically used with neglect patient, to evaluate the change in body perception caused by tool use.

In its version adapted to the body, the bisection task consists of indicating the mid-point of a body limbs, for example the forearm. It has been shown to be an accurate method for estimating the length of body parts (Sposito et al., 2010). Participants performed a 15 min session of tool use, either with a long (60 cm) or with a short (20 cm) tool. After tool use, participants estimated the mid-point of their forearm further away from them compared to pre-tool use, but only when the tool used was the long one. Since the shorter tool was considered "functionally irrelevant" to perform the tool use tasks, the modification of body metrics seemed dependent on the functional importance of the tool imposed by its morphology (Sposito et al., 2012). Miller and colleagues (2014) provided evidence that tool morphology bind the change made to the representation of body limbs by varying tool shape to correspond to different body parts. They designed two experiments; one in which a tool shaped like a hand was used, the other one in which a tool shaped like an arm was used, with a tactile distance judgment task performed before and after each experiment. In this type of task, two tactile point are first presented to a control surface (e.g. the forehead), and then, after a short delay, to the target surface (e.g. the hand). Participants then have to make a verbal judgment about which body part was touched with a greater distance. When the hand-shaped tool was used, tactile size perception

increased for judgement made on the hand but not on the arm. Conversely, with the arm-shaped tool, only judgments made on the arm but not on the hand were increased. These results demonstrate that the morphology of a tool constrains body representational modulation (Miller et al., 2014).

Alongside tool morphology, the effects of tool use on body representation also depend on the action performed with the tool, as evidenced by the previously mentioned patients' studies. Romano and colleagues (2019) findings further supported this idea, when testing different use of the same tool led to different bias in the forearm bisection task. This suggested that specific motor patterns required by the task performed with the tool can induce different changes of body representation (Romano et al., 2019). Similarly, the level of expertise in tool user for specific tools also seems to play a part in the influence of tool use on representation. It is well known that musicians exhibit larger sensorimotor cortical representation of the body part used in their musical training compared to non-musicians (Pantev et al., 2003; Schwenkreis et al., 2007). Furthermore, blind cane users showed an extension of auditory-tactile interactions along the length of the cane when passively holding it. Control participants, by contrast, needed active training with the cane to induce such an extension (Serino et al., 2007).

2.2. Electrophysiological evidence of tool use effects

2.2.1. *Non-human primate studies*

Iriki and colleagues (1996) aimed at studying the neural correlates of the assimilation of a tool into body representation by recording the neural activity of non-human primates using a rake (A Iriki et al., 1996). Neuronal activity was recorded from the intraparietal cortex, where somatosensory and visual information is integrated. Analysis included neurons responding to both somatosensory and visual stimuli, called bimodal neurons (see Figure 4). These types of neurons have two receptive fields: a visual receptive field (vRF) which correspond to the region within the visual field in which stimulation can affect the neuron's response, and a somatosensory receptive field (sRF) which correspond to the stimulated body region to which the neuron respond. The neurons that responded to somatosensory stimuli at the hand (Figure 4a), and to visual stimuli near the hand (Figure 4b) were dubbed 'distal-type' neurons. Iriki and colleagues observed that in some of these bimodal neurons, the vRFs expanded to include the entire length of the tool, after the monkey had used it for a few minutes. Other bimodal neurons with sRFs located around shoulder/neck (named 'proximal type', Figure 4e) had vRFs covering the space reached by the arm (Figure 4f). After tool-use, these proximal vRFs expanded to code the space now accessible with the rake (Figure 4g). Tool use had therefore modified the space

representation around the body, as seen in these results (but see Holmes et al., 2007). Furthermore, it has been hypothesized that the expansion of the vRFs may constitute the neural substrate of tool-assimilation into body representation (A Iriki et al., 1996; Maravita and Iriki, 2004).

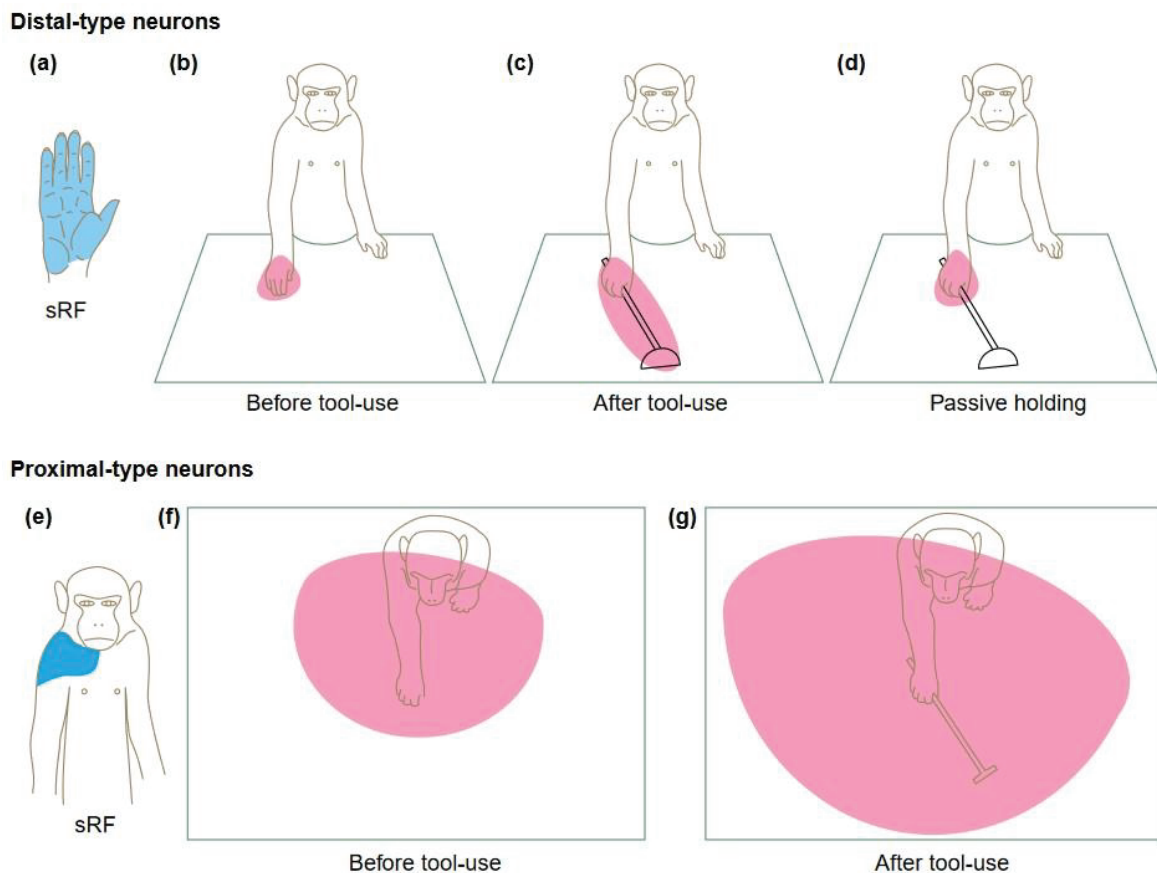


Figure 4. Changes in bimodal receptive field properties following tool-use. The somatosensory receptive fields (sRF) of cells in this regions were identified by light touches, passive manipulation of joints or active hand-use. The visual receptive field was defined as the area in which cellular responses were evoked by visual probes (the most effective ones being those moving towards the somatosensory receptive field). (a) Somatosensory receptive field (blue area) of the ‘distal type’ bimodal neurons and their visual receptive field (pink areas) (b) before tool-use, (c) immediately after tool-use, and (d) when just passively grabbing the rake. (e) Somatosensory receptive field (blue area) of ‘proximal type’ bimodal neurons, and their visual receptive field (pink areas) (f) before and (g) immediately after tool-use. From Maravita & Iriki (2004).

Using a very different tool, a plier, Umiltà and colleagues (2008) also recorded neuronal activity of non-human primates, this time in the motor cortex (MI). Pliers can be distinguished between classic and reverse pliers. With classic pliers, parallel kinematics take place between the hand and the tool, as in when the hand closes, the tool closes too. Whereas with reverse pliers, when the hand is opening, the tool is closing. Albeit both classic and reverse pliers support a similar goal, different kinematic requirements are at stake, opening questions about the neural substrates encoding tool and hand

kinematics. Cortical motor neurons active during hand grasping also became active during grasping with pliers, when the mechanics of pliers mimicked that of the hand (normal pliers), but also when the mechanics was its exact opposite (reverse pliers). These results seem to suggest that tool use can be incorporated into the body representations supported by the premotor cortex. Interestingly, a subset of neurons in MI responded only to the hand configuration (when it closed), regardless of the type of pliers used (Umiltà et al., 2008).

2.2.2. Human studies

The representational plasticity induced by tool-use has more recently been evidenced by electrophysiological studies in humans. Contrary to the monkey's studies, most of these studies use electro-encephalography (EEG) as a non-invasive method. This technique allows researchers to measure brain response directly resulting from a specific event (sensory, cognitive, or motor), a phenomenon referred to as evoked potential or event-related potential (ERP). Forsberg and colleagues (2019) focused for example on the P100 component, which is an ERP elicited by visuo-tactile events, to investigate the effect of tool use on visuo-tactile interactions in near and far space. When a visual stimulus is presented simultaneously to a tactile stimulus on the hand, the P100 has been shown to be enhanced when the visual stimulus is in near space compared to far space (Sambo and Forster, 2009). Before having their brain activity recorded while receiving visuo-tactile stimulation, participants performed a motor task with small tools to hit target keys located in near space, or with long tools to act upon far space targets. While no difference was found in the amplitude of the P100 after the use of short tools, the P100 was enhanced when receiving a tactile stimulation on the hand with a simultaneous visual stimulus in far space, compared to near space, after the use of long tools. This results might be indicative of a transient remapping of space (Forsberg et al., 2019). Similar results were obtained by Ronga and colleagues (2021) when recording electrophysiological response to audio-tactile stimulation after tool use (Ronga et al., 2021).

Miller and colleagues also observed a modulation of the P100 amplitude following tool use. In their study, ERPs were measured while participants had to detect tactile stimuli applied on their hand, before and after two object-interaction conditions—tool use and hand use—in which participants picked up balloons for 8 minutes. To successfully use a tool, sensorimotor models of the body must adapt to its weight and geometry, a recalibration that is not necessary when only the hand is being used. As expected, sustained use of the hands to pick up the balloons did not modulate the amplitude of any ERP. Using a tool, conversely, led to a bilateral modulation of the amplitude of the P100 at posterior recording sites around sensorimotor areas (Miller et al., 2019b). In their case, the enhancement of the P100 reflected the modulation of somatosensory processing by tool use, which is

consistent with the idea that tool use might change body representation. Schaefer and colleagues (2004) used magnetoencephalography (MEG) to record primary somatosensory responses to puffs of air applied to the fingers during tool use, hand use, and rest. They found that tool use (but not hand use) increased the distance between the representations of the thumb and the little finger in primary somatosensory cortex, as measured from somatosensory evoked magnetic fields, providing evidence for body representational plasticity during tool use (Schaefer et al., 2004).

The effect of tool use on space and body representation seems to be overwhelmingly assessed by tactile tasks (Canzoneri et al., 2013; Cardinali et al., 2012, 2011; Sposito et al., 2012). In most of those tasks, the aim is to localize tactile stimuli, as in the tactile distance judgment task for instance. We have seen in the previous section that body representations are required for tactile localization. Since tool use can affect those representations, this might suggest that tool use can also affect tactile localization on the body (Cardinali et al., 2009a, 2011). We will therefore describe in the next section the mechanisms involved in tactile localization on the body surface.

3. How do we localize touch on the body ?

3.1. Frames of reference for localizing tactile inputs

Accurately positioning touch in the space occupied by the body is essential, especially when an action towards the stimuli is planned. For example, if we want to get rid of a fly that landed on our hand, we need to know its exact position, not just on the hand but also in the space around our body. The spatial encoding of a stimulus by the brain requires the use of reference frames (Colby, 1998; Committeri et al., 2004), which can be defined as coordinate systems defining a specific position in two or three dimensional (3D) space. To illustrate the concept of reference frame, picture a person driving a car and another person observing the car (Soechtin and Flanders, 1992). Two reference frames could be used to describe this situation, one fixed to the car and another fixed to the earth. In earth coordinates, the driver is moving, whereas they are stationary in car coordinates. The observer, in turn, is stationary in earth coordinates, but is moving in car coordinates. An object dropped out of the cars' window follows a straight path in car coordinates and a curved one in earth coordinates while falling down. Thus, the anchor of the coordinate system determines the description of events.

All sensory information coming from multiple modalities, not just touch, is encoded relative to spatial reference frames. Visual inputs, for example, can be encoded in retina-centered, or eye-centered coordinates. These reference frames can be shared across modalities and sensory

information is thought to be recoded into a common external spatial reference frame to integrate multisensory information (Pouget, 2002). Indeed, localizing a tactile stimulation require the integration of skin-based coordinates with other information coming from visual, proprioceptive, and vestibular inputs. The position of somatosensory information is therefore coded according to different frames of reference in the brain (Vallar and Maravita, 2009). Touch is initially encoded relative to the skin in an anatomical reference frame, also referred to as skin-based or as somatotopic reference. Since our body parts can move, the brain also needs to take into account the position of the body limbs in external space, i.e. the space that encompass the body. Anatomical coordinates therefore need to be *remapped* into external coordinates. This translation process from anatomical to external information is referred to as *tactile spatial remapping* (Driver and Spence, 1998; Vallar and Maravita, 2009). Touch in 3D space is encoded into external spatial coordinates related to several possible egocentric reference frames, such as a gaze-centered or a head-centered reference frames. The term “external reference frame” is hence typically used as an umbrella term for these various reference frames. It is important to note that these two reference frames, anatomical and external, are egocentric, meaning their origin and axis depend on the location, orientation, and posture of the subject.

3.1.1. Evidence from patients' studies

Initial evidence for anatomical and external coding of tactile events came from studies of patients with tactile extinction. As mentioned in a previous section, extinction is a phenomenon observed following brain damage to one hemisphere, most often the right one. Extinction patients are unable to report a stimulus delivered to the side contralateral to the damaged hemisphere when it is concomitantly presented with a stimulus on the ipsilesional side, whereas it is normally well perceived when presented alone (Bender, 1952; di Pellegrino et al., 1997; Làdavas et al., 1994).

Smania and Aglioti (1995) observed that when right-brain damage (RBD) patients with tactile extinction crossed their hands over the body midline, so that the left hand was in the right part of space and vice versa, their detection rate for tactile stimuli applied to the contralesional hand (i.e. left hand) was significantly higher compared to when the hands were uncrossed (Smania and Aglioti, 1995). Similar results were obtained when the patients crossed their hands while they were both placed in one single hemisphere relative to their body midline (Aglioti et al., 1999). This indicates that the perception of tactile stimuli does not only depend on the hand on which the stimulus is applied, but also on the relative position of the hands in external space. In a single-case study with a RBD patient with tactile extinction, Tinazzi and colleagues applied touch not only to their hands, but also to the thumb or the pinkie of a single hand, and to the sides of a single index, while that hand was placed in

various positions (e.g. palm up/down; in front or behind the back, crossed or uncrossed) (Tinazzi et al., 2000). They reported that in double touch conditions, stimuli coded as left-sided were extinguished, not only when delivered to both hands, but also when delivered on a single hand or a single finger, suggesting that the position of one body part relative to another also matters when perceiving and localizing tactile inputs, and not only the general position of the limbs in space according to the body midline (Aglioti et al., 1999; Tinazzi et al., 2000). Similar pattern was also found by Bartolomeo and colleagues (2004) when double touch was applied on different body parts (hands, knees, and cheeks). In their study, limb crossing improved tactile detection for left body parts, additionally causing a deterioration in performance for stimuli applied to right body parts, even when two non-homologous body parts were stimulated, e.g. the hand and the knee (Bartolomeo et al., 2004).

3.1.2. Evidence from neurotypical participants

Temporal order judgment (TOJ) studies

Tasks manipulating limbs position have largely been used in studies with neurotypical participants to provide evidence for separate anatomical and external coding in localizing tactile stimuli. In a tactile TOJ task, participants are presented with two successive tactile stimuli, one to each hand, and are instructed to report which tactile stimulus is presented first. The stimuli are separated by variable time intervals, i.e. stimulus onset asynchronies (SOA). This task is typically performed while the arms are placed in a canonical, uncrossed posture, or crossed over the body midline, such as the left hand is placed in the right part of space and vice versa. This crossed posture allows one to investigate the involvement of the reference frames of touch by creating a mismatch between them (see Figure 5). Indeed, in the uncrossed posture, touch applied to the right hand is also located in the right hemispace relative to the body midline. When crossing limbs, touch applied to the right hand is now localized in the left hemispace, while the anatomical position of touch hasn't changed.

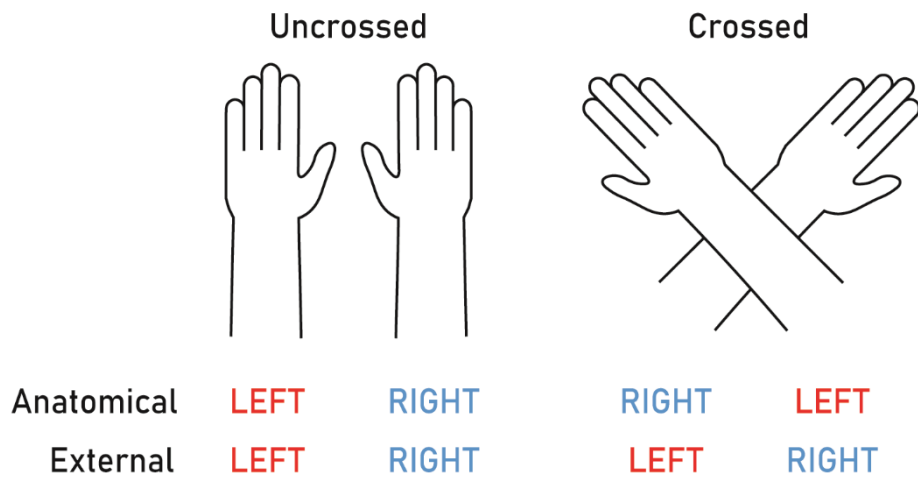


Figure 5. Illustration of the conflict emerging from the crossed hand posture. When the hands are uncrossed, the anatomical and external coordinates of each hand are aligned. When they are crossed over the body midline, a touch on the right hand is still anatomically coded as “right”, but is now externally coded as “left”, as the position of the limbs as changed into external space. Thus, a mismatch between the two coordinates systems emerges from this posture.

Yamamoto and Kitazawa (2001a) have examined participants’ ability to sense the temporal order of two stimuli delivered one to each hand. They observed that participants with uncrossed arms were accurate at assessing the location of the first stimulus, even for very short SOA (<70 ms). However, crossing the arms significantly impaired their performance, as many subjects reported inverted judgment at intervals of around 100–200 ms. Correct judgment was restored as the interval approached 1,500 ms, clearly indicating that the inverted judgment was not caused by a trivial confusion in distinguishing between the two hands (Shinya Yamamoto and Kitazawa, 2001a). The detrimental effect of crossing the hand on TOJ performance has been evidenced by multiple studies having used this paradigm (Azañón and Soto-Faraco, 2007; Roberts et al., 2003; Shore et al., 2005, 2002; for a review see Heed and Azañón, 2014). Remarkably, this effect has proven to be very reliable and stable across studies, in spite of variable differences in the experimental designs. Crossing effect could be observed no matter the response mode: whether the motor response was made with the stimulated finger (Shore et al., 2002), with another finger of the stimulated hand (Sambo et al., 2013) or with foot pedals (Kóbor et al., 2006). It was also observed for verbal answer (Pagel et al., 2009) or even response made by eye saccade (Overvliet et al., 2011a). It was also evidenced with small distance between the stimulated crossed hands (e.g. only 7 cm in (Heed et al., 2012) and only 5 cm in (Roberts et al., 2003)). Moreover, crossing the limbs has been shown to deteriorate participants’ performance when the stimuli differed in terms of frequency (Badde et al., 2015), or when two non-homologous body limbs were stimulated, such as two different fingers belonging from the same or from different hands (Heed et al., 2012), or when the stimulated hand was crossed over the contralateral stimulated

foot (Schicke and Roder, 2006). Crossing hands effects were not only observed when the hands were placed in the space in front of the body, but also when the hands were crossed behind the back of the participants, even though it was considerably reduced in that case (Kóbor et al., 2006).

Since the external position of the stimuli are actually irrelevant to perform the task (i.e. participants have to report on which hand they perceived the first stimulus of the pair irrespective of the position of the hands in external space), this effect has been interpreted as indexing an automatic remapping of tactile inputs into external coordinates, taking the position of the stimulated limbs in space into account (Heed and Azañón, 2014).

Furthermore, Yamamoto and Kitazawa (2001a) also manipulated the orientation of the hands by asking their participants to perform the TOJ task while their hands were placed in six different positions from uncrossed to crossed defined as if the hands were rotating along a circle. They showed that only the positions in which one arm crossed over the other gave rise to a significant impairment of performance (Shinya Yamamoto and Kitazawa, 2001a). This is in line with the findings of Heed and colleagues (2012) who showed that placing one hand on top of the other along the body midline affected the TOJ performance of two tactile stimuli applied on the index fingers but not on the ring fingers. Indeed, whereas both hands share the same spatial location (i.e. in front of the body trunk), the ring finger of the right hand is placed at the right relative to the ring finger of the left hand, just as when the hands are uncrossed in their respective hemispace. In contrast, when one hand is placed on top of the other, the right index finger is positioned at the left of the index finger belonging to the left hand, just as in the crossed hands posture. This indicates that TOJ performance is impaired only when there is a conflict between the two spatial reference frames of the stimulated body parts, while manipulating the posture without creating any mismatch does not seem to influence performance. In that vein, the same authors also demonstrated a reduced effect of crossing the hands when the stimulated little fingers were crossed back to their normal hemispace, as compared to a fully crossed posture, suggesting that the localization of tactile stimuli on a finger was determined by its external location in space, but also by the spatial coordinates of the hand to which it belongs, probably converging through integration mechanisms (Heed et al., 2012).

Other experimental paradigms

Although TOJ task paradigms seems to have been extensively used to investigate the spatial processing of touch, other studies succeeded to evidence the integration of anatomical and external reference frames during the localization of tactile inputs using other paradigms (Azañón et al., 2010a; Azañón and Soto-Faraco, 2008; Medina et al., 2014, 2019; Overvliet et al., 2011; Tamè et al., 2011). For example, Medina and colleagues (2014 & 2019) employed the Simon effect, defined as when

participants respond more quickly when a stimulus is located on the same side of space as the response, even when stimulus position is task-irrelevant (Simon, 1969). Participants performed the task with stimuli delivered to the hands, with arms in crossed or uncrossed posture, and responses were produced with foot pedal. In both postures, participants responded faster when stimuli were presented to the same hand as the response foot (e.g., left hand stimulus, left foot response), showing a robust tactile Simon effect based on an anatomical representation of the limbs (Medina et al., 2014). In a follow-up experiment where, this time, each side of the same hand were stimulated, the same authors (2019) observed a hand-centered Simon effect that was coded in external coordinates (Medina et al., 2019).

In another paradigm, Overvliet and colleagues (2011) measured the saccadic response to somatosensory events in order to investigate the timing of tactile remapping. Saccades are fast voluntary movements of the eyes made to align the fovea with objects of potential interest. Analysis of saccadic movements can provide insights into the early stages of processing, because they are elicited earlier than manual responses (Ludwig and Gilchrist, 2002). Moreover, although typically regarded as visual, saccades can be directed also to auditory or tactile stimuli. As such, Overvliet and colleagues asked participants to direct saccades to a brief tactile stimulus applied on one hand, with the hands being either crossed over the body midline or uncrossed. They were instructed to respond immediately after the tactile stimulus, or else after a variable delay (>600 ms). The authors found that saccade onset latencies, i.e. the time delay between the happening of the tactile event and the start of the saccade, were slower in the crossed hands conditions than in the uncrossed hands condition, illustrating the mismatch between reference frames in the crossed posture. Moreover, in the crossed hands condition, saccades were sometimes initiated to the wrong direction (i.e., towards the side where the hand canonically is) and then corrected in-flight, resulting in what the authors called “a turn-around saccade”. These turn-around saccades, reminding similar findings in monkey studies (Groh and Sparks, 1996) were more likely to occur when participants had to respond immediately after the tactile stimulus, whereas saccades performed after a longer delay went straight to target. This suggest that saccades are initiated using anatomical coordinates and their trajectory are then corrected online when the information in terms of external coordinates is available (i.e. when remapping is completed) (Overvliet et al., 2011).

External coding of touch has also been demonstrated through studies that manipulated the posture of the hands, but without having them crossed. Indeed, manipulating the distance between the two hands has been shown to influence tactile localization by both using TOJ tasks (Roberts et al., 2003; Shore et al., 2005), and congruency-effects (Soto-Faraco et al., 2004). In these studies, the hands were placed either close together or far apart. In the TOJ studies, participants' judgements were less

accurate in the close, as compared to the far hands posture. In the cueing paradigm, the congruency effects (i.e. smaller/larger error rate in localization judgements when the target and the distractor had congruent/incongruent spatial locations) was larger for the close as compared to the far posture, indicating a greater effect of the distractors when the hands were placed close together (Soto-Faraco et al., 2004). Hence these results suggest that the position of the stimulated hands in external space was taken into account and impacted localization performances even when anatomical and external reference frames were still aligned.

Several authors have hypothesized that the remapping of anatomical coordinates into external ones is a highly automatic process (Azañón et al., 2010a; Kitazawa, 2002; Shinya Yamamoto and Kitazawa, 2001a). For instance, Azañón and colleagues (2010) had participants performed tasks where space was made irrelevant, such as a color discrimination task. Participants made faster color judgments when a preceding tactile cue was placed at the same external location of the visual stimulus, whether they responded with a foot pedal or verbally, which suggest that engaging in spatial tasks is not a prerequisite for triggering tactile remapping (Azañón et al., 2010a). Furthermore, Canzoneri and colleagues (2014) used a paradigm requiring participants to localize touch on the skin and then relate skin locations to anatomical body landmarks, under different body posture. They found that body posture influences tactile spatial judgements, even when it is irrelevant to the task, supporting the idea that localizing the body in external space is an automatic process underlying tactile perception (Canzoneri et al., 2014). However, other experiments have cast doubt on whether this is actually the case. For example, if a tactile stimulus is presented during an arm movement, and participants indicate the stimulus's location by pointing to its external location after the movement, they make systematic localization errors (Maij et al., 2017; Watanabe et al., 2009). Importantly, because these errors differ for fast and slow movements, it has been suggested that participants do not compute the precise spatial location of a stimulus when it occurs, but instead infer spatial location post-hoc, by estimating hand location at the perceived time of the tactile stimulus (Maij et al., 2017). Maij and colleagues (2020) investigated the spatial representation of touch when participants have to make spatial decisions about tactile stimuli. Participants were performing a TOJ task in which they had to point to the location of the first of two stimuli received during a bimanual movement. When participants incorrectly chose the hand stimulated second, they pointed to where that hand had been at the time of the first, correct stimulus. Participants derived the reported stimulus location by combining the time of the first, correct stimulus with the trajectory of the second, incorrectly chosen hand, thus indicating a location at which no stimulus had occurred. The authors hence argued that the external coordinates of touch aren't automatically computed but instead constructed post-hoc and on demand (Maij et al., 2020).

3.2. Integration of tactile reference frames

3.2.1. *Integration models*

Different models have been proposed to explain tactile localization. At first, non-integration models suggested that touch location, once it was remapped, was retained only in an external-spatial code, and the original skin location was discarded in the process. To report which body part has been touched, the brain had then to reversely determine which limb was located at the computed external location at the time of the touch (Kitazawa, 2002; Shinya Yamamoto and Kitazawa, 2001a). When considering this hypothesis, TOJ task errors are explained by the idea that participants correctly remap the two tactile stimuli into external space, but then reconstruct erroneously which hand was at the first spatial location.

Others models have since emerged, proposing that both anatomical and external representations of touch remain available after remapping, to be integrated into the localization response. Integrating all available information is advantageous in most situations, as usually anatomical and external reference frames will be aligned at least roughly, for example with respect to left and right. Following this idea, Tamè and colleagues (2019) have hypothesized that previous experience plays a role in the processing of tactile location through the concept of spatial and postural priors. For instance, touches on the right hand would occur more often on the right side and around the center of the body, with respect to the body midline. Therefore, one could preferentially expect the source of the right-hand tactile stimulus as originating from the right hemispace, because it constitutes the most plausible configuration considering past experiences. Similarly, the frequent touches while adopting a particular body posture would promote the emergence of canonical postural priors, that is, stored prototypical postural configurations containing the most plausible body configuration for a given touch. Together, these frequent associations (i.e. co-occurrence of tactile-visual or tactile-postural sensory signals) would be used as a reference for localizing tactile events, providing accurate performance. However, when the body adopts an unusual configuration, such as when the hands are crossed over the body midline, the reliance on these priors would be inefficient. Indeed, in this situation, the spatial priors (i.e. the visual space where the hand normally is and from which one could expect the source of the stimulus to come) would mismatch the online tactile-proprioceptive information which would result in impaired tactile localization (Tamè et al., 2019). Azañón and colleagues (2015) have actually shown that if the crossed posture is maintained in a TOJ task, performance will improve (Azañón et al., 2015), supporting this idea.

Moreover, the weighted integration model (Badde et al., 2015; Badde and Heed, 2016) has taken into account accumulated evidence about the influence of task context on localization performance. This model proposes that touch localization is a constructive process, consisting of at least two separate processes: an automatic remapping of anatomical into external coordinates, and an flexible integration where both sets of coordinates are given differential weights based on contextual demands (Badde et al., 2015; Badde and Heed, 2016). Consequently, in this model, TOJ performance is better in situations that do not contain spatial conflict, such as when the hands are uncrossed, and errors thus reflect the mismatch between different codes used for stimulus location (and their respective weight based on the demands of the task). The resolution of this conflict can take time and be error-prone depending on the weight attributed to each reference frame. Hence, this model views the TOJ paradigm as an implicit index of tactile remapping (Azañón et al., 2015; Badde and Heed, 2016; Heed and Azañón, 2014). Errors implies that participants have correctly remapped the two stimuli into space, but have incorrectly solved the conflict between the different spatial codes of the first stimulus, consequently assigning the incorrect stimulus to the first time point; as a consequence, participants incorrectly report the hand that received the second stimulus.

Although the integration view is the dominant theory of tactile localization at the moment, new evidence has emerged, contradicting the idea that TOJ task actually indexes tactile remapping. Maij et al. (2020) examined errors from a task in which participants received two successive vibrations while hands were in a crossed or uncrossed posture and they moved the hands toward the body to either end in the same posture that they began in, or to end in the opposite posture. Participants were asked to point to the location of the first tactile stimulus with the hand that was vibrated first. Importantly, crossing the hands did not affect errors in pointing to the stimulus location (i.e., tactile localization); instead, crossing the hands influenced hand assignment (i.e., identifying which hand vibrated first). Thus the “time-reconstruction hypothesis” (Maij et al., 2020, 2017), as proposed by the authors, claims that tactile remapping does not occur automatically, but that external representation of touch is constructed post-hoc and on demand. Accordingly, errors in the TOJ task would occur because participants first choose the incorrect hand, and then derive stimulus location based on that hand’s position at the time of the first stimulus.

3.2.2. The role of context

Although the automatic nature of tactile remapping is still debated, there seems to be widespread consensus that each spatial code can have more or less influence depending on the specific situation (i.e. considering individual differences, attention, or task demands, amongst other examples). A number of factors that influence the weighting of spatial information from the different reference

frames have been identified experimentally. We will here briefly review them. These studies show that weighting of tactile spatial information is not determined just by bottom-up processed sensory information, but depends on top-down regulated cognitive factors as well.

Visual information

Visual information about the posture of the hands has been shown to influence the weighting of anatomical and external information. Cadieux & Shore (2013) found a reduced crossing effect in tactile TOJ when participants were blindfolded, as compared to when they performed the task with the eyes open (Cadieux and Shore, 2013). Moreover, in Azañón & Soto-Faraco (2007) study, participants performed a classic tactile TOJ task with the hands either crossed or uncrossed, while watching a pair of rubber hands that were also placed either in a crossed or uncrossed posture (congruent or incongruent with the posture of their own hands). The crossed hands decrement in performance was significantly reduced by the sight of uncrossed rubber hands, hence showing that visual input that provided relevant, but false information also affects tactile localization abilities (Azañón and Soto-Faraco, 2007).

Studies of blind humans further corroborate the relevance of the visual system for reference frame weighting. Röder and colleagues (2004) compared the performance of congenitally blind, late blind, and sighted participants in the tactile TOJ task. Contrary to sighted participants, congenitally blind participants were completely unaffected by the crossing of their hands. However, performance of late blind participants were indistinguishable from that of sighted participants (Röder et al., 2004). These results demonstrate that visual input during development may lead to an impairment of temporal order judgments for tactile stimuli when unusual postures, such as crossing the hands, are adopted in adulthood. Electrophysiological recordings of sighted and congenitally blind participants performing a tactile detection task with their hands either crossed or uncrossed further supported the idea that developmental vision plays a critical role in tactile localization, as a modulation of ERP components reflecting an employment of external coding for tactile attention was only observed for the sighted group but not for the congenitally blind group (Röder et al., 2008a).

Task demands

Specific task requirements and response modalities in a given experiment may directly or indirectly set an external or anatomical context. For example, Schubert and colleagues (2017) demonstrated that task instruction can influence tactile localization performance, for both sighted and congenitally blind participants. They asked participants to localize tactile targets on the palm or back

of one hand, while ignoring simultaneous tactile distractors at congruent or incongruent locations on the other hand. Target locations had to be reported either anatomically (“palm” or “back” of the hand), or externally (“up” or “down” in space), under various hand posture (palms either both faced down, or one faced down and one up). Under anatomical instructions, performance for both groups was more accurate when the distractor and the target tactile inputs were presented at anatomically congruent locations, and conversely regarding spatial instructions (Schubert et al., 2017). ERP evidence for the use of external coding for tactile attention was also found in congenitally blind participants when performing a tactile detection task under external instructions (Eardley and van Velzen, 2011a).

Moreover, similar effects of the task demands on tactile localization capability were found in sighted participants. Unwalla and colleagues (2021) recently demonstrated that the size of the crossing effect observed for sighted individuals performing a tactile TOJ task was dependent over external (which side of space was touched first) or anatomical (which hand was touched first) instructions. Gallace and colleagues (2008) asked participants to perform an elevation judgement task with tactile target presented to either the top or bottom of one of two foam cubes that they held between the thumbs and index of both hands. Distractors were presented on the other foam cube at an elevation that was either congruent or incongruent with respect to the elevation of the target. Moreover, the posture of the hands was also modulated, as in they could be either palm up or palm down, independently of each other. Spatial judgements were made either in external (up vs. down) or anatomical (thumb vs. index) coordinates, with participants indicating them either verbally or with a foot pedal (pressing the toe or the heel). When responding with the foot pedal, a spatial congruency effect was found for external locations: participants responded faster when target and distractor were in externally congruent locations (e.g. thumb up and finger up), no matter if the answer was made in external or anatomical coordinates. However, when responding verbally, the congruency effect followed the frame of reference that was made relevant by the instructions. These results shows that both task instructions and response mode influence the weighting of anatomical and external reference frames (Gallace et al., 2008).

Movement

Movement is another example of contextual situations playing an important role in the use of external spatial coordinates during tactile integration. In the study of Heed and colleagues (2015), sighted and congenitally blind participants performed a tactile TOJ task under external instructions, while executing bimanual arm movements with uncrossed and crossed start and end postures. In the sighted, start posture and planned end posture of the arm movement modulated tactile localization for stimuli presented before and during movement. In the blind group, tactile performance was only

affected for stimuli presented before movement start. Additionally, only the movement's start posture, but not the planned end posture affected their performance. Thus the involvement of movement was shown to impact the use of spatial coordinates for both sighted and blind individuals, even if in a more restrictive way for the latter (Heed et al., 2015b).

Furthermore, Hermosillo and colleagues (2001) also demonstrated that the planning of movement can modulate tactile TOJ performance. Participants had to judge which of two successive vibrotactile stimuli delivered to each index finger arrived first as they were preparing to either cross or uncross their hands. Planning to change the posture from an uncrossed to a crossed arm posture impaired TOJ performance, while the reverse improved participants' performance. And in both cases, these changes occurred before the actual change in hand posture (Hermosillo et al., 2011).

Other contextual cues

Various other contextual factors have also been shown to influence tactile localization processing, such as head orientation (Ho and Spence, 2007) or eye position (Harrar and Harris, 2009). Manipulating participants' mental load during a tactile localization task can also affect their performance, as evidenced by Badde and colleagues (2014). Participants in their study performed a tactile TOJ task, where stimuli were applied to hands in either a crossed or uncrossed posture, while also performing a working memory (WM) task varying in difficulty. The crossing effect was observed to be consistently reduced under processing load as well as varied as a function of the difficulty of the WM task (Badde et al., 2014). Additionally, when asking blindfolded participants to visually imagine their crossed arms as uncrossed while performing a TOJ task, the crossed hand deficit was also shown to decrease (Hermosillo et al., 2011). These results further support the idea that integration of coordinates system is not just influenced by bottom-up process but is also subject to top-down control.

4. The neural correlates of tactile localization

4.1. Cortical network involved in the spatial mapping of touch

4.1.1. Evidence from patients' studies

Head & Holmes (1911) work on sensory disruptions exhibited by brain damaged patients has been amongst the first to highlight the role of the cortex in spatial somatosensory processing (Head and Holmes, 1911). The location of the lesion in patients suffering from spatio-tactile disorder can inform us about the cortical regions involved in tactile localization. For instance, Elithorn and colleagues

(1952) have tested the tactile localization performance of leucotomized patients before and after surgery. Such operation consisted of severing connections in the prefrontal cortex as a treatment for various psychiatric or neurological disorder. They found that errors when localizing tactile stimuli on the fingers increased after surgery, providing evidence that the prefrontal cortex plays a role in tactile localization (Elithorn et al., 1952). Patients in Aglioti and colleagues' study (1995) suffered from lesion of the right somatosensory cortex following a stroke. They were asked to point with their thumb to the position of tactile stimuli applied to the other fingers of the same hand. The task was performed eyes closed, with the right and left hand. When pointing with the right thumb on the right fingers, accuracy of all patients was perfect. However, when localizing stimuli on the contralesional (left) hand with the left thumb, none of them were able to localize the stimulation, and therefore just guessed where to point. In that case accuracy did not differ from chance. Interestingly, if pointing with the right thumb on the left fingers, this time accuracy was above 60% for all patients (Aglioti et al., 1996). Thus, these results shows that bilateral somatosensory cortices are needed to localize touch on the body.

We have previously introduced hemispatial neglect and tactile extinction in this thesis, as behavioral studies including these type of patients informed us on the mechanisms underlying tactile localization. These attentional spatial deficits generally appear after brain lesion, and neuroimaging techniques have helped identified the damaged structures involved. Neglect neural correlates typically include the posterior parietal and premotor cortices (Committeri et al., 2007; Kerkhoff, 2001; Vallar, 1993; Vallar and Perani, 1987). Tactile extinction shares similar neural correlates with neglect; it notably is associated with neural dysfunction in the inferior parietal lobule (de Haan et al., 2012; Hillis et al., 2006). However, contrary to neglect, subcortical lesions are often found in extinction (Vallar et al., 1994). Furthermore, Ben-Shabat and colleagues (2015) investigated brain activation specific to proprioception following stroke. Using fMRI, they found that the supramarginal gyrus (SMG) and the dorsal premotor cortex were activated in healthy participants perceiving their wrist position. Stroke-affected participants exhibited similar proprioception-related brain activation, with the only difference being some reduced laterality in the right SMG. Collectively, these patient studies points to a large cortical network made up of frontal, central, parietal and temporal regions involved in spatial processes such as tactile localization.

4.1.2. Evidence from neurotypical participants

Neural activity recorded from these various cortical areas in non-human primates have supported their role in encoding spatial information. The premotor and parietal cortices have notably been shown to play an important role in the integration of polymodal information into spatial coordinates that can be used for guiding and controlling action (Andersen et al., 1997). For instance, Pesaran and colleagues

(2006) recorded neuronal activity in the dorsal premotor area (PMd) and the medial intraparietal area (MIP) of monkeys during a delayed reach task. The position of the eye, hand, and target independently varied across a range of locations. They found that PMd neurons encoded the position of the target, hand, and eye in a relative position code, while MIP neurons encoded target location in eye-centered coordinates (Pesaran et al., 2006). This is in line with previous report showing that neurons of the premotor cortex code the space immediately surrounding the body using body-part-centered coordinates (Fogassi et al., 1992; for a review see Graziano and Gross, 1998). Furthermore, the intraparietal region has indeed been associated with the coding of supramodal spatial maps (Andersen et al., 1985; Bremmer et al., 2001; Duhamel et al., 1997; for a review, see Cohen and Andersen, 2002) and direct anatomical connections between the two regions have been also reported (Luppino et al., 1999).

Neuroimaging studies in neurotypical humans have drawn strong equivalencies for these regions between humans and monkeys (for a review, see Filimon, 2010). Using functional magnetic resonance imaging (fMRI), Bremmer and colleagues (2001) investigated the neural correlates of polymodal motion processing. Participants were presented with moving stimuli that were either visual, tactile or auditory. Motion information of each modality showed increased neural activity in their respective sensory cortices (relative to their respective control) as well as increased activity in posterior parietal cortex and premotor cortex. In particular, tactile motion information (relative to the tactile control condition) showed increased neural activity in the primary and secondary somatosensory cortex bilaterally, posterior parietal cortex bilaterally, and right lateral premotor cortex (Bremmer et al., 2001). Interestingly, these results add evidence for an early interhemispheric integration of tactile information between the two sides of the body (for a review, see Tamè et al., 2019). In another fMRI study, Tamè and colleagues (2012) observed the somatosensory cortex activity of participants receiving pairs of vibrotactile stimuli to the fingertips of the index and middle fingers. While the overall BOLD (blood-oxygen-level dependent) signal evoked by the stimulation was primarily contralateral in SI and was more bilateral in SII, both cortices were sensitive to ipsilateral as well as to contralateral inputs. Moreover, differential activity was observed following stimulation of homologous (same hand) or nonhomologous (different hand) fingers. These results show that the role of SI and SII in the spatial coding of touch isn't restricted to discriminating between body parts but also to integrating the somatosensory input from the two sides of the body (Tamè et al., 2012).

Considering its significance in understanding how tactile events are processed, investigators have looked at the neural correlates of the crossing effect. Crossing the hands while performing tactile TOJ tasks has thus been related to increased brain activity in a large cortical network, including premotor and posterior parietal areas (Crollen et al., 2017; Takahashi et al., 2013; Wada et al., 2012).

Lloyd and colleagues (2003) have indeed found that the representation of tactile stimuli presented to the right hand positioned across the body midline (i.e. in the left hemispace) recruited both the left parietal and left premotor cortex. In their fMRI study, participants passively received vibrotactile stimulation to the right hand, which was positioned either on the right side of the body or across the body midline on the left side of the body (Lloyd et al., 2003). Their results suggest the involvement of premotor and parietal areas into the encoding of limb position. Wada and colleagues (2012) found similar results when asking participants to perform a TOJ task in the fMRI. When adopting a crossed hand posture, activation in the left posterior parietal cortex (PPC) increased. Furthermore, activity in this area was positively linked with the degree of reversal of TOJ judgements (Wada et al., 2012).

As a matter of fact, Pellijeff and colleagues (2006) found an association between maintaining and updating postural (i.e., non-visual) representations of the upper limb and activity of the superior parietal cortex. They investigated reaching movements executed without vision: when comparing BOLD activity associated with reaches involving a novel postural configuration of the limb, against reaches involving the repetition of a recently used limb configuration, they observed an increased activation of the superior parietal cortex bilaterally.

Besides fMRI, premotor and posterior parietal areas in human have also been repeatedly associated with the external coding of touch by means of transcranial magnetic stimulation (TMS), which is a technique allowing to artificially and transitory disrupt cortical activity at a targeted location (Azañón et al., 2010b; Bolognini and Maravita, 2007a; Ruzzoli and Soto-Faraco, 2014). Ruzzoli and Soto-Faraco (2014) applied rhythmic TMS (rTMS) at a frequency of 10 Hz over the intraparietal sulcus (IPS) of participants performing a tactile detection task with tactile stimuli presented unpredictably to the left or right index finger. They found that, as compared to stimulation over SI as a control condition, 10-Hz rTMS over the IPS had a negative impact on tactile detection on the contralateral hand but resulted in enhanced performance on the hand ipsilateral in external space, independent of whether hands were held in an uncrossed or crossed posture. This indicates that the effect produced by the modulation of IPS on the detection of tactile stimuli were dependent of the position of the stimulated hand in external space, but not of the anatomical position of the stimulus (Ruzzoli and Soto-Faraco, 2014). Similar results were found when participants judged the elevation of touches on their (unseen) forearm relative to touches on their face (Azañón et al., 2010b). Single-pulsed TMS over the PPC impaired their localization performance compared to a control site (vertex), whereas proprioceptive judgments of arm elevation or tactile localization on the skin remained unaffected. These findings have highlighted the causal role of human PPC in encoding touch into external space.

4.2. Electrophysiological evidences of reference frames

4.2.1. *Evoked potentials*

By using techniques such as magnetoencephalography (MEG) and electroencephalography (EEG), researchers have been able to investigate the neural processes behind tactile localization. As previously mentioned, evoked potentials, or ERPs, reflect the brain response to a specific sensory, cognitive, or motor event. A tactile stimulus will elicit a series of somatosensory evoked potentials (SEPs) detectable at the scalp level (Allison et al., 1992a; Eisen and Elleker, 1980a). The repetition of the exact same stimulus will reduce the amplitude of the SEPs. As such if a variation in the stimulus parameters is introduced after a series of repetition, the amplitude of SEP resulting from the treatment of that particular parameter will have increased. Extra components can also appear as a results of change, a phenomenon referred to as the somatosensory mismatch negativity, which has been observed in other sensory modalities as well (Näätänen, 1995; Näätänen et al., 2007; Tales et al., 1999). This principle can therefore be used to study the ERP correlates of tactile localization by changing the position of tactile stimuli. For instance, Kekoni and colleagues (1997) had participants receive repetitive tactile stimuli on their hands by the means of vibrators. Stimuli were of the same frequency and amplitude in vibrations. Deviant stimuli only differed by their position on the skin and were presented randomly during the sequence of standard stimuli. Participants ignored all stimulations, as they were reading during the EEG recording. Results showed an increase of amplitude of the P50 and P100 over centro-parietal electrodes in response to deviants, corresponding to SEPs happening 50 and 100 ms after stimulus onset respectively. Moreover, an extra negative component between 100-200 ms latency was observed over fronto-central electrodes (Kekoni et al., 1997). Using a similar paradigm, Shinozaki and colleagues (1998) also observed a frontal negativity ranging from 70 to 140 ms elicited by a change of position of the tactile stimulation (Shinozaki et al., 1998). The latency of these various SEPs informs us on the timing of the spatial processing of touch. Moreover, their localization over the scalp correspond to the brain regions found in fMRI studies. Interestingly, Cardini and colleagues (2011) showed that visual feedback of the stimulated hand during a tactile discrimination task modulated SEPs, notably the P50 and N140. This is in line with the founding that visual information influence tactile localization (Cadieux and Shore, 2013; Röder et al., 2004).

When using paradigm involving posture change, such as crossing the limbs, these electrophysiological studies have offered compelling evidence about the use and integration of reference frames for tactile localization (Ley et al., 2015; Soto-Faraco and Azañón, 2013). Soto-Faraco & Azañón (2013) investigated the neural signature of the initial steps of tactile remapping by comparing SEPs following contact on one finger while the participant had either their hands uncrossed

or crossed. They found initial signs of tactile remapping at around 70 ms latency, consisting of a negative deflection for the crossed-hand posture. This effect, which overlaps in time with the somatosensory component N80, was clearly lateralized to the left scalp. It was localized over fronto-temporal electrodes at early stages and extended to left temporo-parietal electrodes at about 170 ms. Moreover, this lateralized pattern of brain activity was independent of the hand being stimulated, and it is therefore suggestive of a hemispheric functional asymmetry. When looking at later latencies (200 to 350ms), posture effects in SEPs were also stronger over the left hemisphere but extended toward central and right locations at longer latencies. Finally, the authors were able to correlate these electrophysiological differences with their behavioral index of remapping, i.e. the crossing effect on TOJ performance. In particular, the magnitude of the N80 negative shift at left temporo-parietal electrodes and, to some extent, at later stage windows, was correlated with the magnitude of the crossed-hands effect in precision. This suggests that the electrophysiological difference observed reflects neural correlates underlying tactile remapping, and more precisely the conflict between reference frames (Soto-Faraco and Azañón, 2013a).

Numerous ERP studies on tactile localization involving the crossed posture have actually focused on tactile attention (i.e. the spatial orienting process happening BEFORE touch). Nevertheless, these studies still proved invaluable to our understanding of tactile spatial codes. For instance, Eimer and colleagues (2003) measured lateralized ERPs sensitive to the direction of attentional shifts following visual precues directing attention to the relevant location of tactile events. In their task, participants had to detect infrequent tactile targets delivered to the hand located on the cued side, while the hand were either crossed over the body midline or uncrossed. One ERP component measured over fronto-central electrodes (the anterior directing attention negativity, or ADAN) was delayed and reversed polarity when the hands were crossed compared to when they were uncrossed. In contrast, another elicited component measured over occipito-parietal electrodes (late directing attention positivity, or LDAP) remained unaffected by hand posture. These results suggest that different spatial coordinate systems may be used by separable attentional control processes: an anterior one that rely on anatomical coordinates and a posterior one that rely on external coordinates (Eimer et al., 2003). Using a similar procedure, Röder and colleagues (2008) also found an effect of hand posture on the amplitude of ERPs measured in sighted participants, but not in blind participants (Röder et al., 2008a). It is important to note that participants in both studies performed the task under anatomical instructions, i.e. focusing on the (right or left) hand, no matter its position in space. Contrastingly, Eardley & van Velzen (2011) employed the same task but with external instructions, i.e. focusing on the (right or left) side of space (relative to body midline), independently of the hand posture. They found that the polarity of the ADAN was reversed in the cue-touch interval, as well as a significant delay when hands were crossed, not only for sighted but also for early blind participants (Eardley and

van Velzen, 2011a). These results illustrate the mismatch of reference frames when crossing the hands, and also add evidence to the role contextual factors, here developmental vision but also task instruction (in comparison to the Röder et al. study) can play in how spatial coordinates systems are used.

4.2.2. *Oscillatory brain activity*

Oscillatory brain activity is observed when groups of neurons synchronize their firing repetitively, possibly, because they are transiently involved in the same computation. It has been associated with a number of cognitive functions, including somatosensory processing (Cheyne et al., 2003; Feurra et al., 2011; Neuper et al., 2006). Neural oscillations have been categorized based on their frequency range: for instance, the alpha rhythm varies in its peak frequency between individuals in the range of 7–14 Hz (Saskia Haegens et al., 2014) whereas the beta rhythm typically encompass frequency between 14 to 35 Hz. Both of these rhythms have been involved in the encoding of tactile spatial information. Buchholz and colleagues (2011 & 2013) investigated anatomical and external spatial reference frames in the context of planning a movement to a remembered tactile targets. In their MEG studies, participants had to fix their gaze on the ring finger of one of their hand while receiving a tactile target stimulus at the same hand's index or little finger. After a delay, they were asked to execute either an eye (V. N. Buchholz et al., 2011a) or a hand movement (Buchholz et al., 2013) to the remembered target location. Time-frequency analysis within the delay period revealed of significant modulation of posterior-parietal alpha power in the in the contralateral compared to the ipsilateral hemisphere relative to the tactile stimulus location in an eye-centered reference frame, that is, left versus right visual hemifields. In contrast, central alpha-, and central and posterior beta power were modulated in the contralateral compared to the ipsilateral hemisphere relative to the anatomical stimulus location, that is, left versus right hand, and unaffected by the external spatial location of the target (V. N. Buchholz et al., 2011a; Buchholz et al., 2013). Thus, posterior-parietal oscillatory alpha-band activity appeared to be involved in the encoding of an eye-centered external reference frame for vision and touch. Somatosensory processing, on the other hand, seemed to be reflected by beta-band rhythm in central regions. Corroborating this finding, Blohm and colleagues (2018) linked alpha and beta oscillations to the transformation of spatial code for reaching through the entire occipital-parietal-frontal reach network (Blohm et al., 2018).

Furthermore, Schubert and colleagues (2019) probed the reference frames encoded by oscillatory activity during tactile processing by asking sighted and blind participants to perform a tactile detection task while adopting either an uncrossed or crossed hand posture. An auditory cue indicated them which hand to attend prior to stimulation. They then had to detect rare tactile deviant stimuli at

the cued hand while ignoring tactile deviants at the other hand, and tactile standard stimuli at both hands. In sighted participants, an attentional effect was observed on the alpha-band over ipsilateral centroparietal and occipital cortex. Hand crossing attenuated this attentional modulation predominantly over ipsilateral posterior-parietal cortex (Schubert et al., 2019). However, no crossing effect was found in the oscillatory activity of blind participants, which we now know could be explained by the employment of anatomical instructions in Schubert's task, since crossing effects have been observed in blind participants when external instructions were used (Eardley and van Velzen, 2011a). Still, these results are in line with those of Ruzzoli & Soto-Faraco (2014) who found that frequency-specific (10 Hz) tuning of the PPC induced spatially specific enhancement of tactile detection that was expressed in an external reference frame, supporting the idea that oscillatory alpha-band activity plays a pivotal role in the neural coding of external spatial information for touch (Ruzzoli and Soto-Faraco, 2014).

5. How do we localize touch on a hand-held tool ?

5.1. A barely explored phenomenon

As previously stated, tactile perception is not restricted to the boundary of the skin but can be extended through hand-held tools (Vaught et al., 1968). For instance, in Yoshioka and colleagues' study (2007), participants touched familiar textured surfaces (familiar as in, encountered in daily life, e.g., corduroy, paper, wood...) with their bare finger as well as with a hand-held tool. They had to then rate dissimilarity between two different surface in both conditions. Results showed that the texture percept is similar though not identical in the two condition (bare finger and through tool). Furthermore, roughness of surface was rated similarly in both conditions (Yoshioka et al., 2007). This suggests that tactile information extracted from the tool can be processed similarly as when directly received on the skin. Nonetheless, tool-mediated sensing is still a poorly understood aspect of the daily human experience.

Yamamoto et al. (2001b) adapted the TOJ paradigm with tactile stimuli applied on tools. Participants had to judge the order of two successive stimulation delivered to the tip of sticks held in each hand. The task was performed in four different postures: arms uncrossed & sticks uncrossed (Figure 6.a.), arms uncrossed & sticks crossed (Figure 6.c.), arms crossed & sticks uncrossed (Figure 6.d.) and arms crossed & sticks crossed (Figure 6.b). When arms and sticks were uncrossed, performance was excellent, even at very short SOA (<100 ms). When the arms were crossed without crossing the sticks, errors increased, especially for short SOA (between 100 and 400 ms). This is similar to the performance obtained when tactile stimuli are applied directly on the hands (Shore et al., 2002;

Shinya Yamamoto and Kitazawa, 2001a). When crossing the sticks without crossing the arms, similar results were obtained. However, when crossing both, errors dropped and performance improved. These results show that the judgment of temporal order depended critically on which hemisphere the tip of each stick occupied in reference to the anatomical laterality of the hand holding the stick. (Shinya Yamamoto and Kitazawa, 2001b). The same experiment was reproduced using L-shaped sticks instead of straight ones, with similar results obtained (Yamamoto et al., 2005). Participants reported the order of stimuli correctly in most trials when the tip of each L-shaped stick occupied the hemisphere ipsilateral to the anatomical laterality of the hand holding the L-shaped stick (Figure 6. e-g). However, they misreported the order of stimuli presented at moderately short SOA (<300 ms) when the tip of the stick occupied the hemisphere contralateral to the anatomical laterality of the hand holding it (Figure 6. h-i). These results support the idea that tactile stimuli delivered to the tip of the sticks are processed by the brain in the same way as tactile stimuli applied on the hands (Yamamoto et al., 2005; Shinya Yamamoto and Kitazawa, 2001b).

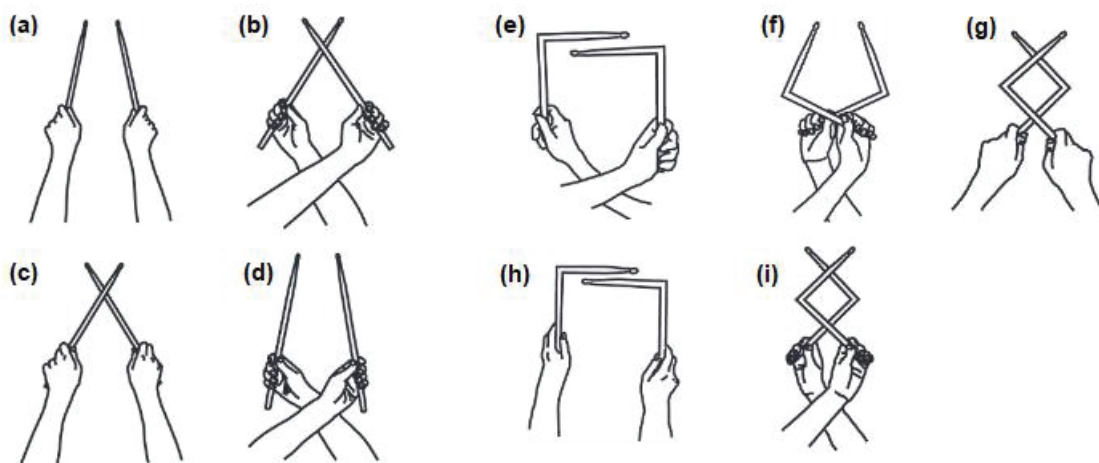


Figure 6. Posture used in TOJ paradigm with tools.

On the right, (a-d) postures used with straight sticks held in each hand. On the left, (e-i) postures used with L-shaped sticks. On the top row, (a,b,e,f,g) postures where the tip of each stick occupied the hemisphere ipsilateral to the anatomical laterality of the hand holding it. On the bottom row, (c,d,h,i) postures where the tip of each stick occupied the hemisphere contralateral to the anatomical laterality of the hand holding it. Adapted from Yamamoto & Kitazawa (2001b) and Yamamoto and al. (2005).

As a matter of fact, we can feel touch through the entire surface of a tool such as the cane, not just through the tip. For example, a surgeon is able to precisely manipulate a scalpel, getting sensory feedback through the whole length of the blade, just as we can when cutting food with a knife (Nou et al., 2020). More importantly, we can accurately sense where an object contacts the surface of a hand-held tool, just as is possible on our own skin, as demonstrated by Miller and colleagues (2018). In their

study, participants used a wooden rod to contact an object in one of seven different locations along the tool shaft (Figure 7. a.): after each hit, participants had to indicate the point of contact on a graphical representation of the rod. Localization occurred after contact with an object through either self-generated action (active sensing) or passive reception of impact (passive sensing). Given that participants could not see their hand or the rod, the localization task could rely only on their somatosensory perception. Participants were able to detect where an object contacted the surface of the rod with great accuracy when actively hitting the object, as well as when passively receiving contact (Luke E. Miller et al., 2018a). In another study, Frissen and colleagues (2022) even found that participants can accurately localize an object rolling inside a hand-held container (Frissen et al., 2022). Although, in that case, auditory cues were shown to be of great importance to estimate the rolled distance, no auditory feedback was given to participants in Miller's study.

To understand how the tool communicates impact location to the hand, Miller and colleagues (2018) then recorded vibrations on the handle of the rod and on the index finger of three participants while they performed the localization task. It revealed that the rod mechanically transduces impact location into vibratory motifs, each contact point giving rise to a different pattern of vibrations highly consistent across trials (Figure 7. b.). The use of a classifier on this dataset showed that the location-specific pattern of each motif emerged extremely rapidly, with classification accuracy reaching 90% within approximately 8 ms after impact. Since mechanoreceptors in the hand, mostly the Pacinian corpuscles, have been proposed to have an important role in encoding vibrations transmitted through hand-held objects (Brisben et al., 1999), Miller and colleagues hypothesized that Pacinian corpuscles transduce the vibratory motifs from the tool into neural response patterns that retain the location-specifying information. To test that hypothesis, they simulated the spiking responses of a population of 42 Pacinian mechanoreceptors (Figure 7. c.) to the mechanical vibrations of the tool. Simulated spikes were phase-locked with the vibratory motifs (Figure 7. d.). Additionally, impact location from the population spike-timing could also be accurately decoded with a classifier, with classification accuracy reaching 90% within approximately 25 ms after impact. All of these evidence suggest the nervous system contains mechanisms to extract and process location information from the tool (Luke E. Miller et al., 2018a).

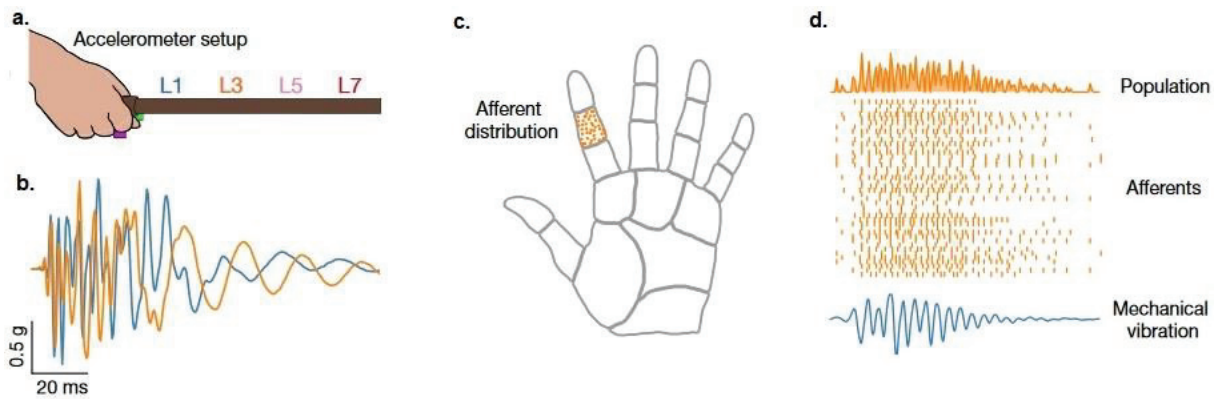


Figure 7. Impact location on a hand-held tool is encoded in vibratory motifs that are transduced by mechanoreceptors of the hand.

(a). Contact on the tool happened at seven different locations. Accelerometers were used to record vibrations from the tool and index finger of participants. (b) Vibratory motifs emerging from contact location at two different positions. (c) The distribution of 42 simulated Pacinian mechanoreceptors in the middle phalanx of the index finger. (d) Mechanical vibration (first 150 ms after impact) on a randomly chosen trial from the dataset of one participant. Vibrations led to temporally precise response patterns across the individual afferents (orange raster plot) and the population response (top). Adapted from Miller et al. (2018).

5.2. Aims and hypotheses

Since tools have such a prominent role in our daily life, tactile information received through hand-held tools are as important as the ones received directly on our body. Information about the nature of the tactile source even seems to be preserved in that case, as we can perceive touch location on a hand-held tool as accurately as on our own skin. As we have seen in previous section of this dissertation, somatosensory stimuli happening on the body are mapped in reference frames, which are reflected in the brain oscillatory activity. However, it is yet unknown if similar spatial codes are used to localize touch on hand-held tools.

Decades of studies on tool use have shown that tools extend our sensorimotor abilities, therefore suggesting that the brain re-uses body-related mechanisms when performing an action with a tool. Recent investigation about tactile localization on tools further support this idea (Luke E. Miller et al., 2018a; Yamamoto et al., 2005; Shinya Yamamoto and Kitazawa, 2001b). Nonetheless, the neural mechanisms underlying the spatial perception of tactile stimuli on external objects have received little attention so far. Hence the purpose of this work was to investigate which neural processes are involved when localizing touch on a hand-held tool, and if those are shared with similar body-related action.

To this aim, we focused our research on the electrophysiological correlates of tool-extended tactile localization. Localization tasks were designed to isolate the tactile modality while EEG was used

to record participants' neural activity. In **study 1**, we assessed the cortical dynamics of participants performing a tactile localization task in which tactile stimuli were applied to a tool held in their dominant hand. In a second experiment, tactile stimuli were applied on their forearm, which allowed us to compare body-related and tool-related dynamics. We hypothesized that the brain uses the tool as a sensory extension of the body, and as such, re-uses neural mechanisms devoted to the body.

In **study 2**, we investigated the oscillatory correlates of tactile localization on the tools. We performed time-frequency decomposition on the dataset of study 1. Since alpha and beta-band activity have been implicated in the spatial encoding of touch on the body, we hypothesized that both oscillations band would be involved when localizing tactile inputs on a hand-held rod.

In **study 3**, we aimed at pinpointing the role of these oscillations during tool-extended sensing. We designed a cued tactile localization task where tactile stimuli were applied to either hands or the tips of hand-held rods. The posture of the hands/tool-tips was uncrossed or crossed at participants' body midline in order for us to disentangle brain responses related to different coordinate systems. We hypothesized that oscillatory activity would similarly reflect the use of spatial codes for encoding touch on the body and on the tools.

Experimental studies

Study 1:

Somatosensory Cortex Efficiently Processes Touch Located Beyond the Body

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Keywords: touch, sensorimotor, efficient coding, somatosensory cortex, tool use, sensory embodiment, extended sensing

Summary

Tool use is a universal feature of humankind. Tools allow us to explore our environment and expand our sensorimotor abilities. However, despite two decades of research, it remains unknown how this could be instantiated at the neural level. To this aim, the present study combined behaviour, electrophysiology and neuronal modelling to characterize how the human brain could treat a tool like a sensory extension of the body. We designed a tactile localization task where two tactile stimuli were successively applied in the same or in different locations on a hand-held tool (either near the tip, or near the hand of the user). A second, similar task was performed, this time with tactile stimuli applied on the forearm of participants. In addition to being able to directly compare body and tool-related dynamics, this experimental design allowed us to exploit repetition effect of the contact location. As with the body, participants localise touches on a hand-held tool with near-perfect accuracy, replicating Miller et al. (2018) results. This behaviour is owed to the ability of the somatosensory system to rapidly and efficiently use the tool as a tactile extension of the body. Using electroencephalography (EEG), we found that where a hand-held tool was touched was immediately coded in the neural dynamics of primary somatosensory and posterior parietal cortices of healthy participants. Moreover, we found similar neural responses in a proprioceptively deafferented patient with spared touch perception, supporting the idea that location-information is extracted from the rod's vibrational patterns, as evidenced by Miller et al. (2019) study. The second EEG experiment showed that touches on the tool and arm surfaces were localized by similar stages of cortical processing. Multivariate decoding algorithms and cortical source reconstruction provided further evidence that early limb-based processes were repurposed to map touch on a tool, as we notably found similar regions involved for localizing on each surface. Based on these results, we propose that an elementary strategy the human brain uses to sense with tools is to recruit primary somatosensory dynamics otherwise devoted to the body.

Abstract

The extent to which a tool is an extension of its user is a question that has fascinated writers and philosophers for centuries (Clark, 2008). Despite two decades of research (Cardinali et al., 2009b; Atsushi Iriki et al., 1996; Martel et al., 2016b; Miller et al., 2017a; Luke E Miller et al., 2018; Umiltà et al., 2008), it remains unknown how this could be instantiated at the neural level. To this aim, the present study combined behaviour, electrophysiology and neuronal modelling to characterize how the human brain could treat a tool like an extended sensory ‘organ’. As with the body, participants localise touches on a hand-held tool with near-perfect accuracy (Luke E Miller et al., 2018). This behaviour is owed to the ability of the somatosensory system to rapidly and efficiently use the tool as a tactile extension of the body. Using electroencephalography (EEG), we found that where a hand-held tool was touched was immediately coded in the neural dynamics of primary somatosensory and posterior parietal cortices of healthy participants. We found similar neural responses in a proprioceptively deafferented patient with spared touch perception, suggesting that location-information is extracted from the rod’s vibrational patterns. Simulations of mechanoreceptor responses (Saal et al., 2017) suggested that the speed at which these patterns are processed is highly efficient. A second EEG experiment showed that touches on the tool and arm surfaces were localized by similar stages of cortical processing. Multivariate decoding algorithms and cortical source reconstruction provided further evidence that early limb-based processes were repurposed to map touch on a tool. We propose that an elementary strategy the human brain uses to sense with tools is to recruit primary somatosensory dynamics otherwise devoted to the body.

Results and Discussion

In somatosensory perception, there is evidence in many species that intermediaries are treated like non-neural sensory extensions of the body (Burton, 1993). For example, some spiders actively use their web as an extended sensory ‘organ’ to locate prey (Japyassú and Laland, 2017). Analogously, humans can use tools to sense the properties of objects from a distance (Kilteni and Ehrsson, 2017; Saig et al., 2012; S Yamamoto and Kitazawa, 2001), such as when a blind person uses a cane to probe the surrounding terrain. This sensorimotor ability is so advanced that humans can almost perfectly localize touch on the surface of a tool (Luke E Miller et al., 2018), suggesting a strong parallel with tactile localisation on the body. Characterizing the neural dynamics of tool-extended touch localization provides us with a compelling opportunity to investigate the boundaries of somatosensory processing and hence the question of *sensory embodiment*: To what extent does the human brain treat a tool like an extended sensory ‘organ’?

From a theoretical perspective (Luke E Miller et al., 2018), the sensory embodiment of a tool predicts that—as is the case with biological sense organs—the cerebral cortex (i) rapidly extracts location-based information from changes in a tool’s sensory-relevant mechanical state (e.g., vibrations) and (ii) makes this information available to the somatosensory system in an efficient manner. The peripheral code for touch location is likely different for skin (e.g., a place code) and tools (e.g. a temporal code; ref. 7). Transforming a temporal to a spatial code—a necessary step for tool-extended localization—is a non-trivial task for the brain. We predict that, to do so efficiently, (iii) the brain repurposes low-level processing stages dedicated to localizing touch on the body to localize touch on a tool. Direct evidence for sensory embodiment requires understanding how the structural dynamics of tools couple to the neural dynamics of the cortex. Such evidence can be obtained using neuroimaging methods with high temporal resolution. To this aim, we combined EEG and computational modelling to test the aforementioned predictions.

The cerebral cortex rapidly processes where a tool was touched

In an initial experiment ($n=16$), participants localized touches applied on the surface of a one-meter wooden rod (Figure 1A) while we recorded their cortical dynamics using EEG. We designed a delayed match-to-sample task that forced participants to compare the location of two touches (delivered via solenoids; Supplementary Figure 1A) separated in time (Figure 1B). If the two touches were felt to be in different locations, participants made no overt response. If they were felt to be in the same location, participants used a pedal with their ipsilateral left foot to report whether the touches were close or far from their hand. Participants never used the rod before the experiment and never received performance feedback. As a result, participants had to rely on pre-existing internal models of tool dynamics (Imamizu et al., 2000). Regardless, accuracy was near ceiling for all participants (mean: $96.4 \pm 0.71\%$; range: 89.7–99.5%), consistent with our prior finding (Luke E Miller et al., 2018).

When a stimulus feature is repeatedly presented to a sensory system, the responses of neural populations representing that feature are suppressed (Grill-Spector et al., 2006). Effects of repetition are a well-accepted method for timestamping when specific features in a complex input are extracted (Schendan and Kutas, 2003). Repetition paradigms have previously been used to characterize how sensory signals are mapped by sensorimotor cortices (Shen et al., 2018; Strömmer et al., 2014; Tamè et al., 2015; Van Pelt et al., 2010). Our experimental paradigm allowed us to leverage these repetition suppression effects to characterize when the brain extracted where a rod has been touched. Specifically, the amplitude of evoked brain responses reflecting the processing of impact location will be reduced if the rod is hit at the same location twice in a row compared to two distinct locations (Figure 1C).

We first characterized the cortical dynamics of tool-extended touch localization. Touching the surface of the rod led to widespread evoked responses over contralateral regions (Supplementary Figures 1, 3), starting ~24 milliseconds after contact (Supplementary Figure 1B); this time-course is consistent with the known conduction delays between upper limb nerves and primary somatosensory cortex (Eisen and Elleker, 1980b). A nonparametric cluster-based permutation analysis identified significant location-based repetition suppression in a cluster of sensorimotor electrodes between 48–108 milliseconds after contact ($P=.003$; Figure 1D-I; Supplementary Table 1; Supplementary Figures 1C-D, 3). This cluster spanned two well-characterized processing stages previously identified for touch on the body: (a) recurrent sensory processing within primary somatosensory (SI) and motor (MI) cortices between 40–60 milliseconds after stimulation (Allison et al., 1992b), which has been implicated in spatial processing (Akatsuka et al., 2007a; Cardini et al., 2011a); and (b) feedforward and feedback processing between SI, MI, and posterior parietal regions between 60–100 milliseconds after stimulation (Cauler and Kulics, 1991; Jones et al., 2007a), proposed to contribute to transforming a sensory map into a higher-level spatial representation (Shen et al., 2018; Soto-Faraco and Azañón, 2013b). This suppression was too quick to reflect signals related to motor preparation/inhibition, which generally occur ~140 milliseconds after touch (Nakata et al., 2004).

Location-based repetition suppression is driven by vibratory signals

We previously suggested that, during tool-extended sensing, where a rod is touched is encoded pre-neuronally by patterns of vibration (i.e., vibratory motifs; Supplementary Figure 1E-F). When transiently contacting an object, specific resonant modes (100–1000 Hz for long wooden rods) are selectively excited, giving rise to vibratory motifs that unequivocally encode touch location [7, Supplementary Information]. These rapid oscillations are superimposed onto a slowly-evolving rigid motion that places a load on the participant's fingers and wrist. Given that the somatosensory system is sensitive to both slow-varying loads (via proprioception) and rapid vibrations imposed to the hand (via touch), these two signals are difficult to disentangle experimentally.

To adjudicate between the contribution of each aspect of the mechanical signal, we repeated Experiment 1 with a deafferented participant (DC) who lost proprioception in her right upper limb (33% accuracy in clinical testing) following the resection of a tumour near the right medulla oblongata (Lucilla Cardinali et al., 2016). Importantly, light touch was largely spared in her right limb (100% accuracy). DC completed the EEG experiment while holding a rod in her deafferented hand and intact left hand (separate blocks). Her behavioural performance was good for both the intact (72%) and deafferented (77%) limbs. Crucially, her neural dynamics exhibited the observed repetition suppression for both limbs, with a magnitude comparable to that of the healthy participants

(Figure 1F, I; Supplementary Figure 2). Though not excluding possible contributions from slow varying rigid motion (when available), this result strongly suggests that the observed suppression was largely driven by information encoded by vibrations.

Processing of vibratory motifs is temporally efficient

We used a biologically plausible skin-neuron model (Saal et al., 2017) to quantify how efficiently the brain extracts touch location on a tool. According to principles of efficient coding, sensory cortices attempt to rapidly and sparsely represent the spatiotemporal statistics of the natural environment with minimal information loss (Simoncelli and Olshausen, 2001). DC's results suggest that the brain uses vibratory motifs to extract contact location on a rod. It has been hypothesized that the spiking patterns of Pacinian afferents encode object-to-object contact during tool use (Roland S Johansson and Flanagan, 2009), a claim that we found model-based evidence for [7]. This temporal code must be decoded in somatosensory processing regions, perhaps as early as the cuneate nucleus (Jörntell et al., 2014b).

We derived an estimate of 'maximal efficiency' by quantifying the time course of location-encoding in a simulated population of Pacinian afferents in the hand (Figure 2A-B). Support-vector machine (SVM) classification revealed a temporal code that was unambiguous about contact location within 20 milliseconds (Figure 2C). This code was efficient, corresponding to 4.6 ± 1.7 spikes per afferent. Taking into account the known conduction delays between first-order afferents and SI (Eisen and Elleker, 1980b), this finding—along with our prior study [7]—suggests that location-encoding within 35–40 milliseconds would reflect an efficient representational scheme. The early suppression observed in Experiment 1 (Figure 1D-I) is consistent with this estimate. This suggests that somatosensory cortex views these temporal spike patterns as meaningful tactile features, allowing humans to efficiently use a rod as an extended sensor.

Rapid processing of contact location on the arm

To identify when touch location on the body is processed, we conducted a second EEG experiment with ten participants from Experiment 1. In this experiment, touch was applied at two locations on the ventral surface of the forearm (Figure 3A). We found significant repetition suppression effects corresponding to a cluster extending 44–144 milliseconds after contact ($P=.005$; Figure 3B-C; Supplementary Table 2). Suppression within this time window was found in almost all ten participants (Figure 3D) and spanned the two processing stages observed in Experiment 1. This timing is in line with previous studies that have identified location-based suppression following touch on the body, including the arm (Shen et al., 2018).

Despite differences in the structure of the earliest SEPs following touch on the rod and tool (Supplementary Figure 3), the suppression observed across experiments was not significantly different ($P > .2$). The similarity between surfaces was also evident when inspecting the scalp topographies for both surfaces (Figure 3E), suggestive of similar neural dynamics. When interpreting these results, it is crucial to recall that the peripheral neural codes carrying information about where a rod or arm is touched are likely different: Our modelling results suggest that where a rod is touched is represented by a spike-timing code [Figure 2; ref. 7], whereas where the arm is touched is assumed to be represented by a place code (Maria et al., 2016). Therefore, though not all early cortical responses are identical between touch on the arm and tool, the observed temporal overlap of suppression between surfaces suggests that the somatosensory cortex resolves these basic coding differences relatively early.

Similar neural dynamics reflect the processing of touch location on a tool and arm

We used multivariate analyses to better test the hypothesis that the brain uses similar processing stages for localizing touch on the arm and tool. First, using a representational decoding approach (van Ede et al., 2019), we investigated whether the suppression observed in the arm dataset could predict the suppression observed in the tool dataset. We found statistically significant cross-surface decoding from cortical activity over sensorimotor channels starting within 52 milliseconds of touch on either surface ($P < .001$; Figure 3F); decoding was not possible from channels over temporal cortex. Furthermore, hierarchical clustering grouped neural responses by trial condition (i.e., same, different location) and not touched surface (Figure 3G).

We trained an SVM to distinguish between all four trial types, grouped by both surface and trial condition. Significant classification accuracy ($>25\%$) was found for both early (52 ms; Accuracy: $44.8 \pm 2.1\%$; one-sample t -test: $P < .001$) and late (80 ms; Accuracy: $49.5 \pm 2.1\%$; one-sample t -test: $P < .001$) neural responses (Figure 3H). We then characterized the types of misclassifications in the confusion matrix at both time points (Figure 3I; Supplementary Figure 4A-C). The SVM was more likely to identify the correct trial condition than the correct surface (Figure 3J; both $P_s < .05$). In sum, these results reveal the rapid emergence of statistically similar repetition suppression in the somatosensory system following touch on the arm and tool.

Similar cortical sources localize touch on a tool and arm

Finally, we compared the cortical sources for localizing touch on each surface. For the tool (Figure 4A) and the arm alike (Figure 4B), the earliest stages of shared suppression (52 ms) were localized in the hand and arm regions of SI and MI ($P < .05$, FDR-corrected), respectively. The suppression in SI during

tool-sensing may reflect the efficient detection of a location-specific tactile feature (i.e., vibratory motifs). Alternatively, given the results of our multivariate analyses, the observed suppression may reflect a point in time when SI has already extracted touch location from motifs. This would suggest that SI can resolve differences in peripheral neural codes and represent touch location on both the body and tool using a common format.

After primary sensorimotor regions, the processing of touch location for the tool (Figure 4C) and arm (Figure 4D) spread throughout the posterior parietal cortex (PPC). These regions construct higher-level spatial representations (Bolognini and Maravita, 2007b; Verena N Buchholz et al., 2011) and even represent hands and tools within a shared coordinate system (Naito et al., 2008a; Naito and Ehrsson, 2006). They thus play an important role in tool use (Atsushi Iriki et al., 1996; Johnson-Frey, 2004). The current results suggest that the PPC is involved in deriving a spatial code for where a tool was touched. A direct comparison of both surfaces at this processing stage found several shared sources in SI, MI, and PPC (Supplementary Figure 4D), consistent with our scalp-level multivariate analyses (Figure 3; Supplementary Figure 4A-C).

General discussion and implications

Identifying the spatial boundaries of a cognitive system requires characterizing how neural activity couples the body with external objects during thinking, acting, and perceiving (Chiel and Beer, 1997). For humans, tool use is a textbook example of an extended body (Cardinali et al., 2009b; Atsushi Iriki et al., 1996; Martel et al., 2016b; Miller et al., 2017a; Luke E Miller et al., 2018; Umiltà et al., 2008) since it marks a step in human evolution when our ancestors could act on their environments in ways otherwise impossible. We show that tools are fundamental to human behaviour in a previously underappreciated way: they expand the *somatosensory boundaries* of our body at the neural level. Hence, rather than stopping at the skin, our results suggest that somatosensory processing extends beyond the nervous system to include the tools we use.

We propose that an elementary strategy the human brain uses to sense with tools consists in sharing similar primary sensory dynamics devoted to the body. This allows a tool to be used as an extended, non-neural sense organ that can efficiently probe the user's surroundings. This finding challenges the long-held view which portrays SI as a layered structure of low-level feature detectors.

Instead our finding suggests that the SI dynamics instantiate high-level sensorimotor models of an organism (Brecht, 2017; Giurgola et al., 2019), including biological and extended parts.

Is the ability to sense with a tool merely a human case of detecting substrate vibrations? Indeed, it is well known that many species take advantage of information transported by material substrates [9]. Though some processing aspects of extended sensing may apply to objects that cannot be manipulated, there are several reasons for viewing tool-extended sensing as a unique case. The dexterity and tactile sensitivity of the human hand, along with its corresponding neural machinery (Peeters et al., 2009), likely evolved because they aided in the manipulation of tools (Young, 2003). Sensitivity to vibrations during tool use is largely attributed to Pacinian mechanoreceptors, which are critical for fine object manipulation (Roland S Johansson and Flanagan, 2009). Our results may thus reflect neural processes that developed for sensing with tools.

Unlike other instances of sensitivity to substrate vibrations, sensing with tools is a process that is most effective during active manipulation. When a blind person uses a cane to sense the environment, they adapt how the cane is gripped and swept against surfaces to optimize sensory feedback (e.g., vibrations), a strategy referred to as information self-structuring (Lungarella and Sporns, 2006). In our prior study, we found that fine-grained accuracy was significantly better during fully active compared to partially passive sensing [7]. Though the present study utilized a partially passive sensing mode (owing to experimental constraints), participants often reported selecting a grip that made it easier to discriminate between close and far hits [see also, ref. 7]. Thus, tool-extended sensing is an active process and not a passive pick-up of information.

The boundaries of somatosensory processing is a key theoretical question that has practical, real-world implications. A growing movement in bioengineering attempts to design *biomimetic* prosthetic limbs that provide somatosensory feedback to users, with limited—yet, encouraging—success (Bensmaia and Miller, 2014). For a prosthetic device to provide rich perceptual interaction with the world, its wearer must be able to perceive and act upon tactile events across its entire surface.

Tactile feedback is typically provided via invasive procedures, such as peripheral nerve stimulation (Valle et al., 2018) and intracortical microstimulation (Flesher et al., 2016). The present results suggest that a complementary, non-invasive means to restore sensory feedback would be to design prostheses that possess well designed structural dynamics in response to interactions with touching objects. Optimised transmission of these vibratory dynamics could leverage the identified sensorimotor mechanisms for mapping touch on a tool to aid in the use of a prosthetic device as an extended sensor.

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Author contributions: L.E.M., V.H., and A.F., conceived of the experimental idea. L.E.M. and A.F. designed the EEG experiments. L.E.M. C.F., and V.R. collected and analysed the EEG data. L.E.M. designed and analysed the neuronal modelling experiment. J.L. and S.B. performed the assessments for participant DC. E.K. and R.S. built the solenoid setup. L.E.M., N.B., V.H., and A.F. wrote the paper. All authors approved of the final submission. **Declaration of interests:** The authors declare no competing interests.

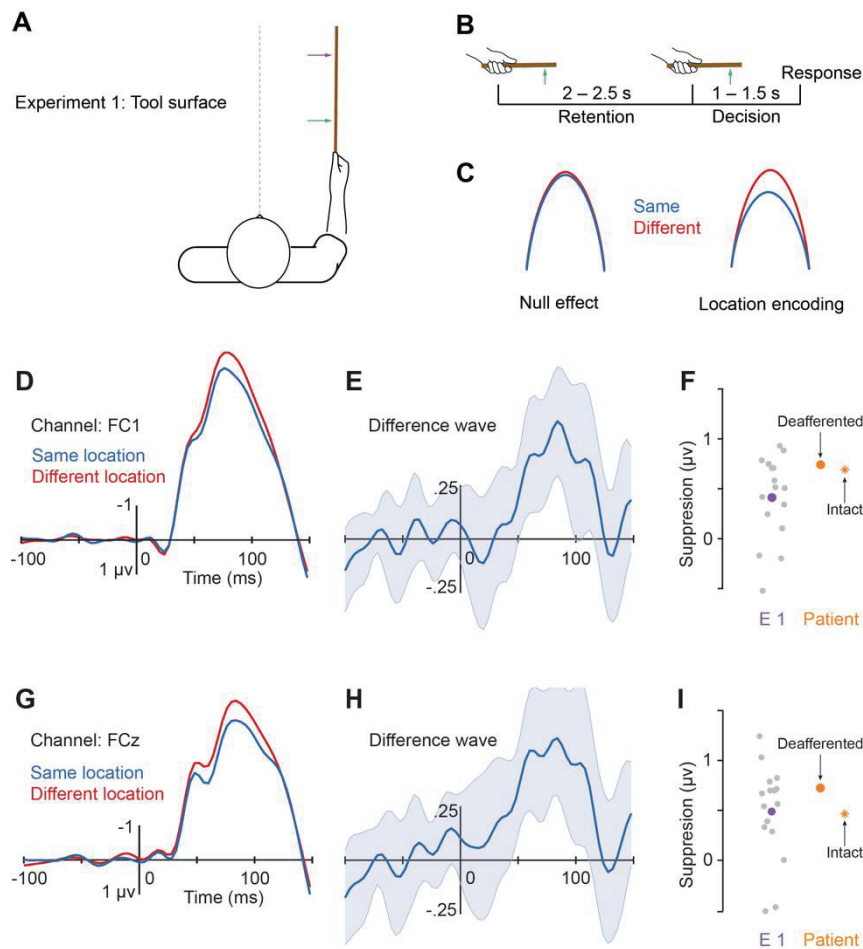


Figure 1. Rapid processing of object location during tool-extended sensing.

(A) Participants ($n=16$) performed a 2-interval delayed match-to-sample task for touches applied at two locations (coloured arrows) on the surface of a tool held in their right hand. This task forced participants to discriminate where the tool was touched (see STAR Methods). (B) Trial structure of the delayed match-to-sample task. For presentation purposes, only a portion of the rod is shown. Green arrows represent where the rod was hit. (C) Idealized possible results for a single SEP: Repetition suppression in the amplitude of the evoked potential (right) indicates location encoding at that specific stage of somatosensory processing. (D-F) Representative results are shown for (D-E) channel FC1 and (G-I) channel FCz. In both, we found a significant reduction in SEP amplitude (D, G) when the hit was at the same location (blue) compared to a different location (red). (E, H) The difference waves (Different–Same) clearly show rapid suppression in both channels. Shaded areas = the 95% confidence interval. (F, I) Individual differences for the suppression (average between 52–108 ms) at both channels from Experiment 1 (mean=purple dot; individuals=grey dot) and from the deafferented participant, DC (orange dots). The suppression observed in DC was on the high-end compared to our healthy participants.

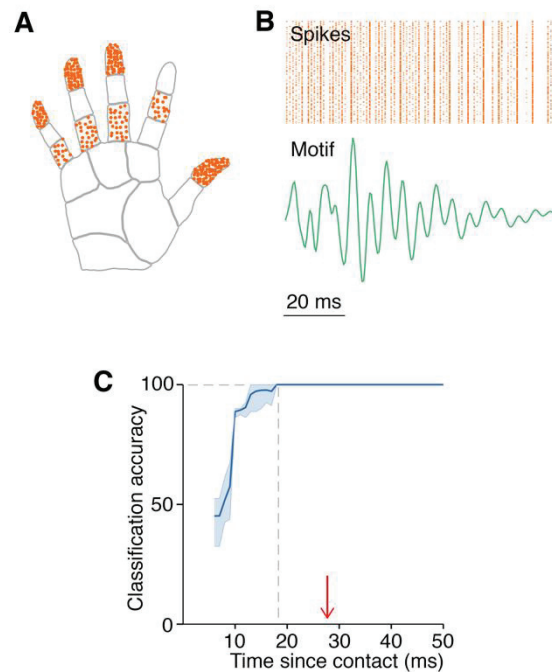


Figure 2. Afferent simulations demonstrated efficient encoding of location during tool-extended sensing.

(A) We used a skin-neuron model (TouchSim) to simulate a population of 286 Pacinian corpuscles (PCs) in the hand. (B) We simulated PC spikes (orange ticks) in response to the location-specific vibratory motif (green curve). (C) Given the spike-timing of the PC population, we could decode location with 100% accuracy given a window-size of 18 ms (grey dashed line). We took this value to represent the minimal information needed to extract contact location if somatosensory encoding was maximally efficient. The red arrow indicates what we actually observed after removing the 20 ms conduction delay between the periphery and SI (Eisen and Elleker, 1980b). Shaded regions represent the range of accuracy for 100 permutations.

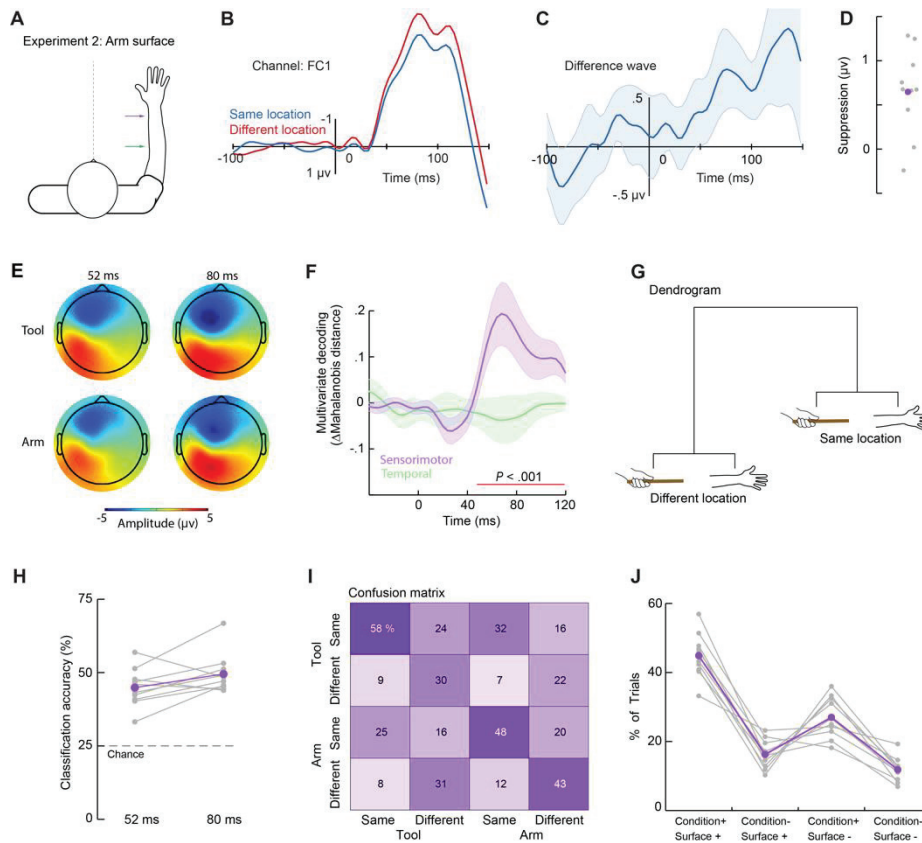


Figure 3. Similar processing of touch location on the arm and tool.

(A) Participants performed the exact paradigm as Experiment 1 (Figure 1A-C) with the exception that the stimulated surface was the arm. (B) As with the first experiment, we found a significant reduction in SEP amplitude (between 52 to 144 ms) when the hit was in the same location on the arm (blue) compared to a different location (red). (C) The time-course of this suppression is more evident in the difference wave. Shaded areas = the 95% confidence interval. (D) We found suppression in the majority of participants (8 out of 10; mean=purple dot; individuals=grey dots). (E) Scalp topographies at early (52 ms) and late (80 ms) time points for touch on the tool (top row) and arm (bottom). To illustrate the general similarity between surfaces, we have collapsed scalp topographies across both the same and different conditions. (F) Cross-surface multivariate decoding of suppression for each participant ($n=10$) and at several time points (-40 to 120 ms). Decoding is expressed as the difference in the Mahalanobis distance between matching and non-matching trial conditions (i.e., same location vs. different location). For sensorimotor channels (purple), we observed a significant cluster ($P < .001$; red line) of positive similarity between suppression on the tool and arm starting at 52 ms and continuing throughout our trial window. No significance was found for temporal channels (green). Shaded areas = ± 1 s.e.m. for decoding across participants. (G) Hierarchical clustering grouped neural responses by trial condition and not by surface touched. (H) SVM classification accuracy (mean=purple dot; individuals=grey dots) for both early and late time points were significantly greater than chance

(dashed grey line). (I) Confusion matrix for classifier trained on the early time point (52 ms). Numbers correspond to the percentage of time the classifier chose that trial type. (J) For ease of interpretation, we deconstructed the confusion matrix (early time point) into all categories of classifications (mean=purple; individuals=grey). This includes accurate classification (condition+, surface+) and the three types of misclassifications. The majority of misclassifications were based on shared trial condition, not shared surface.

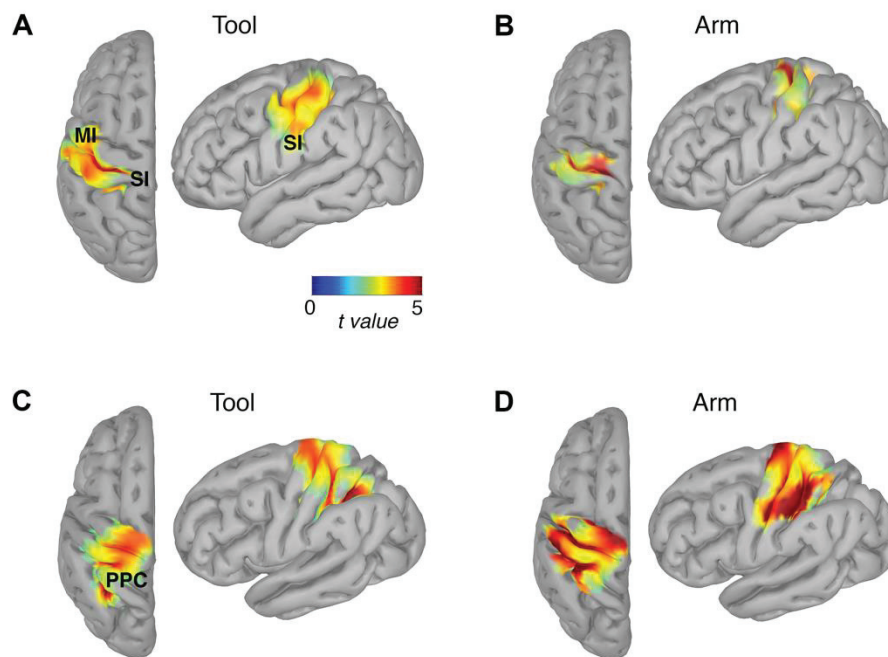


Figure 4. Neural correlates of touch location on a tool and forearm

(A-B) Suppression shortly after contact (52 ms) on the (A) rod and (B) arm was confined to primary somatosensory and motor cortices. (C-D) Activity 80 ms after contact on the (C) rod and (D) arm then spread to nearly identical regions in the posterior parietal cortex.

LEAD CONTACT AND MATERIALS AVAILABILITY

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Luke E. Miller (L.Miller@donders.ru.nl). This study did not generate new unique reagents.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

16 right-handed subjects (mean age: 26.5 years, range 20 to 34 years, 5 males) free of any known sensory, perceptual, or motor disorders, volunteered to participate in Experiment 1. Ten of these participants also completed Experiment 2. A neurological patient (DC; female, 50 years of age) also completed Experiment 1. All subjects provided written informed consent according to national guidelines of the ethics committee (CPP SUD EST IV).

Method details

Experimental Setup

In Experiment 1, Participants sat in a chair with their right arm placed on an adjustable armrest. A wooden rod (length: 100 cm; cross-sectional radius: 0.75 cm) was held in their right hand, with the tip of the stick resting on a support so that it would stay stable and parallel to the participant's midline. A fixation cross was displayed on a computer screen ~100 cm in front of the participant. A left foot double-pedal (Leptron Footswitch 548561) was used to make responses in the task (see below).

The rod was contacted with solenoids (Mecalectro 8.19.AB.83) at two different location (see Figure 1A): ~16 cm from the hand (close location) and ~63 cm from the hand (far location). The solenoids were powered with 36W in order to achieve a sufficient impact level and were controlled via custom Matlab code. Each had an identical acceleration profile, ensuring that contact force (~14 N) did not vary from trial-to-trial. Furthermore, the acceleration onset of the solenoid was controlled with sub-millisecond precision (SD of acceleration onset: 0.26 ms), guaranteeing good time-locking for the EEG analysis (see below). All solenoids were secured by adjustable tripods, which were used to place the solenoid 1 cm below the surface of the rod. To ensure uniform and consistent contact between solenoids and the body of the rod, a plastic disc (4 cm diameter) was added at the tip of each solenoid's metal point.

Two precautions were taken to mask the sound generated by the solenoids: (i) white noise was played continuously over noise-cancelling earphones (Bose QuietComfort 20) at a level that made the solenoids almost inaudible; (ii) a 'decoy' solenoid was placed next to the rod and in between the other two solenoids so that the activation of each solenoid was always accompanied by an activation

of the decoy, further obscuring auditory cues to solenoid position. All solenoids were supported by adjustable tripods at the same height. Visual cues were prevented by spreading a black sheet between the screen and subjects' neck to cover their hands and the stick.

The experimental setup was almost exactly the same as Experiment 1. Participants sat in a chair with their right elbow and hand each placed on an armrest. Stimulation was applied to the ventral surface of their right forearm, which was positioned between each arm rest. As with the prior experiment, the solenoids were positioned at two locations, ~5 cm from the crook of the arm and ~5 cm from the wrist, and 1 cm below the surface.

Delayed match-to-sample paradigm

Participants performed a delayed match-to-sample task (DMS) whereby they had to decide whether two mechanical stimulations were in the same or different location on either the rod (Experiment 1) or the arm (Experiment 2). Specifically, participants were instructed to report whether the two contacts were in the same or a different location, using foot pedals placed under their left foot (i.e., ipsilateral to the site of stimulation). When the two locations of contact were different, participants made no overt response. When they were in the same location, we required them to make explicit judgments about whether they were close to the hand (raising their heel) or far from the hand (raising their toe). This ensured that our paradigm did not fall prey to the known criterion effects in based same vs. different psychophysical tasks. Furthermore, no feedback was ever given to participants on whether their responses were correct or incorrect, ensuring that they could not learn arbitrary rules to distinguish close or far. All stimulus presentation and behavioural response collection was controlled via custom scripts in Matlab (MathWorks).

The structure of each trial was as follows. Each trial began with a fixation cross presented at the centre of the computer screen, which blinked after 1000 ms to inform the participants that a contact was coming soon and to therefore pay attention. After a delay period (between 1000-1500 ms, randomly chosen from a uniform distribution), mechanical stimulation was applied to the experimental surface (i.e., rod or arm) at one of the two locations (close or far; pseudo-randomly chosen). During a retention period, participants kept the location of contact in working memory (between 2000-2500 ms, randomly chosen from a uniform distribution); this retention period ended with the application of the second stimulus (location chosen pseudo-randomly). Participants then decided about whether the second hit was in the same location as the first and kept this decision in mind during a further delay period (between 1000-1500 ms, randomly chosen from a uniform distribution). This delay period ended when the fixation cross changed to an 'X', signifying to the

subject to make a response (see above). The 'X' turned back into a fixation cross just after the response was made, or after 2000 ms if no response, and the next trial began.

Subjects performed four blocks of 100 trials each (400 trials in total), in which stimulus location was pseudo-randomly interleaved for each hit. Thus, there were 200 contacts per location for each of the two hits (400 close and 400 far contacts in total). Furthermore, on half of the trials the two hits were in the same location and on the other half the two hits were in different locations. Each trial lasted between 5000 and 8500 ms. A brief rest period was provided between blocks during which the subjects could move their hands and eyes freely. For two participants in each experiment, one block of data was not recorded due to experimenter error; their full dataset therefore only contains three blocks.

Clinical testing and details for participant DC

We have previously completed a tool-use experiment with participant DC (Lucilla Cardinali et al., 2016). DC is a right-handed 50-year old woman who underwent surgery in March 2006 to remove a vascular tumour in the proximity of the right medulla oblongata. Following surgery, DC lost proprioception and kinaesthesia in her right upper limb, which remains deafferented to this day. Light touch on her right upper limb is largely spared. She currently prefers manipulating objects and use tools with her right hand (self-report and Edinburgh Handedness Index), and often compensates with visual feedback. The sensorimotor functions of all other limbs were unaffected by the surgery.

Clinical examination with the Rivermead Assessment of Somatosensory Performance [49] was performed prior to her inclusion in the present study. This test confirmed that, for both hands, she could perfectly discriminate sharp/dull probes, detect surface pressure, and localize touches (100% accuracy). Her ability to discriminate proprioceptive movements of her elbow, wrist, and thumb were perfect for her left upper limb (100% accuracy). On the contrary, she was highly impaired when discriminating proprioceptive movements of three joints (i.e., elbow, wrist, and thumb) for her right upper limb (33% accuracy).

Participant DC completed the procedures from Experiment 1 with both her intact (left) and deafferented (right) hand in separate blocks (block order: left, right, right, left). The experimental procedures were identical to described above. In debriefing, DC reported that she did not feel her wrist moving during the experiment.

Electroencephalographic (EEG) recording parameters

EEG data were recorded continuously using a 65 channel ActiCap system (Brain Products). Horizontal and vertical electro-oculograms (EOGs) were recorded using electrodes placed below the left eye, and

near the outer canthi of the right eye. Impedance of all electrodes was kept at <20 k Ω . FCz served as the reference during recording. EEG and EOG signals were low-pass filtered online at 0.1 Hz, sampled at 2500 Hz, and then saved to a disk.

Preprocessing of the EEG data

EEG signals were preprocessed using the EEGLab Toolbox [50]. The preprocessing steps for each participant were as follows: We appended all four blocks of the experiment into a single dataset, resampled the signal at 250 Hz, and high-pass filtered at 1 Hz. We then epoched the data into a time window of 3 seconds, 1 second before and 2 seconds after the hit (time zero). We then isolated epochs related to the second hit, as this was the focus of our analysis (see below); each epoch was categorized as reflecting the same location as the first hit ('same' condition) or a different location ('different' condition). Next, we removed signal artefacts with two steps: First, we removed eye blinks and horizontal eye movements from the signal using independent components analysis [51] and a semi-automated algorithm called SASICA [52]. Second, we excluded the first ten trials of the experiment, trials that were interrupted by the experimenter, all trials where subjects answered incorrectly, and manually rejected trials that were contaminated by muscle artefacts or other forms of signal noise. In all, this led to a mean exclusion of 35.5 trials in Experiment 1 (range: 14–56) and 24.1 trials in Experiment 2 (range: 12–43). Next, we used the EEGLab function *pop_reref* to add FCz (the online reference) back into the dataset. Finally, we re-referenced the data to the average voltage across the scalp and re-epoched the data into a time window of 250 milliseconds, –100 milliseconds before and 150 milliseconds after the hit. We chose this time window because it captures three mid-latency somatosensory evoked potentials (SEPs) related to the early stages of perceptual processing [22], the P50, N80 and P100.

Vibration recordings

We previously demonstrated that information about impact location is initially encoded by the modal response of a rod when contacted [7]. We recorded these vibrations in order to estimate how mechanoreceptors in the hand respond to impact at the two locations in Experiment 1. All vibrations were recorded using a miniature tri-axis analogue accelerometer (Analog Devices; Model ADXL335), which have low mass (40.0 mg), a wide frequency bandwidth (0–1,600 Hz in X and Y; 0–550 Hz in Z), and high dynamic range (–3.6 to 3.6 g).

Vibrations were recorded from the base of the tool shaft as one of the authors (V.R.) held the rod in place. The modal response of the rod was measured forty times for each location. We restricted the recording to the Z-axis as this contained the bulk of the impact response. The signal was digitized with a 14-bit resolution and sampled at a frequency of 2 kHz over a three-second window using a data

acquisition device (National Instruments; Model USB-6009). We then converted the signal into three temporal derivatives (acceleration, velocity, and displacement) and high-pass filtered it at 100 Hz using a 3rd order zero-phase Butterworth FIR filter. All data was recorded and processed using Matlab 2017b (The MathWorks).

Skin-neuron model

Pacinian mechanoreceptors in the hand have previously been proposed to play a role in encoding vibrations during tool-surface contact [33]. We recently provided evidence, using a biologically plausible computational skin-neuron model (TouchSim; ref. 8), that they re-encode where a tool has been touched [7]. Matlab code to implement the model is freely available online (<http://bensmaialab.org/download/>). The reader should refer to the original article for an in-depth treatment of the methods and model validation.

We used TouchSim to simulate the responses of a population of Pacinian mechanoreceptors (286 in total) to the vibrations described above. The population was confined to skin surfaces that are tangential to the force of impact when holding the rod. The vibration on each trial (see above) was used as the input for each mechanoreceptor in the population. To more realistically simulate the mechanoreceptors, the temporal profile of their responses included stochastic noise and considered known mechanical and spiking delays. We then derived the population-level response pattern by summing the spiking of each individual mechanoreceptor.

QUANTIFICATION AND STATISTICAL ANALYSIS

Cluster-based analysis of EEG signals

The goal of each experiment was to identify time windows where the amplitude of SEPs was modulated by whether the location of contact was repeated or not (see Main Text). We hypothesized that the evoked response to the second hit would be smaller when the stimulus was at the same location as the first (i.e., ‘same’ condition), compared to when it was at a different location (i.e., ‘different’ condition). We therefore focused our analysis on the evoked responses to the second stimulus presentation. Identical results were found when this procedure was performed on the two contact locations separately (data not shown); we therefore combined them into a single dataset for the final analysis. To identify time windows of suppression, we used a nonparametric cluster-based permutation test [53], a popular data-driven approach that robustly controls for the multiple comparison problem inherent in M/EEG analysis. We focused this analysis on electrodes over temporal and sensorimotor regions contralateral to the stimulation: P7, P5, P3, P1, Pz, TP9, TP7, CP5, CP3, CP1, CPz, T7, C5, C3, C1, Cz, FT9, FT7, FC5, FC3, FC1, FCz, F7, F5, F3, F1, and Fz. The sensorimotor electrodes

are the most common sites of the three SEPs corresponding to the chosen time window [22] and the temporal electrodes served as neutral electrodes where no suppression was expected.

Multivariate pattern decoding of EEG signals

Decoding was performed on the datasets from the ten participants that took part in both Experiment 1 and 2. The trial-by-trial EEG signal is dominated by low-frequency oscillations, which swamp the evoked responses. Therefore, in order to place greater emphasis on the evoked SEPs, we subtracted the EEG following the first hit from the second hit on every trial. Trials were then classified by the two above-mentioned trial conditions: Same and Different.

Representational distance approach: To test the hypothesis that similar processing stages are used to localize touch on an arm and tool, we compared the similarity of the multivariate neural patterns of suppression for both surfaces at each time point (-40 to 120 ms after touch) using the Mahalanobis distance (MD) metric [35]. All trials in both the tool and arm datasets were divided into the conditions 'same location' and 'different location'. Then, for each trial in the participant's tool dataset, we calculated its MD from the average of all trials in the participant's arm dataset whose condition was either matching or non-matching. For example, a trial in the 'same' condition from the tool dataset could be compared against the average of the 'same' condition (match) or the 'different' condition (non-matching) in the arm dataset. The degree of decoding for each time point was then quantified by subtracting the condition-matched MD from the condition-mismatched MD.

If the multivariate neural patterns of suppression in the arm dataset were in fact predictive of the patterns of suppression in the tool dataset, per our hypothesis, the condition-matched MD should yield smaller values than the condition-mismatched MD. We assessed this using the nonparametric cluster-based permutation test described above. Prior to this analysis, the trial-averaged MD values for each participant were smoothed using a Gaussian-kernel with a standard deviation of 8 ms. This approach increases the sensitivity of the analysis [35] and did not have an effect on our pattern of results. We restricted the present analysis (and therefore the multivariate patterns) to nine of the sensorimotor channels from the significant cluster in Experiment 1 (CP3, CP1, CPz, C3, C1, Cz, FC3, FC1, FCz) and seven ventral electrodes where no significant classification was expected (P7, TP9, TP7, T7, FT9, FT7, F7).

Hierarchical clustering: The full dataset for each participant contains four distinct trial types that are derived from the combinations of trial condition and the surface touched. We used hierarchical clustering to assess their representational similarity. The Euclidean distance between the trial-average neural patterns for each trial type was calculated for each participant. We then averaged the matrix of Euclidean distances across all participants and clustered the data using the *hclust* function in R version

3.2.3. [54]. This was done for two time points: (i) the earliest time point (52 ms) of significant cross-surface decoding described above; (ii) a later time point (80 ms) corresponding to the peak of the N80 (Supplementary Figures 1 & 3). We restricted the present analysis to nine of the sensorimotor channels from the significant cluster in Experiment 1 (CP3, CP1, CPz, C3, C1, Cz, FC3, FC1, FCz).

Support vector classification: For each participant, we attempted to classify the four distinct trial types in their full dataset using a support vector machine (SVM) [55] with a radial basis kernel. Our classification scheme used 5-fold cross validation. Thus, we trained the classifier on four subsamples of the data (i.e., 80% of the trials) and tested classifier performance on the leftover subsample (i.e., the remaining 20% of the trials). Each fold had an equal number of items per trial type. The hyperparameters of the SVM, C and γ , were tuned using grid search; tuning occurred separately for each of the five classification iterations. The features for classification were the neural patterns of suppression for each of the two time points mentioned above (i.e., 52 and 80 ms). Classification was performed using the e1071 package [56] and its interface with LIBSVM [57]. This was implemented with R version 3.2.3. [55]. Chance classification (i.e., random guessing) was 25%. Classification was done separately for each participant. We restricted the present analysis to nine of the sensorimotor channels from the significant cluster in Experiment 1 (CP3, CP1, CPz, C3, C1, Cz, FC3, FC1, FCz).

To further explore the performance of the classifier, we assessed the confusion matrix for each participant. There were four possible types of classifier judgments. The classifier could be completely accurate about both condition and surface (condition+, surface+). The classifier could also produce three types of possible misclassifications: (i) accurate about surface only (condition-, surface+); (ii) accurate about condition only (condition+, surface-), and (iii) fully inaccurate (condition-, surface-). Different proportions of misclassification are informative about which categories are considered most similar and distinct by the classifier.

Source reconstruction

The cortical sources underlying the observed repetition suppression in both experiments were estimated using Standardized Low Resolution Brain Electromagnetic Tomography (sLORETA) [53], which approximates the generators underlying a given scalp topography by finding a discrete solution to the inverse problem. A boundary element method (OpenMEEG) was used to create a realistic head model (15000 vertices) to constrain source reconstruction [59]. This process was implemented using the Brainstorm toolbox [60], which is freely available for download online under the GNU general public license (<http://neuroimage.usc.edu/brainstorm>). Sources were reconstructed separately for each experimental condition ('same' and 'different') and were statistically compared using a paired permutation-based t -test (1000 repetitions) at the group-level (FDR corrected at $P < .05$). Given prior

studies on the sources between 40 and 100 milliseconds after stimulation [22, 23, 27, 28], we constrained our analyses to a region-of-interest covering contralateral MI, SI, and the PPC (1300 vertices). Our analysis focused on two time points in the observed windows of suppression discussed above: 52 and 80 ms. Qualitatively similar results were found when using a cluster-based approach to source reconstruction (data not shown).

We further compared the sources for each surface, tool and arm, in the ten participants who completed both experiments. We first investigated the interaction between condition ('same', 'different') and surface (tool, arm) by using the above methods to compare the sources of suppression (i.e., the arithmetic difference between both conditions) for both surfaces. Given that this analysis yielded no results, we combined the data from both experiments into a single dataset in order to identify regions that coded for contact location on both the tool and arm.

Support vector classification of simulated spikes

We sought to derive a theoretical lower bound on how efficiently the brain could extract where a rod was touched. This involved three steps: (i) recording the rod's modal responses to being impacted (see above); (ii) simulating how this response is encoded by mechanoreceptors in the hand (see above); (iii) using machine learning to classify how quickly impact location emerges in mechanoreceptor spiking.

We classified impact location from the population response using a support vector machine (SVM) [55] with a radial basis kernel. Our classification scheme used 5-fold cross validation. Thus, we trained the classifier on four subsamples of the data (i.e., 80% of the trials) and tested classifier performance on the leftover subsample (i.e., the remaining 20% of the trials). Each fold had an equal number of items per impact location. The hyperparameters of the SVM, C and γ , were tuned using grid search; tuning occurred separately for each of the five classification iterations. We specifically sought to characterize when a location-specific pattern emerged in the PC population's spiking pattern. The features for classification were therefore subsets of this population spiking across multiple temporal window sizes (5 to 50 ms, in steps of 1 ms). Classification was performed using the e1071 package [56] and its interface with LIBSVM [57]. This was implemented with R version 3.2.3. [54]. Chance classification (i.e., random guessing) was ~50%.

References

1. Clark, A. (2008). *Supersizing the mind: Embodiment, action, and cognitive extension* (New York: Oxford University Press).
2. Iriki, A., Tanaka, M., and Iwamura, Y. (1996). Coding of modified body schema during tool use by macaque postcentral neurones. *Neuroreport* 7, 2325–2330.
3. Umiltà, M., Escola, L., Intskirveli, I., Grammont, F., Rochat, M., Caruana, F., Jezzini, A., Gallese, V., and Rizzolatti, G. (2008). When pliers become fingers in the monkey motor system. *Proc. Natl. Acad. Sci.* 105, 2209–2213.
4. Cardinali, L., Frassinetti, F., Brozzoli, C., Urquizar, C., Roy, A.C., and Farnè, A. (2009). Tool-use induces morphological updating of the body schema. *Curr. Biol.* 19, 1157.
5. Miller, L.E., Cawley-Bennett, A., Longo, M.R., and Saygin, A.P. (2017). The recalibration of tactile perception during tool use is body-part specific. *Exp. Brain Res.* 235, 2917–2926.
6. Martel, M., Cardinali, L., Roy, A.C., and Farnè, A. (2016). Tool-use: An open window into body representation and its plasticity. *Cogn. Neuropsychol.* 33, 82–101.
7. Miller, L.E., Montroni, L., Koun, E., Salemme, R., Hayward, V., and Farnè, A. (2018). Sensing with tools extends somatosensory processing beyond the body. *Nature* 561, 239–242.
8. Saal, H.P., Delhay, B.P., Rayhaun, B.C., and Bensmaia, S.J. (2017). Simulating tactile signals from the whole hand with millisecond precision. *Proc. Natl. Acad. Sci.* 114, E5693–E5702.
9. Burton, G. (1993). Non-Neural extensions of Haptic Sensitivity. *Ecol. Psychol.* 5, 105–124.
10. Japyassú, H.F., and Laland, K.N. (2017). Extended spider cognition. *Anim. Cogn.* 20, 375–395.
11. Yamamoto, S., and Kitazawa, S. (2001). Sensation at the tips of invisible tools. *Nat. Neurosci.* 4, 979–980.
12. Saig, A., Gordon, G., Assa, E., Arieli, A., and Ahissar, E. (2012). Motor-Sensory Confluence in Tactile Perception. *J. Neurosci.* 32, 14022–14032.
13. Kiltani, K., and Ehrsson, H.H. (2017). Sensorimotor predictions and tool use: Hand-held tools attenuate self-touch. *Cognition* 165, 1–9.
14. Imamizu, H., Miyauchi, S., Tamada, T., Sasaki, Y., Takano, R., Pütz, B., Yoshioka, T., and Kawato, M. (2000). Human cerebellar activity representing acquired internal model of a new tool. *Nature* 403, 192–195.

15. Grill-Spector, K., Henson, R., and Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends Cogn. Sci.* 10, 14–23.
16. Schendan, H.E., and Kutas, M. (2003). Time course of processes and representations supporting visual object identification and memory. *J. Cogn. Neurosci.* 15, 111–135.
17. Tamè, L., Pavani, F., Papadelis, C., Farnè, A., and Braun, C. (2015). Early integration of bilateral touch in the primary somatosensory cortex. *Hum. Brain Mapp.* 36, 1506–1523.
18. Shen, G., Smyk, N.J., Meltzoff, A.N., and Marshall, P.J. (2018). Neuropsychology of human body parts: Exploring categorical boundaries of tactile perception using somatosensory mismatch responses. *J. Cogn. Neurosci.* 30, 1858–1869.
19. Van Pelt, S., Toni, I., Diedrichsen, J., and Medendorp, W.P. (2010). Repetition Suppression Dissociates Spatial Frames of Reference in Human Saccade Generation. *J. Neurophysiol.* 104, 1239–48
20. Strömmer, J.M., Tarkka, I.M., and Astikainen, P. (2014). Somatosensory mismatch response in young and elderly adults. *Front. Aging Neurosci.* 6, 1–9.
21. Eisen, A., and Elleker, G. (1980). Sensory nerve stimulation and evoked cerebral potentials. *Neurology* 30, 1097–1105.
22. Allison, T., McCarthy, G., and Wood, C.C. (1992). The relationship between human long-latency somatosensory evoked potentials recorded from the cortical surface and from the scalp. *Electroencephalogr. Clin. Neurophysiol. Potentials Sect.* 84, 301–314.
23. Cardini, F., Longo, M.R., and Haggard, P. (2011). Vision of the Body Modulates Somatosensory Intracortical Inhibition. *Cereb. Cortex* 21, 2014–2022.
24. Akatsuka, K., Wasaka, T., Nakata, H., Kida, T., Hoshiyama, M., Tamura, Y., and Kakigi, R. (2007). Objective examination for two-point stimulation using a somatosensory oddball paradigm: An MEG study. *Clin. Neurophysiol.* 118, 403–411.
25. Cauller, L.J., and Kulics, A.T. (1991). The neural basis of the behaviorally relevant N1 component of the somatosensory-evoked potential in SI cortex of awake monkeys: evidence that backward cortical projections signal conscious touch sensation. *Exp. Brain Res.* 84, 607–619.
26. Jones, S.R., Pritchett, D.L., Stufflebeam, S.M., Hamalainen, M., and Moore, C.I. (2007). Neural Correlates of Tactile Detection: A Combined Magnetoencephalography and Biophysically Based Computational Modeling Study. *J. Neurosci.* 27, 10751–10764.
27. Soto-Faraco, S., and Azañón, E. (2013). Electrophysiological correlates of tactile remapping. *Neuropsychologia* 51, 1584–1594.

28. Nakata, H., Inui, K., Nishihira, Y., Hatta, A., Sakamoto, M., Kida, T., Wasaka, T., and Kakigi, R. (2004). Effects of a go/nogo task on event-related potentials following somatosensory stimulation. *Clin. Neurophysiol.* 115, 361–368.
29. Cardinali, L., Brozzoli, C., Luauté, J., Roy, A.C., and Farnè, A. (2016). Proprioception Is Necessary for Body Schema Plasticity: Evidence from a Deafferented Patient. *Front. Hum. Neurosci.* 10.
30. Simoncelli, E.P., and Olshausen, B.A. (2001). Natural Image Statistics and Neural Representation. *Annu. Rev. Neurosci.* 24, 1193–1216.
31. Johansson, R.S., and Flanagan, J.R. (2009). Coding and use of tactile signals from the fingertips in object manipulation tasks. *Nat. Rev. Neurosci.* 10, 14–20.
32. Jörntell, H., Bengtsson, F., Geborek, P., Spanne, A., Terekhov, A. V., and Hayward, V. (2014). Segregation of tactile input features in neurons of the cuneate nucleus. *Neuron* 83, 1444–1452.
33. Maria, R., Panchuelo, S., Ackerley, R., Glover, P.M., Bowtell, R.W., Wessberg, J., Francis, S.T., and Mcglone, F. (2016). Mapping quantal touch using 7 Tesla functional magnetic resonance imaging and single-unit intraneural microstimulation. *Elife*, 1–19.
34. van Ede, F., Chekroud, S.R., Stokes, M.G., and Nobre, A.C. (2019). Concurrent visual and motor selection during visual working memory guided action. *Nat. Neurosci.* 22, 477–483.
35. Bolognini, N., and Maravita, A. (2007). Proprioceptive Alignment of Visual and Somatosensory Maps in the Posterior Parietal Cortex. *Curr. Biol.* 17, 1890–1895.
36. Buchholz, V.N., Jensen, O., and Medendorp, W.P. (2011). Multiple reference frames in cortical oscillatory activity during tactile remapping for saccades. *J. Neurosci.* 31, 16864–71.
37. Naito, E., and Ehrsson, H.H. (2006). Somatic sensation of hand-object interactive movement is associated with activity in the left inferior parietal cortex. *J. Neurosci.* 26, 3783–3790.
38. Naito, E., Scheperjans, F., Eickhoff, S.B., Amunts, K., Roland, P.E., Zilles, K., and Ehrsson, H.H. (2008). Human superior parietal lobule is involved in somatic perception of bimanual interaction with an external object. *J. Neurophysiol.* 99, 695–703.
39. Johnson-Frey, S.H. (2004). The neural bases of complex tool use in humans. *Trends Cogn. Sci.* 8, 71–78.
40. Chiel, H.J., and Beer, R.D. (1997). The brain has a body: Adaptive behavior emerges from interactions of nervous system, body and environment. *Trends Neurosci.* 20, 553–557.
41. Brecht, M. (2017). The Body Model Theory of Somatosensory Cortex. *Neuron* 94, 985–992.

42. Giurgola, S., Pisoni, A., Maravita, A., Vallar, G., and Bolognini, N. (2019). Somatosensory cortical representation of the body size. *Hum. Brain Mapp.* 40, 3534–3547.
43. Peeters, R., Simone, L., Nelissen, K., Fabbri-Destro, M., Vanduffel, W., Rizzolatti, G., and Orban, G.A. (2009). The Representation of Tool Use in Humans and Monkeys: Common and Uniquely Human Features. *J. Neurosci.* 29, 11523–11539.
44. Young, R.W. (2003). Evolution of the human hand : the role of throwing and clubbing. *J. Anat.* 202, 164–174.
45. Lungarella, M., and Sporns, O. (2006). Mapping information flow in sensorimotor networks. *PLoS Comput. Biol.* 2, 1301–1312.
46. Bensmaia, S.J., and Miller, L.E. (2014). Restoring sensorimotor function through intracortical interfaces: Progress and looming challenges. *Nat. Rev. Neurosci.* 15, 313–325.
47. Flesher, S.N., Collinger, J.L., Foldes, S.T., Weiss, J.M., Downey, J.E., Tyler-Kabara, E.C., Bensmaia, S.J., Schwartz, A.B., Boninger, M.L., and Gaunt, R.A. (2016). Intracortical microstimulation of human somatosensory cortex. *Sci. Transl. Med.* 8.
48. Valle, G., Mazzoni, A., Iberite, F., D’Anna, E., Strauss, I., Granata, G., Controzzi, M., Clemente, F., Rognini, G., Cipriani, C., et al. (2018). Biomimetic Intraneural Sensory Feedback Enhances Sensation Naturalness, Tactile Sensitivity, and Manual Dexterity in a Bidirectional Prosthesis. *Neuron* 100, 37–45.
49. Winward, C.E., Halligan, P.W. & Wade, D.T. The rivermead assesement of somatosensory performance (RASP): standardization and reliability data. *Clin. Rehabil.* 16, 523–533 (2002).
50. Delorme, A. & Makeig, S. EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J. Neurosci. Methods* 134, 9–21 (2004).
51. Makeig, S., Bell, A. J., Jung, T.-P. & Sejnowski, T. J. Independent Component Analysis of Electroencephalographic Data. *Adv. Neural Inf. Process.* 8, 145–151 (1996).
52. Chaumon, M., Bishop, D. V. M. & Busch, N. A. A practical guide to the selection of independent components of the electroencephalogram for artifact correction. *J. Neurosci. Methods* 250, 47–63 (2015).
53. Maris, E. & Oostenveld, R. Nonparametric statistical testing of EEG- and MEG-data. *J. Neurosci. Methods* 164, 177–190 (2007).
54. R.C. Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. (2014).
55. C. Cortes, & V. Vapnik. Support-vector networks. *Machine learning* 20, 273-297 (1995).

56. D. Meyer, E. Dimitriadou, K. Hornik, A. Weingessel, & F. Leisch. e1071: Misc Functions of the Department of Statistics, Probability Theory Group (Formerly: E1071), TU Wien. R package version 1.6-7. (2015).
57. C.C. Chang & C.J. Lin. LIBSVM: a library for support vector machines. *ACM Transactions on Intelligent Systems and Technology (TIST)* 2, 27 (2011).
58. Pascual-Marqui, R. D. Standardized low-resolution brain electromagnetic tomography (sLORETA): technical details. *Methods Find. Exp. Clin. Pharmacol.* 24, 5–12 (2002).
59. Gramfort, A., Papadopoulo, T., Olivi, E. & Clerc, M. OpenMEEG: Opensource software for quasistatic bioelectromagnetics. *Biomed. Eng. Online* 9, 1–20 (2010).
60. Tadel, F., Baillet, S., Mosher, J. C., Pantazis, D. & Leahy, R. M. Brainstorm: A user-friendly application for MEG/EEG analysis. *Comput. Intell. Neurosci.* 2011, (2011).

Study 2:

Alpha Oscillations Are Involved in Localizing Touch on Handheld Tools

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Summary

The sense of touch is not restricted to the body but can also extend to external objects. When we use a hand-held tool to contact an object, we feel the touch on the tool and not in the hand holding the tool. The ability to perceive touch on a tool actually extends along its entire surface, allowing the user to accurately localize where it is touched similarly as they would on their body. While the neural mechanisms underlying the ability to localize touch on the body have been largely investigated, those underlying tactile localization on a tool have been mostly unexplored. We aimed to fill this gap by recording the EEG signal of participants while they localized tactile stimuli on a hand-held rod. While the first study looked at post-touch ERP, we focus here on post-touch oscillatory activity. Oscillations in the alpha (7-14 Hz) and beta (15-30 Hz) range have been previously linked to distinct spatial codes used to localize touch on the body: beta activity reflects the mapping of touch in skin-based coordinates, whereas alpha activity reflects the mapping of touch in external space. Since localizing touch on a hand-held tool seems to require similar mechanisms than for localizing touch on the body, we expected alpha and beta to both be involved in the former process. We based our analysis on repetition effect of contact location. We found that alpha activity was solely modulated by the location of tactile stimuli applied on a hand-held rod, while beta power was insignificantly affected by it. Source reconstruction suggested that this alpha power modulation was localized in a network of fronto-parietal regions previously implicated in higher-order tactile and spatial processing. These sources notably included SI, SII, dorsal and ventral premotor cortices, occipito-parietal cortex, and the superior temporal gyrus. These findings are the first to implicate alpha oscillations in tool-extended sensing and suggest an important role for processing touch in external space when localizing touch on a tool.

Abstract

The sense of touch is not restricted to the body but can also extend to external objects. When we use a hand-held tool to contact an object, we feel the touch on the tool and not in the hand holding the tool. The ability to perceive touch on a tool actually extends along its entire surface, allowing the user to accurately localize where it is touched similarly as they would on their body. While the neural mechanisms underlying the ability to localize touch on the body have been largely investigated, those allowing to localize touch on a tool are still unknown. We aimed to fill this gap by recording the EEG signal of participants while they localized tactile stimuli on a hand-held rod. We focused on oscillatory activity in the alpha (7-14 Hz) and beta (15-30 Hz) range, as they have been previously linked to distinct spatial codes used to localize touch on the body. Beta activity reflects the mapping of touch in skin-based coordinates, whereas alpha activity reflects the mapping of touch in external space. We found that alpha activity was solely modulated by the location of tactile stimuli applied on a hand-held rod. Source reconstruction suggested that this alpha power modulation was localized in a network of fronto-parietal regions previously implicated in higher-order tactile and spatial processing. These findings are the first to implicate alpha oscillations in tool-extended sensing and suggest an important role for processing touch in external space when localizing touch on a tool.

KEYWORDS: Tactile localization – Tool use - Extended sensing – Alpha oscillations

Introduction

Space is a crucial aspect of touch. Whether a mosquito lands on your arm, or a cat rubs against your leg, tactile events share the common feature of originating from somewhere, usually on the body. The sense of touch though, is not restricted to processing events on the body surface, as humans can also perceive tactile contact on external objects. For example, a blind person can use a white cane to locate obstacles in their immediate surroundings. Even in the sighted, when a person touches an object with the tip of a hand-held tool, the object is perceived to be at the tip instead of at the hand that holds the tool (Vaught et al., 1968; Yamamoto et al., 2005; Yamamoto and Kitazawa, 2001). Humans can also sense several of an object's properties with a tool, such as its surface texture (Klatzky and Lederman, 1999; Yoshioka et al., 2007), softness (LaMotte, 2000), length (Peck et al., 1996) and position in space (Carello et al., 1992; Giudice et al., 2013).

Importantly, the ability to perceive touch on a tool extends along its entire surface, allowing humans to accurately localize where a hand-held tool is touched as they would on their own body (Miller et al., 2018). It was also found that where a tool is touched is likely rapidly encoded by location-specific patterns of vibration, termed vibratory motifs. Simulations with a biologically plausible skin-neuron model (Saal et al., 2017) suggested that these motifs are likely re-encoded by the spiking patterns of the hand's mechanoreceptors, reflecting the initial transformation underlying the extraction of contact location on a rod. However, the nature of these mechanisms, particularly at the cortical level, is still largely unexplored. The aim of the present study is therefore to address the question of how the brain extracts 'where' a tool has been touched.

Since it is essential to identify the position of a tactile object in order to interact with it, more than a century of research has characterized the perceptual processes underlying tactile localization at a behavioral level ((Badde et al., 2015; Cholewiak and Collins, 2003; Fuchs et al., 2019; Harrar and Harris, 2009; Ho and Spence, 2007; Liu and Medina, 2021; Mancini et al., 2011; Miller et al., 2020; Parrish, 1897; Sadibolova et al., 2018; Stevens, 1992; Weber, 1846); for a review see (Heed et al., 2015)). These studies have identified different spatial codes that are utilized to localize tactile stimuli. The location of touch is thought to be initially encoded in skin-based coordinates—also called anatomical coordinates—and later integrated with extra-cutaneous information (e.g., proprioception) to remap its location in coordinates anchored to external space (Aglioti et al., 1999; Azañón and Soto-Faraco, 2008; Badde et al., 2015, 2014; Longo et al., 2015; Schicke and Roder, 2006; Shore et al., 2005, 2002). There has been extensive investigation on how these spatial codes are implemented at the neural level ((Celesia, 1979; Ghazanfar et al., 2000; Johansson and Flanagan, 2009; Johnson and Lamb,

1981; Tamè et al., 2015); for a review see (Dijkerman and de Haan, 2007)). Early activity in primary somatosensory cortex (SI) likely implements an anatomical code, as its layout is spatially organized in a limb-centric fashion (Penfield and Boldrey, 1937; Schnitzler et al., 1995). External coding, on the other hand, requires the involvement of a larger network that includes secondary somatosensory cortex (SII) and fronto-parietal regions (Azañón et al., 2010; Graziano and Gross, 1998; Reed et al., 2005; Soto-Faraco and Azañón, 2013; Takahashi et al., 2013; Wada et al., 2012).

Over the last decade, research using magnetoencephalography (MEG) and electroencephalography (EEG) has identified oscillatory mechanisms that underlie these processes. Touching the skin leads to a desynchronization in two main low-frequency bands, alpha (7-14 Hz) (Cheyne et al., 2003; Haegens et al., 2014; Neuper et al., 2006; Salenius et al., 1997; Salmelin and Hari, 1994) and beta (15-30 Hz) (Neuper et al., 2006; Pfurtscheller et al., 2001; Salmelin and Hari, 1994). Both frequency bands have been implicated in the spatial processing of touch (Heed et al., 2015). The alpha band has mainly been involved in the mapping of touch in the external coordinate system (Buchholz et al., 2013, 2011; Ruzzoli and Soto-Faraco, 2014; Schubert et al., 2019, 2015). Activity in the beta band, on the other hand, seems to exclusively reflect the mapping of touch in skin-centered coordinates (Buchholz et al., 2013, 2011b; Schubert et al., 2015). To date, whether these frequency bands also relate to spatial processing of touch on hand-held tools remains unknown. Our goal here was therefore to fill this gap.

We used EEG to investigate the oscillatory correlates of tool-extended tactile localization. Participants performed a delayed match-to-sample task that required them to judge the relative location of two successive contacts on a hand-held rod. Our previous event-related potentials (ERP) investigation (Miller et al., 2019) identified signatures of tactile localization starting as early as 48 ms after touch on a tool. Multivariate decoding algorithms and cortical source reconstruction suggested that the somatosensory cortex reuses low-level neural processes devoted to mapping touch on the body for mapping touch on the tool. Expanding on these previous results, we report here on the induced oscillations following touch localization on a tool. Given their role on mapping touch on the body, we focused our attention on the activity of the two aforementioned frequency bands: alpha and beta. Since tool use shares similar neural processes with body-related actions (Gallivan et al., 2013; Johnson-Frey, 2004) and based on our ERPs findings, we hypothesized that activity in both frequency bands would index spatial coding of touch on a hand-held tool.

Method

Analyses were performed on a dataset for which we have previously analysed ERPs following tactile stimulation (Miller et al., 2019). Here we focused on the induced oscillations and not oscillations phase-locked to the event.

Participants

16 right-handed participants (mean age: 26.5 years, range 20 to 34 years, 5 males) free of any known sensory, perceptual, or motor disorders, volunteered to participate in the experiment. We chose this sample size in accordance to previous studies about somatosensory oscillations (Haegens et al., 2011; Schubert et al., 2015). The experiment was performed in accordance with the ethical standards laid down in the Declaration of Helsinki (2013) and all participants provided written informed consent according to national guidelines of the ethics committee (CPP SUD EST IV).

Setup

Participants sat in a chair with their right arm placed on an adjustable armrest. During the task, they fixated on a central cross (2 cm wide) that was displayed on a 16" monitor ~100 cm in front of them and aligned with their body midline. A one-meter long wooden rod was placed in their right hand, with the tip of the rod resting on a support so that it would stay stable and parallel to the participant's body midline. Two solenoids (Mecalectro 8.19-.AB.83; 24 V, supplied with 36 W) were used to contact the rod at two different locations with a force of ~15 N: ~16 cm from the hand (close location) and ~63 cm from the hand (far location). To ensure uniform and consistent contact between solenoids and the body of the rod, a plastic disc (4 cm diameter) was attached perpendicular to the tip of each solenoid's metal rod. Participants used a double-pedal (Lepton Footswitch 548561) under their left foot to report their judgments.

In order to mask the sound generated by the solenoids, white noise was played continuously over noise-cancelling earphones (Bose QuietComfort 20) and a third solenoid was placed next to the rod between the other two solenoids; this 'decoy' solenoid was used to mask any residual auditory spatial cue to the location of impact. All solenoids were supported by adjustable tripods at the same height. Visual feedback was also prevented by spreading a black sheet between the screen and the participants' neck to cover their hands and the stick.

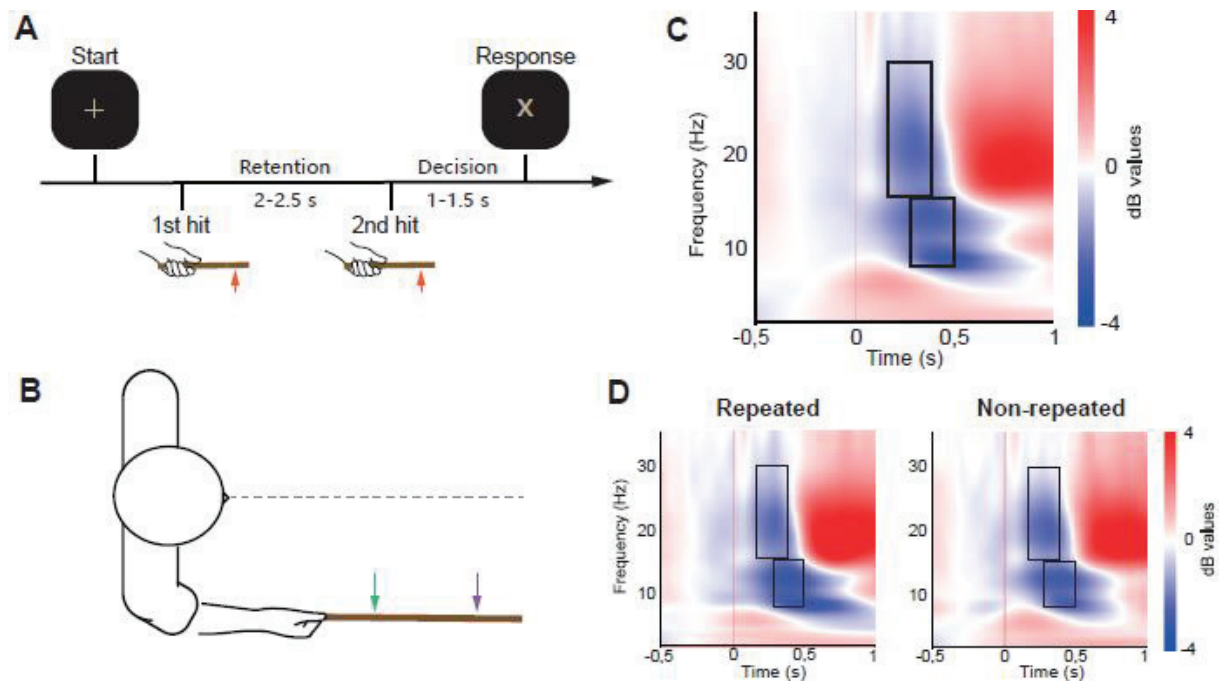


Figure 3. Experimental setup and paradigm

(A) Trial structure of the delayed match-to-sample task. For presentation purposes, only a portion of the rod is shown and black boxes represent the computer screen. (B) Participants ($n=16$) performed a 2-interval delayed match-to-sample task for touches applied at two locations (colored arrows) on the surface of a tool held in their right hand. This task forced participants to discriminate where the tool was touched. (C-D) Induced temporal dynamics of the after-hit period over contralateral somatosensory cortex. Oscillatory dynamics of C3 electrode for: (C) all epochs combined, (D) epochs where location of the second hit was the same as the first hit (left panel) and epochs where location of the second hit was different than the first (right panel). Modulations are displayed as compared relative to baseline (-500 to -100 ms). Selected time windows for analysis are represented by grey rectangle for each frequency band: 300-500 ms for alpha and 200-400 ms for beta.

Experimental paradigm

Participants performed a delayed match-to-sample task designed to measure repetition effects on brain responses (Grill-Spector et al., 2006) during tactile localization on a tool (Figure 1B). In each trial, two hits were successively applied to the surface of the rod (Figure 1A). Participants had then to decide whether the second hit was in the same location (same close or far from the hand), or in a different location with respect to the first hit. Participants never wielded the rod before performing the task and never received feedback about their performance, ensuring that they could not learn arbitrary rules to distinguish close or far.

Each trial (Figure 1A) started when a fixation cross was displayed at the center of the screen. After 1000 ms, the fixation cross blinked to inform participants that the rod was about to be contacted. After a variable delay (between 1000–1500 ms; randomly chosen from a uniform distribution), a first stimulus was applied to the stick at one of the two locations (close or far; pseudorandomized), followed by a further delay (between 2000–2500 ms; randomly chosen from a uniform distribution) during which participants had to retain in memory the location of contact. The second stimulus (location chosen pseudorandomly) was then presented after which participants made a decision about whether the second hit was in the same or a different location as the first hit. They were instructed to wait until the fixation cross changed to an X (between 1000–1500 ms), prompting them to respond. The X turned back into a fixation cross just after the response was made, or after 2000 ms if no response. The next trial began after a fixed delay of 1000 ms.

Participants were instructed to discriminate whether the two contacts were in the same or a different location, using the foot pedals in the following way: if they judged that both hits were close to the hand they lifted their heel releasing the lower pedal. If they judged that both hits were far from the hand they lifted their toes releasing the upper pedal. If the two stimuli were different (close/far or far/close) they had to refrain from responding. To ensure that motor and perceptual processes wouldn't overlap in the EEG data, participants used their left foot to make the response, thus engaging the sensorimotor system in the right hemisphere (i.e., ipsilateral to the stimulated hand). Participants performed four blocks of 100 trials each (400 trials in total), in which stimulus location was pseudorandomly interleaved for each hit. There were 200 contacts per location for each of the two hits by block (400 close and 400 far contacts in total). Furthermore, on half of the trials the two hits were in the same location and on the other half the two hits were in different locations. Each trial lasted between 5000 and 8500 ms. A brief rest period was provided between blocks during which participants could move their hands and eyes freely.

EEG recording

EEG data were recorded continuously using a 65 channel ActiCap system (Brain Products). Horizontal and vertical electro-oculograms (EOGs) were recorded using electrodes placed below the left eye, and near the outer canthi of the right eye. Impedance of all electrodes was kept at <20 k Ω . FCz served as the online reference. EEG and EOG signals were low-pass filtered online at 0.1 Hz, sampled at 2500 Hz, and then saved to disk.

Stimulus presentation and behavioral response collection were performed using MatLab on the experimental control computer, which was synchronized and communicated with the EEG data recording system. The trial events were sent to the EEG data recording system via a parallel port.

Pre-processing of the EEG data

EEG signals were preprocessed using the EEGLab Toolbox (Delorme and Makeig, 2004). The preprocessing steps for each participant were as follows: each participant's four blocks of the experiment were appended into a single dataset. The signal was resampled at 250 Hz and high-pass filtered at 1 Hz. Faulty channels were interpolated using a spherical spline. We then epoched data into a time window of 3 seconds, 1 second before and 2 seconds after the second hit (time zero). Next, we removed signal artifacts with two steps: first, we removed eye blinks and horizontal eye movements from the signal using independent components analysis (ICA (Delorme and Makeig, 2004)) and a semi-automated algorithm called SASICA (Chaumon et al., 2015). Second, we excluded the first ten trials of the experiment, trials that were interrupted by the experimenter, all incorrectly answered trials, and manually rejected trials that were contaminated by muscle artifacts or other forms of signal noise. A response was determined as correct if: when the same two contacts happened, the participant responded for same, and gave the right location (far or close); when different contacts happened, the participant made no response. Only trials with correct response were kept for the analysis (mean accuracy = $96.4 \pm 0.71\%$; range: 89.7%–99.5%). In total, this led to a mean exclusion of 35.5 trials per participant (range: 14–56). Next, we used the EEGLab function `pop_reref` to add FCz (the online reference) back into the dataset. Finally, we re-referenced the data to the average voltage across the scalp.

Time-frequency decomposition

Time-frequency decomposition was performed using the open source toolbox Brainstorm (Tadel et al., 2011) in Matlab. The raw signal of each epoch was decomposed into frequencies between 1–35 Hz (linearly spaced) using Complex Morlet wavelets with a central frequency of 1 Hz and a full-width half maximum of 3 s. These parameters were chosen to ensure that our time-frequency decomposition had good spectral and temporal resolution within the chosen frequency range. The evoked activity was removed from the signal before time-frequency decomposition since it has already been analyzed in a previous study (Miller et al., 2019). Signal was then normalized in decibel (dB) to its ratio with the respective channel mean power during a baseline period ranging from -500 to -100 ms before hit. This period was free of any stimulus-induced activity that would extend into the baseline due to the temporal smoothing of the wavelet transformation, which is especially problematic for the lower frequencies (Cohen, 2014).

EEG data analysis

Alpha- and beta-band activity were defined here as 7–14 Hz and 15–30 Hz respectively. Based on the observation of the oscillatory temporal dynamics during the time period after the hit (collapsed across all participants and conditions, see Figure 1C), we selected two time windows for analysis for each of our frequency band of interest: 200-400 ms for beta-band, and 300-500 ms for the alpha-band. This is a bias-free method for choosing time windows upon which running the analysis (Cohen, 2014).

We based our main analysis on repetition effects as a way of capturing correlates of localization devoid of potential low level confounds, such as intensity differences. Repeating a stimulus has been shown to modulate the power in frequency bands that index the processing of that feature (Grill-Spector et al., 2006). Thus, if the second hit occurred in the same location as the first hit, the power in frequency band(s) indexing spatial processing should significantly differ from when the second hit was in a different location. In order to reveal the modulation of activity related to contact location processing, we statistically compared activity when location of the second hit was repeated (in reference to the first hit of the same trial) versus when it was not repeated. To this aim, we averaged the power of each frequency band, as well as the time points within the given time window and compared the scalp topography of each condition (repeated, non-repeated) using a cluster-based permutation test (Maris and Oostenveld, 2007). Analysis was two-tailed with a cluster-level significance threshold set to 0.05 and 1000 permutations run.

Source reconstruction

We performed source reconstruction for each epoch using the open source toolbox Brainstorm (Tadel et al., 2011). First, a head model was computed using OpenMEEG BEM model (Gramfort et al., 2010). A noise covariance matrix for every participant was computed over a baseline time window of -500 to -100 ms before stimulation. Sources were then estimated using the Standardized low resolution brain electromagnetic tomography (sLORETA (Pascual-Marqui, 2002)) approach with unconstrained dipole orientations across the surface.

We then performed time-frequency decomposition on the source files to localize significant power modulations in the alpha-band, since it returned significant location repetition effects. The signal at each vertex was decomposed into the mean of frequencies going from 7 to 14 Hz using Complex Morlet wavelets with a central frequency of 1 Hz and a full-width half maximum of 3 s. The signal was then normalized in decibel (dB) to its ratio with the respective channel mean power during a baseline period ranging from -500 to -100 ms before hit. A similar statistical comparison as the previous analysis was then applied in order to reveal the cerebral regions involved in processing contact location. We analyzed the difference in alpha power between each condition (repetition vs.

non-repetition) during the same time windows (300 to 500 ms after hit) using a cluster-based comparison (Maris and Oostenveld, 2007).

Results

Temporal dynamics of alpha and beta over contralateral somatosensory cortex

We first examined the temporal dynamics of oscillations at C3, an electrode directly above sensorimotor cortex (Oostenveld and Praamstra, 2001). Tactile stimulation on the rod led to a pattern of low-frequency power modulations (Figure 1C) over sensorimotor cortex that was consistent with prior work (Cheyne et al., 2003; Nierula et al., 2013). Specifically, we observed a desynchronization of alpha power between ~250 to 600 ms after touch, and narrower desynchronization of beta power between 200 to 500 ms. Desynchronization within these time periods has been observed in previous studies (Neuper et al., 2006; Salmelin and Hari, 1994), including those related to spatial processing within each frequency band (Buchholz et al., 2013, 2011; Schubert et al., 2019, 2015).

Based on these changes in power spectra, analysis of alpha (Fig. 2) and beta (Fig. 3) was performed on distinct time windows that captured desynchronization of all of the frequencies in each band.

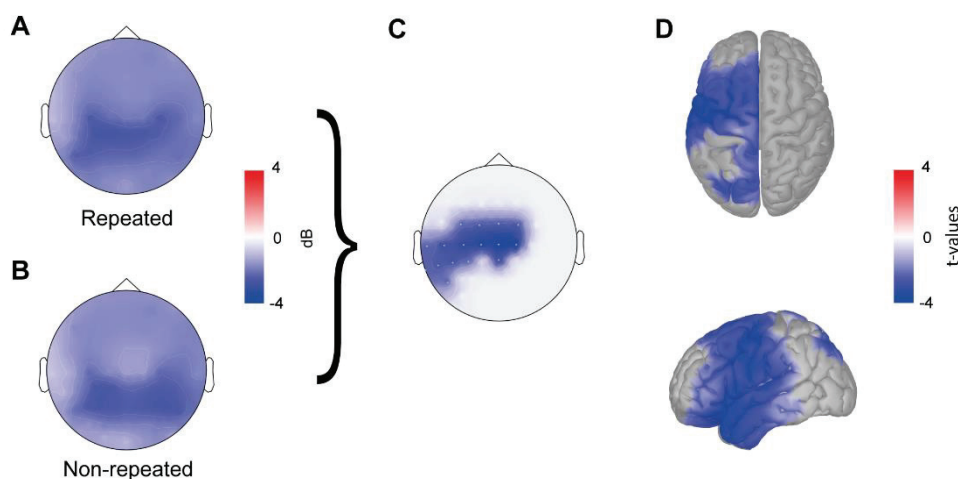


Figure 2 Alpha power modulation depends on contact location

(A-B) Average alpha-band (7–14 Hz) activity relative to baseline for the selected time windows (300-500 ms) following contact on the rod, when: A. location of the second hit was the same as the first hit and (B) location of the second hit was different than the first. (C) Scalp topography of the alpha power difference relative to contact location (Repeated vs. Non-repeated analysis, $p = 0.024$). (D) Source localization of the significant alpha power difference ($p = 0.006$). T-scale on the right is used for both (C) and (D).

Suppression in the alpha-band was dependent on location-based repetition

Touch on the rod led to widespread desynchronization in alpha power across the scalp, between 300 to 500 ms after touch. Consistent with previous studies (Buchholz et al., 2011; Schubert et al., 2019), this desynchronization was largely concentrated over centro-parietal channels bilaterally. As can be seen in Fig. 2A and B, the overall pattern of desynchronization on the scalp was largely independent of whether touch location was repeated or not (Figure 2A and B). Instead, location repetition modulated the gain of this desynchronization. We found significant differences in alpha power above central and parietal channels over the sensorimotor cortex contralateral to the stimulation (cluster-based p-value= 0.024). This difference was contralateral to the location of touch (Figure 2C), suggesting that the modulation observed is related to the tactile location processing and not to the motor preparation of the response.

We followed up by identifying the cortical sources underlying the observed alpha modulation. We found widespread repetition effects in alpha throughout the frontal, parietal, and temporal cortices (Figure 2D, $p = 0.006$). These sources notably include SI, SII, dorsal and ventral premotor cortex, occipito-parietal cortex, and the superior temporal gyrus (STG).

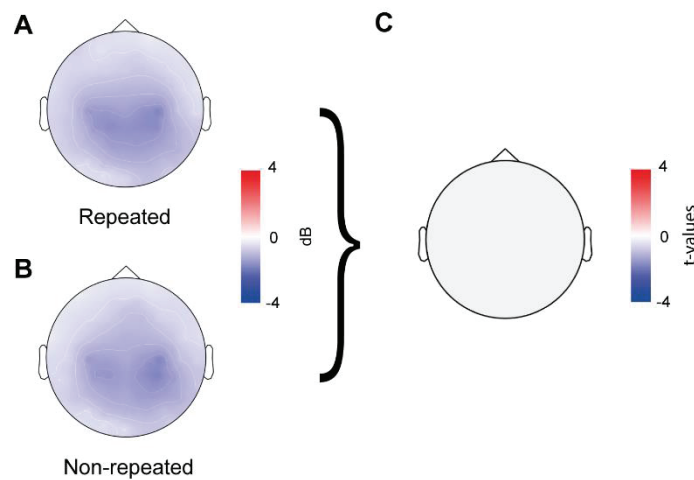


Figure 3. Beta power modulation doesn't depend on contact location

(A-B) Average beta-band (15–30 Hz) activity relative to baseline for the selected time windows (200-400 ms) following contact on the rod, when: (A) location of the second hit was the same as the first hit and (B) location of the second hit was different than the first. (C) Scalp topography of the beta power difference relative to contact location (Repeated vs. Non-repeated analysis, no cluster found).

Beta-band activity was independent from location-based repetition

We observed a desynchronization of beta power over bilateral centro-parietal channels between 200 to 400 ms after touch on the rod. As can be seen in Figure 3A and B, whether location was repeated or not did not affect the scalp distribution of desynchronization. Indeed, a cluster-based permutation test for the selected time window revealed no significant difference in beta power (Figure 3C). Therefore, in contrast to the alpha band and with our initial hypothesis, we did not observe repetition effects in the beta band.

Discussion

The present study aimed to investigate whether oscillatory activity linked to spatial coding of touch on the body (Buchholz et al., 2013, 2011; Ruzzoli and Soto-Faraco, 2014; Schubert et al., 2018, 2015) is also involved in sensing location through a hand-held tool. To this end, we compared oscillatory EEG responses in the alpha (7–14 Hz) and beta (15–30 Hz) bands during a delayed match-to-sample task where two successive touches were applied to either the same or different location on a hand-held wooden rod. Contact location information was isolated based on repetition effects, by comparing oscillatory power when location was repeated to when it was not.

We found that the post-stimulus desynchronization of alpha activity between 300 to 500 ms after touch was differentially affected by whether contact location was repeated. In contrast, we did not observe any repetition effects in the post-stimulus desynchronization of beta activity. Moreover, source estimation of the observed alpha modulation showed that it originated in a contralateral fronto-parietal network that is known to be involved in tactile localization. These findings provide novel evidence for the involvement of alpha-band activity in spatial coding of touch on a tool.

Owing to the remarkable accuracy with which humans can similarly localize touch on their arm and on a hand-held tool, previous work hypothesized that similar mechanisms may be involved in both (Miller et al., 2018; Yamamoto et al., 2005). In a recent event-related potentials study, we provided evidence that location information encoded in the tool's vibratory pattern is rapidly extracted and processed (<100 ms post-touch) by somatosensory and parietal cortices. Furthermore, these location-related neural responses were similar to those observed when touch was on the arm; this suggests that the brain may reuse neural mechanisms dedicated to processing touch on the body to process touch on a tool (Miller et al., 2019).

The present study focused on assessing whether alpha and beta oscillations—known to be associated to localizing touch on the body in external and anatomical reference frames, respectively (Buchholz et al., 2013, 2011; Schubert et al., 2019, 2015)—are also involved in localizing touch on a tool. In keeping with previous reports, we observed a post-touch desynchronization in both alpha and

beta power when touch was applied to a hand-held tool. In addition, their temporal distributions were consistent with what has been previously shown for touch on the skin (Cheyne et al., 2003; Gaetz and Cheyne, 2006). Importantly, repeating contact location on the tool allowed us to isolate oscillatory activity specific to spatial processing. That is, a repetition effect in oscillatory power served as a signature of localization-related processing. We identified such a signature in the alpha-band activity, with a significant effect of repetition on desynchronization in the hemisphere contralateral to the stimulation (Figure 2A-C). This suggests that alpha-band activity is involved in touch localization on a tool.

In contrast, the magnitude of the beta desynchronization was not modulated by whether touch location on the tool was repeated or not (Figure 3), suggesting that it may not play a role in localizing touch on a tool. Instead, beta-band desynchronization may reflect neural activity associated with stimulus discrimination and decision making (Haegens et al., 2017; Nakata et al., 2013). Moreover, various motor processes such as motor preparation, motor imagery, and motor intent can also modulate cortical beta oscillations (Miller et al., 2010; Pfurtscheller and Neuper, 1997). This alludes to a potential role for beta-band activity in encoding non-location specific processes, though future investigation is required to determine its role.

These findings raise the question as to which aspects of sensorimotor processing are reflected in the observed alpha desynchronization. One possibility, which we can readily rule out, is that it reflects motor preparatory activity. Such activity would likely be observed contralateral to the foot used for the response (i.e., the left) and therefore right lateralized (i.e., ipsilateral to the stimulation). However, the repetition effects in both the sensor-level activity (Figure 2A-C) and the sources (Figure 2D) were all lateralized to the left hemisphere (i.e., contralateral to stimulation), underscoring its relation to the processing of tactile information and not motor preparation.

The repetition effects in alpha-band activity instead likely reflect the processing of spatial tactile information on the surface of a hand-held tool. As previously discussed, alpha activity has been implicated in tactile spatial processing, being thought to play a prominent role in the coding of external spatial information for touch (Buchholz et al., 2013, 2011; Ruzzoli and Soto-Faraco, 2014; Schubert et al., 2019). Our findings provide initial evidence that alpha activity is also involved in tactile localization on a tool, thus possibly implicating the use of an external reference frame for the coding of tactile information on tools. As the tool itself is outside of the body, it might seem logical that tool-extended tactile localization takes place in an external reference frame. However, some alpha-activity has been linked to the use of skin-based information when touch is applied on the skin (Schubert et al., 2015). Thus, a “tool-centered” reference frame might not be purely external, but could also involve its own form of anatomical coding, similar to what happens for tactile localization on the body. One potential limitation of our study is that we did not directly compare body-related oscillations in the same

participants. While a second experiment in Miller et al (2019) did measure brain responses following touch on the forearm, its sample size was not optimized for Time Frequency analysis and thus precluded a direct comparison here. While future studies are needed, our conclusions are drawn based on the abundant previous literature indicating that alpha band oscillations are linked to spatial coding of touch on the body (Buchholz et al., 2013, 2011c; Ruzzoli and Soto-Faraco, 2014; Schubert et al., 2019, 2015).

Our source localization of the repetition effect in the alpha-band activity is consistent with this proposition. Repeating the location of touch modulated activity in a left-lateralized cortical network that included motor and somatosensory cortices, premotor (PMC) and posterior parietal cortices (PPC), and temporal regions (Figure 2D). Studies in both human and non-human primates have implicated these regions—particularly the PMC and PPC—in processing touch in external space (Avillac et al., 2005; Azañón et al., 2010; Bremmer et al., 2001; Lloyd et al., 2003). Furthermore, alpha oscillatory activity in these regions appears to play a crucial role in this process (Buchholz et al., 2011; Ruzzoli and Soto-Faraco, 2014; Schubert et al., 2019).

Post-touch alpha oscillations may reflect the orienting of attention in external space (Ossandón et al., 2020), which is involved in the alignment of sensory modalities under a common coordinate system (Ruzzoli and Soto-Faraco, 2014). Indeed, the PMC and PPC are crucial for the reference frame transformations underlying multimodal integration (Avillac et al., 2005; Bolognini and Maravita, 2007; Bremmer et al., 2001; Graziano and Gross, 1998). Vallar and Maravita have argued that both regions are also important for making the experience of space integrated and unitary across modalities (Vallar and Maravita, 2009). Consistent with this proposal, alpha-band activity has also been implicated in spatial processing of visual (Foster et al., 2017, 2016; Rihs et al., 2007; Samaha et al., 2016) and auditory (Deng et al., 2020; Frey et al., 2014) stimuli. In the context of these findings, the observed alpha desynchronization during tool extended sensing might reflect a supramodal mechanism for spatial localization.

Several studies have found that using a tool modulates body representations for action (Berti and Frassinetti, 2000; Cardinali et al., 2012, 2009; Gentilucci et al., 2004; Martel et al., 2019) and somatosensory perception (Canzoneri et al., 2013; Maravita et al., 2002; Miller et al., 2014, 2017b; Sposito et al., 2012). Our results support and help qualify the notion that tools are incorporated into the body representation (Cardinali et al., 2009), as not only low-frequency modulations for touch applied on a hand-held object were similar to when touch is applied on the skin (Cheyne et al., 2003; Nierula et al., 2013; Salenius et al., 1997) but they were also localized in brain regions previously implicated in localizing touch on the body (Avillac et al., 2005; Azañón et al., 2010; Lloyd et al., 2003; Miller et al., 2019). Furthermore, fronto-parietal alpha-connectivity emerged only when touch was

applied to the self-body but not when applied to an object (Pisoni et al., 2018). In this context, our finding suggests that the tool is treated more like a body part and less like an object.

Previous tool-use studies have found that active wielding (Bruno et al., 2019; Cardinali et al., 2016; Galigani et al., 2020) may be necessary for tool embodiment. Participants in the present study never actively wielded the rod, which seems contradictory with this proposition. However, even if no motor movements were made, our task required participants to actively treat the rod as a sensory surface, taking sensory input and placing it within a spatial model of the tool. This can be viewed as a form of active use. Consistent with our finding, several other studies have also found that sensory feedback is important for embodiment (Cardinali et al., 2011; Martel et al., 2019; Miller et al., 2017a; Serino et al., 2015) . Sensing with a hand-held tool appears to be sufficient for tool embodiment, which might reflect the deployment of body related neural processes to sensing with tools. This capacity to extract information from a hand-held tool, as displayed in the present and previous studies (Miller et al., 2019, 2018), might have conferred an evolutionary advantage to the genus homo and possibly played a role in humans' sophisticated mastery of tools.

Overall, while our findings are clear in suggesting a role of alpha oscillations in localizing touch on a hand-held tool, the nature of the spatial representation remains unclear. The present study was not aimed at disentangling the actual coordinate(s) system(s) reflected in tool-extended sensing. Indeed, isolating tactile reference frames typically requires manipulating the posture of an effector, such as crossing the hands. When the hands are crossed, anatomical (e.g. right hand) and external (e.g. left side) reference frames can be spatially dissociated. Thus, to precisely pinpoint the spatial code(s) used in tool-extended tactile localization, future studies are needed that manipulate tool posture in a similar way, possibly allowing to dissociate the signatures of anatomical and external reference frames.

CONCLUSION

To conclude, we newly report that alpha activity is specifically modulated by the location of tactile stimuli applied on a hand-held rod. The neural sources of this alpha power modulation were localized to a network of parieto-frontal areas previously implicated in tactile and spatial processing. While further studies are needed to deepen the specific role of brain oscillations in processing touch on tools, we provide novel evidence involving alpha band activity in tool-extended sensing.

DATA AVAILABILITY

All data will be available in an online repository upon acceptance.

CONFLICT OF INTEREST

The authors declare no conflict in interest.

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AUTHOR CONTRIBUTIONS

CF, LEM and AF conceived of the experimental idea, designed the EEG experiment, and wrote the paper. CF and LEM collected and analyzed the data. RS and EK built the solenoid setup. All authors approved of the final submission.

REFERENCES

- Aglioti, S., Smania, N., Peru, A., 1999. Frames of Reference for Mapping Tactile Stimuli in Brain-Damaged Patients. *Journal of Cognitive Neuroscience* 11, 67–79. <https://doi.org/10.1162/089892999563256>
- Avillac, M., Denève, S., Olivier, E., Pouget, A., Duhamel, J.-R., 2005. Reference frames for representing visual and tactile locations in parietal cortex. *Nature Neuroscience* 8, 941–949. <https://doi.org/10.1038/nn1480>
- Azañón, E., Longo, M.R., Soto-Faraco, S., Haggard, P., 2010. The Posterior Parietal Cortex Remaps Touch into External Space. *Current Biology* 20, 1304–1309. <https://doi.org/10.1016/j.cub.2010.05.063>
- Azañón, E., Soto-Faraco, S., 2008. Changing Reference Frames during the Encoding of Tactile Events. *Current Biology* 18, 1044–1049. <https://doi.org/10.1016/j.cub.2008.06.045>
- Badde, S., Röder, B., Heed, T., 2015. Flexibly weighted integration of tactile reference frames. *Neuropsychologia* 70, 367–374. <https://doi.org/10.1016/j.neuropsychologia.2014.10.001>
- Badde, S., Röder, B., Heed, T., 2014. Multiple spatial representations determine touch localization on the fingers. *Journal of Experimental Psychology: Human Perception and Performance* 40, 784–801. <https://doi.org/10.1037/a0034690>
- Berti, A., Frassinetti, F., 2000. When Far Becomes Near: Remapping of Space by Tool Use. *Journal of Cognitive Neuroscience* 12, 415–420. <https://doi.org/10.1162/089892900562237>

- Bolognini, N., Maravita, A., 2007. Proprioceptive Alignment of Visual and Somatosensory Maps in the Posterior Parietal Cortex. *Current Biology* 17, 1890–1895. <https://doi.org/10.1016/j.cub.2007.09.057>
- Bremmer, F., Schlack, A., Duhamel, J.-R., Graf, W., Fink, G.R., 2001. Space Coding in Primate Posterior Parietal Cortex. *NeuroImage* 14, S46–S51. <https://doi.org/10.1006/nimg.2001.0817>
- Bruno, V., Carpinella, I., Rabuffetti, M., De Giuli, L., Sinigaglia, C., Garbarini, F., Ferrarin, M., 2019. How Tool-Use Shapes Body Metric Representation: Evidence From Motor Training With and Without Robotic Assistance. *Front. Hum. Neurosci.* 13, 299. <https://doi.org/10.3389/fnhum.2019.00299>
- Buchholz, V.N., Jensen, O., Medendorp, W.P., 2013. Parietal Oscillations Code Nonvisual Reach Targets Relative to Gaze and Body. *Journal of Neuroscience* 33, 3492–3499. <https://doi.org/10.1523/JNEUROSCI.3208-12.2013>
- Buchholz, V.N., Jensen, O., Medendorp, W.P., 2011a. Multiple Reference Frames in Cortical Oscillatory Activity during Tactile Remapping for Saccades. *Journal of Neuroscience* 31, 16864–16871. <https://doi.org/10.1523/JNEUROSCI.3404-11.2011>
- Buchholz, V.N., Jensen, O., Medendorp, W.P., 2011b. Multiple Reference Frames in Cortical Oscillatory Activity during Tactile Remapping for Saccades. *Journal of Neuroscience* 31, 16864–16871. <https://doi.org/10.1523/JNEUROSCI.3404-11.2011>
- Buchholz, V.N., Jensen, O., Medendorp, W.P., 2011c. Multiple Reference Frames in Cortical Oscillatory Activity during Tactile Remapping for Saccades. *Journal of Neuroscience* 31, 16864–16871. <https://doi.org/10.1523/JNEUROSCI.3404-11.2011>
- Canzoneri, E., Ubaldi, S., Rastelli, V., Finisguerra, A., Bassolino, M., Serino, A., 2013. Tool-use reshapes the boundaries of body and peripersonal space representations. *Experimental Brain Research* 228, 25–42. <https://doi.org/10.1007/s00221-013-3532-2>
- Cardinali, L., Brozzoli, C., Finos, L., Roy, A.C., Farnè, A., 2016. The rules of tool incorporation: Tool morpho-functional & sensori-motor constraints. *Cognition* 149, 1–5. <https://doi.org/10.1016/j.cognition.2016.01.001>
- Cardinali, L., Brozzoli, C., Urquizar, C., Salemme, R., Roy, A.C., Farnè, A., 2011. When action is not enough: Tool-use reveals tactile-dependent access to Body Schema. *Neuropsychologia* 49, 3750–3757. <https://doi.org/10.1016/j.neuropsychologia.2011.09.033>
- Cardinali, L., Frassinetti, F., Brozzoli, C., Urquizar, C., Roy, A.C., Farnè, A., 2009. Tool-use induces morphological updating of the body schema. *Current Biology* 19, 1157. <https://doi.org/10.1016/j.cub.2009.06.048>
- Cardinali, L., Jacobs, S., Brozzoli, C., Frassinetti, F., Roy, A.C., Farnè, A., 2012. Grab an object with a tool and change your body: tool-use-dependent changes of body representation for action. *Exp Brain Res* 218, 259–271. <https://doi.org/10.1007/s00221-012-3028-5>
- Carello, C., Fitzpatrick, P., Turvey, M.T., 1992. Haptic probing: Perceiving the length of a probe and the distance of a surface probed. *Perception & Psychophysics* 51, 580–598. <https://doi.org/10.3758/BF03211655>
- Celesia, G.G., 1979. Somatosensory Evoked Potentials Recorded Directly From Human Thalamus and Sm I Cortical Area. *Archives of Neurology* 36, 399–405. <https://doi.org/10.1001/archneur.1979.00500430029003>

- Chaumon, M., Bishop, D.V.M., Busch, N.A., 2015. A practical guide to the selection of independent components of the electroencephalogram for artifact correction. *Journal of Neuroscience Methods* 250, 47–63. <https://doi.org/10.1016/j.jneumeth.2015.02.025>
- Cheyne, D., Gaetz, W., Garnero, L., Lachaux, J.-P., Ducorps, A., Schwartz, D., Varela, F.J., 2003. Neuromagnetic imaging of cortical oscillations accompanying tactile stimulation. *Cognitive Brain Research* 17, 599–611. [https://doi.org/10.1016/S0926-6410\(03\)00173-3](https://doi.org/10.1016/S0926-6410(03)00173-3)
- Cholewiak, R.W., Collins, A.A., 2003. Vibrotactile localization on the arm: Effects of place, space, and age. *Perception & Psychophysics* 65, 1058–1077. <https://doi.org/10.3758/BF03194834>
- Cohen, M.X., 2014. *Analyzing Neural Time Series Data: Theory and Practice*. MIT Press.
- Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods* 134, 9–21. <https://doi.org/10.1016/j.jneumeth.2003.10.009>
- Deng, Y., Choi, I., Shinn-Cunningham, B., 2020. Topographic specificity of alpha power during auditory spatial attention. *NeuroImage* 207, 116360. <https://doi.org/10.1016/j.neuroimage.2019.116360>
- Dijkerman, H.C., de Haan, E.H.F., 2007. Somatosensory processes subserving perception and action. *Behavioral and Brain Sciences* 30, 189. <https://doi.org/10.1017/S0140525X07001392>
- Foster, J.J., Bsaies, E.M., Jaffe, R.J., Awh, E., 2017. Alpha-Band Activity Reveals Spontaneous Representations of Spatial Position in Visual Working Memory. *Current Biology* 27, 3216–3223.e6. <https://doi.org/10.1016/j.cub.2017.09.031>
- Foster, J.J., Sutterer, D.W., Serences, J.T., Vogel, E.K., Awh, E., 2016. The topography of alpha-band activity tracks the content of spatial working memory. *Journal of Neurophysiology* 115, 168–177. <https://doi.org/10.1152/jn.00860.2015>
- Frey, J.N., Mainy, N., Lachaux, J.-P., Muller, N., Bertrand, O., Weisz, N., 2014. Selective Modulation of Auditory Cortical Alpha Activity in an Audiovisual Spatial Attention Task. *Journal of Neuroscience* 34, 6634–6639. <https://doi.org/10.1523/JNEUROSCI.4813-13.2014>
- Fuchs, X., Wulff, D.U., Heed, T., 2019. Online sensory feedback during active search improves tactile localization (preprint). *Neuroscience*. <https://doi.org/10.1101/590539>
- Gaetz, W., Cheyne, D., 2006. Localization of sensorimotor cortical rhythms induced by tactile stimulation using spatially filtered MEG. *NeuroImage* 30, 899–908. <https://doi.org/10.1016/j.neuroimage.2005.10.009>
- Galigani, M., Castellani, N., Donno, B., Franza, M., Zuber, C., Allet, L., Garbarini, F., Bassolino, M., 2020. Effect of tool-use observation on metric body representation and peripersonal space. *Neuropsychologia* 148, 107622. <https://doi.org/10.1016/j.neuropsychologia.2020.107622>
- Gallivan, J.P., McLean, D.A., Valyear, K.F., Culham, J.C., 2013. Decoding the neural mechanisms of human tool use. *eLife* 2, e00425. <https://doi.org/10.7554/eLife.00425>
- Gentilucci, M., Roy, AliceC., Stefanini, S., 2004. Grasping an object naturally or with a tool: are these tasks guided by a common motor representation? *Exp Brain Res* 157. <https://doi.org/10.1007/s00221-004-1863-8>

- Ghazanfar, A.A., Stambaugh, C.R., Nicolelis, M.A.L., 2000. Encoding of Tactile Stimulus Location by Somatosensory Thalamocortical Ensembles. *J. Neurosci.* 20, 3761–3775. <https://doi.org/10.1523/JNEUROSCI.20-10-03761.2000>
- Giudice, N.A., Klatzky, R.L., Bennett, C.R., Loomis, J.M., 2013. Perception of 3-D location based on vision, touch, and extended touch. *Exp Brain Res* 224, 141–153. <https://doi.org/10.1007/s00221-012-3295-1>
- Gramfort, A., Papadopoulos, T., Olivi, E., Clerc, M., 2010. OpenMEEG: opensource software for quasistatic bioelectromagnetics 20.
- Graziano, M.S., Gross, C.G., 1998. Spatial maps for the control of movement. *Current Opinion in Neurobiology* 8, 195–201. [https://doi.org/10.1016/S0959-4388\(98\)80140-2](https://doi.org/10.1016/S0959-4388(98)80140-2)
- Grill-Spector, K., Henson, R., Martin, A., 2006. Repetition and the brain: neural models of stimulus-specific effects. *Trends in Cognitive Sciences* 10, 14–23. <https://doi.org/10.1016/j.tics.2005.11.006>
- Haegens, S., Handel, B.F., Jensen, O., 2011. Top-Down Controlled Alpha Band Activity in Somatosensory Areas Determines Behavioral Performance in a Discrimination Task. *Journal of Neuroscience* 31, 5197–5204. <https://doi.org/10.1523/JNEUROSCI.5199-10.2011>
- Haegens, S., Vazquez, Y., Zainos, A., Alvarez, M., Jensen, O., Romo, R., 2014. Thalamocortical rhythms during a vibrotactile detection task. *Proceedings of the National Academy of Sciences* 111, E1797–E1805. <https://doi.org/10.1073/pnas.1405516111>
- Haegens, S., Vergara, J., Rossi-Pool, R., Lemus, L., Romo, R., 2017. Beta oscillations reflect supramodal information during perceptual judgment. *Proc Natl Acad Sci USA* 114, 13810–13815. <https://doi.org/10.1073/pnas.1714633115>
- Harrar, V., Harris, L.R., 2009. Eye position affects the perceived location of touch. *Exp Brain Res* 198, 403–410. <https://doi.org/10.1007/s00221-009-1884-4>
- Heed, T., Buchholz, V.N., Engel, A.K., Röder, B., 2015. Tactile remapping: from coordinate transformation to integration in sensorimotor processing. *Trends in Cognitive Sciences* 19, 251–258. <https://doi.org/10.1016/j.tics.2015.03.001>
- Ho, C., Spence, C., 2007. Head orientation biases tactile localization. *Brain Research* 1144, 136–141. <https://doi.org/10.1016/j.brainres.2007.01.091>
- Johansson, R.S., Flanagan, J.R., 2009. Coding and use of tactile signals from the fingertips in object manipulation tasks. *Nat Rev Neurosci* 10, 345–359. <https://doi.org/10.1038/nrn2621>
- Johnson, K.O., Lamb, G.D., 1981. Neural mechanisms of spatial tactile discrimination: neural patterns evoked by braille-like dot patterns in the monkey. *The Journal of Physiology* 310, 117–144. <https://doi.org/10.1113/jphysiol.1981.sp013540>
- Johnson-Frey, S.H., 2004. The neural bases of complex tool use in humans. *Trends in Cognitive Sciences* 8, 71–78. <https://doi.org/10.1016/j.tics.2003.12.002>
- Klatzky, R.L., Lederman, S.J., 1999. Tactile roughness perception with a rigid link interposed between skin and surface. *Perception & Psychophysics* 61, 591–607. <https://doi.org/10.3758/BF03205532>
- LaMotte, R.H., 2000. Softness Discrimination With a Tool. *Journal of Neurophysiology* 83, 1777–1786. <https://doi.org/10.1152/jn.2000.83.4.1777>

- Liu, Y., Medina, J., 2021. Visuoproprioceptive conflict in hand position biases tactile localization on the hand surface. *Journal of Experimental Psychology: Human Perception and Performance* 47, 344–356. <https://doi.org/10.1037/xhp0000893>
- Lloyd, D.M., Shore, D.I., Spence, C., Calvert, G.A., 2003. Multisensory representation of limb position in human premotor cortex. *Nature Neuroscience* 6, 17–18. <https://doi.org/10.1038/nn991>
- Longo, M.R., Mancini, F., Haggard, P., 2015. Implicit body representations and tactile spatial remapping. *Acta Psychologica* 160, 77–87. <https://doi.org/10.1016/j.actpsy.2015.07.002>
- Mancini, F., Longo, M.R., Iannetti, G.D., Haggard, P., 2011. A supramodal representation of the body surface. *Neuropsychologia* 49, 1194–1201. <https://doi.org/10.1016/j.neuropsychologia.2010.12.040>
- Maravita, A., Spence, C., Kennett, S., Driver, J., 2002. Tool-use changes multimodal spatial interactions between vision and touch in normal humans. *Cognition* 83, B25–B34. [https://doi.org/10.1016/S0010-0277\(02\)00003-3](https://doi.org/10.1016/S0010-0277(02)00003-3)
- Maris, E., Oostenveld, R., 2007. Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods* 164, 177–190. <https://doi.org/10.1016/j.jneumeth.2007.03.024>
- Martel, M., Cardinali, L., Bertonati, G., Jouffrais, C., Finos, L., Farnè, A., Roy, A.C., 2019. Somatosensory-guided tool use modifies arm representation for action. *Sci Rep* 9, 5517. <https://doi.org/10.1038/s41598-019-41928-1>
- Miller, K.J., Schalk, G., Fetz, E.E., den Nijs, M., Ojemann, J.G., Rao, R.P.N., 2010. Cortical activity during motor execution, motor imagery, and imagery-based online feedback. *Proceedings of the National Academy of Sciences* 107, 4430–4435. <https://doi.org/10.1073/pnas.0913697107>
- Miller, L.E., Cawley-Bennett, A., Longo, M.R., Saygin, A.P., 2017a. The recalibration of tactile perception during tool use is body-part specific. *Experimental Brain Research* 235, 2917–2926. <https://doi.org/10.1007/s00221-017-5028-y>
- Miller, L.E., Fabio, C., Ravenda, V., Bahmad, S., Koun, E., Salemme, R., Luauté, J., Bolognini, N., Hayward, V., Farnè, A., 2019. Somatosensory Cortex Efficiently Processes Touch Located Beyond the Body. *Current Biology* S0960982219313831. <https://doi.org/10.1016/j.cub.2019.10.043>
- Miller, L.E., Fabio, C., van Beers, R., Farnè, A., Medendorp, W.P., 2020. A neural surveyor in somatosensory cortex (preprint). *Neuroscience*. <https://doi.org/10.1101/2020.06.26.173419>
- Miller, L.E., Longo, M.R., Saygin, A.P., 2017b. Visual illusion of tool use recalibrates tactile perception. *Cognition* 162, 32–40. <https://doi.org/10.1016/j.cognition.2017.01.022>
- Miller, L.E., Longo, M.R., Saygin, A.P., 2014. Tool morphology constrains the effects of tool use on body representations. *Journal of Experimental Psychology: Human Perception and Performance* 40, 2143–2153. <https://doi.org/10.1037/a0037777>
- Miller, L.E., Montroni, L., Koun, E., Salemme, R., Hayward, V., Farnè, A., 2018. Sensing with tools extends somatosensory processing beyond the body. *Nature* 561, 239–242. <https://doi.org/10.1038/s41586-018-0460-0>
- Nakata, H., Sakamoto, K., Otsuka, A., Yumoto, M., Kakigi, R., 2013. Cortical rhythm of No-go processing in humans: An MEG study. *Clinical Neurophysiology* 124, 273–282. <https://doi.org/10.1016/j.clinph.2012.06.019>

- Neuper, C., Wörtz, M., Pfurtscheller, G., 2006. ERD/ERS patterns reflecting sensorimotor activation and deactivation, in: *Progress in Brain Research*. Elsevier, pp. 211–222. [https://doi.org/10.1016/S0079-6123\(06\)59014-4](https://doi.org/10.1016/S0079-6123(06)59014-4)
- Nierula, B., Hohlefeld, F.U., Curio, G., Nikulin, V.V., 2013. No somatotopy of sensorimotor alpha-oscillation responses to differential finger stimulation. *NeuroImage* 76, 294–303. <https://doi.org/10.1016/j.neuroimage.2013.03.025>
- Oostenveld, R., Praamstra, P., 2001. The five percent electrode system for high-resolution EEG and ERP measurements. *Clinical Neurophysiology* 7.
- Ossandón, J.P., König, P., Heed, T., 2020. No Evidence for a Role of Spatially Modulated α -Band Activity in Tactile Remapping and Short-Latency, Overt Orienting Behavior. *J. Neurosci.* 40, 9088–9102. <https://doi.org/10.1523/JNEUROSCI.0581-19.2020>
- Parrish, C.S., 1897. Localisation of Cutaneous Impressions by Arm Movement without Pressure upon the Skin. *The American Journal of Psychology* 8, 250. <https://doi.org/10.2307/1410941>
- Pascual-Marqui, R.D., 2002. Standardized low resolution brain electromagnetic. *Clinical Pharmacology* 16.
- Peck, A.J., Jeffers, R.G., Carello, C., Turvey, M.T., 1996. Haptically Perceiving the Length of One Rod by Means of Another. *Ecological Psychology* 8, 237–258. https://doi.org/10.1207/s15326969eco0803_3
- Penfield, W., Boldrey, E., 1937. SOMATIC MOTOR AND SENSORY REPRESENTATION IN THE CEREBRAL CORTEX OF MAN AS STUDIED BY ELECTRICAL STIMULATION. *Brain* 60, 389–443. <https://doi.org/10.1093/brain/60.4.389>
- Pfurtscheller, G., Neuper, C., 1997. Motor imagery activates primary sensorimotor area in humans. *Neuroscience Letters* 239, 65–68. [https://doi.org/10.1016/S0304-3940\(97\)00889-6](https://doi.org/10.1016/S0304-3940(97)00889-6)
- Pfurtscheller, G., Woertz, M., Krausz, G., Neuper, C., 2001. Distinction of different fingers by the frequency of stimulus induced beta oscillations in the human EEG. *Neuroscience Letters* 4.
- Pisoni, A., Romero Lauro, L.J., Vergallito, A., Maddaluno, O., Bolognini, N., 2018. Cortical dynamics underpinning the self-other distinction of touch: A TMS-EEG study. *NeuroImage* 178, 475–484. <https://doi.org/10.1016/j.neuroimage.2018.05.078>
- Reed, C.L., Klatzky, R.L., Halgren, E., 2005. What vs. where in touch: an fMRI study. *NeuroImage* 25, 718–726. <https://doi.org/10.1016/j.neuroimage.2004.11.044>
- Rihs, T.A., Michel, C.M., Thut, G., 2007. Mechanisms of selective inhibition in visual spatial attention are indexed by β -band EEG synchronization. *Eur J Neurosci* 25, 603–610. <https://doi.org/10.1111/j.1460-9568.2007.05278.x>
- Ruzzoli, M., Soto-Faraco, S., 2014. Alpha Stimulation of the Human Parietal Cortex Attunes Tactile Perception to External Space. *Current Biology* 24, 329–332. <https://doi.org/10.1016/j.cub.2013.12.029>
- Saal, H.P., Delhaye, B.P., Rayhaun, B.C., Bensmaia, S.J., 2017. Simulating tactile signals from the whole hand with millisecond precision. *Proceedings of the National Academy of Sciences* 114, E5693–E5702. <https://doi.org/10.1073/pnas.1704856114>
- Sadibolova, R., Tamè, L., Longo, M.R., 2018. More than skin-deep: Integration of skin-based and musculoskeletal reference frames in localization of touch. *Journal of Experimental Psychology: Human Perception and Performance* 44, 1672–1682. <https://doi.org/10.1037/xhp0000562>

- Salenius, S., Schnitzler, A., Salmelin, R., Jousmäki, V., Hari, R., 1997. Modulation of Human Cortical Rolandic Rhythms during Natural Sensorimotor Tasks. *NeuroImage* 5, 221–228. <https://doi.org/10.1006/nimg.1997.0261>
- Salmelin, R., Hari, R., 1994. Spatiotemporal characteristics of sensorimotor neuromagnetic rhythms related to thumb movement. *Neuroscience* 60, 537–550. [https://doi.org/10.1016/0306-4522\(94\)90263-1](https://doi.org/10.1016/0306-4522(94)90263-1)
- Samaha, J., Sprague, T.C., Postle, B.R., 2016. Decoding and Reconstructing the Focus of Spatial Attention from the Topography of Alpha-band Oscillations. *Journal of Cognitive Neuroscience* 28, 1090–1097. https://doi.org/10.1162/jocn_a_00955
- Schicke, T., Roder, B., 2006. Spatial remapping of touch: Confusion of perceived stimulus order across hand and foot. *Proceedings of the National Academy of Sciences* 103, 11808–11813. <https://doi.org/10.1073/pnas.0601486103>
- Schnitzler, A., Salmelin, R., Salenius, S., Jousmäki, V., Hari, R., 1995. Tactile information from the human hand reaches the ipsilateral primary somatosensory cortex. *Neuroscience Letters* 200, 25–28. [https://doi.org/10.1016/0304-3940\(95\)12065-C](https://doi.org/10.1016/0304-3940(95)12065-C)
- Schubert, J.T.W., Buchholz, V.N., Föcker, J., Engel, A.K., Röder, B., Heed, T., 2019. Alpha-band oscillations reflect external spatial coding for tactile stimuli in sighted, but not in congenitally blind humans. *Sci Rep* 9, 9215. <https://doi.org/10.1038/s41598-019-45634-w>
- Schubert, J.T.W., Buchholz, V.N., Föcker, J., Engel, A.K., Röder, B., Heed, T., 2015. Oscillatory activity reflects differential use of spatial reference frames by sighted and blind individuals in tactile attention. *NeuroImage* 117, 417–428. <https://doi.org/10.1016/j.neuroimage.2015.05.068>
- Schubert, J.T.W., Buchholz, V.N., Foecker, J., Engel, A.K., Roder, B., Heed, T., 2018. Alpha-band oscillations reflect external spatial coding for tactile stimuli in sighted, but not in congenitally blind humans. *bioRxiv*. <https://doi.org/10.1101/442384>
- Serino, A., Canzoneri, E., Marzolla, M., di Pellegrino, G., Magosso, E., 2015. Extending peripersonal space representation without tool-use: evidence from a combined behavioral-computational approach. *Front. Behav. Neurosci.* 9. <https://doi.org/10.3389/fnbeh.2015.00004>
- Shore, D.I., Gray, K., Spry, E., Spence, C., 2005. Spatial Modulation of Tactile Temporal-Order Judgments. *Perception* 34, 1251–1262. <https://doi.org/10.1068/p3313>
- Shore, D.I., Spry, E., Spence, C., 2002. Confusing the mind by crossing the hands. *Cognitive Brain Research* 14, 153–163. [https://doi.org/10.1016/S0926-6410\(02\)00070-8](https://doi.org/10.1016/S0926-6410(02)00070-8)
- Soto-Faraco, S., Azañón, E., 2013. Electrophysiological correlates of tactile remapping. *Neuropsychologia* 51, 1584–1594. <https://doi.org/10.1016/j.neuropsychologia.2013.04.012>
- Sposito, A., Bolognini, N., Vallar, G., Maravita, A., 2012. Extension of perceived arm length following tool-use: Clues to plasticity of body metrics. *Neuropsychologia* 50, 2187–2194. <https://doi.org/10.1016/j.neuropsychologia.2012.05.022>
- Stevens, J.C., 1992. Aging and Spatial Acuity of Touch. *Journal of Gerontology* 47, P35–P40. <https://doi.org/10.1093/geronj/47.1.P35>

- Tadel, F., Baillet, S., Mosher, J.C., Pantazis, D., Leahy, R.M., 2011. Brainstorm: A User-Friendly Application for MEG/EEG Analysis. *Computational Intelligence and Neuroscience* 2011, 1–13. <https://doi.org/10.1155/2011/879716>
- Takahashi, T., Kansaku, K., Wada, M., Shibuya, S., Kitazawa, S., 2013. Neural Correlates of Tactile Temporal-Order Judgment in Humans: an fMRI Study. *Cerebral Cortex* 23, 1952–1964. <https://doi.org/10.1093/cercor/bhs179>
- Tamè, L., Pavani, F., Braun, C., Salemme, R., Farnè, A., Reilly, K.T., 2015. Somatotopy and temporal dynamics of sensorimotor interactions: evidence from double afferent inhibition. *Eur J Neurosci* 41, 1459–1465. <https://doi.org/10.1111/ejn.12890>
- Vallar, G., Maravita, A., 2009. Personal and Extrapersonal Spatial Perception, in: Berntson, G.G., Cacioppo, J.T. (Eds.), *Handbook of Neuroscience for the Behavioral Sciences*. John Wiley & Sons, Inc., Hoboken, NJ, USA, p. neubb001016. <https://doi.org/10.1002/9780470478509.neubb001016>
- Vaught, G.M., Simpson, W.E., Ryder, R., 1968. Feeling with a stick. *Perceptual and Motor Skills* 26, 848–848. <https://doi.org/10.2466/pms.1968.26.3.848>
- Wada, M., Takano, K., Ikegami, S., Ora, H., Spence, C., Kansaku, K., 2012. Spatio-Temporal Updating in the Left Posterior Parietal Cortex. *PLoS ONE* 7, e39800. <https://doi.org/10.1371/journal.pone.0039800>
- Weber, E., 1846. Tastsinn und Gemeingefühl [On the sense of touch and ‘common sensibility’]. E. H. Weber on the Tactile Senses, Earlbaum, Taylor & Francis, Hove, UK.
- Yamamoto, S., Kitazawa, S., 2001. Sensation at the tips of invisible tools. *Nature neuroscience* 4, 979–980.
- Yamamoto, S., Moizumi, S., Kitazawa, S., 2005. Referral of Tactile Sensation to the Tips of L-Shaped Sticks. *Journal of Neurophysiology* 93, 2856–2863. <https://doi.org/10.1152/jn.01015.2004>
- Yoshioka, T., Bensmaïa, S.J., Craig, J.C., Hsiao, S.S., 2007. Texture perception through direct and indirect touch: An analysis of perceptual space for tactile textures in two modes of exploration. *Somatosensory & Motor Research* 24, 53–70. <https://doi.org/10.1080/08990220701318163>

Study 3:

Alpha oscillations reflect similar mapping mechanisms for localizing touch on hands and tools

Abbreviated title: *Similar tactile mapping processes for body and tools*

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Summary

Numerous studies have suggested that tools become incorporated into a representation of our body. A prominent hypothesis suggests that our brain re-uses body-based neural processing to swiftly adapt to the use of tools. However, little is known about how this is implemented at the neural level. Here we used the ability to localize touch on both tools and body parts as a case study to fill this gap. It was recently shown by Miller et al. (2018) that participants can localize tactile information received along the entire surface of a hand-held tool as accurately as on their own body. Previous EEG studies have found that the alpha (7-14 Hz) and beta (15-30 Hz) frequency bands are involved in the spatial processing of touch on the body in distinct reference frames. Alpha activity reflects sensorimotor transformations that map touch in external spatial coordinates, whereas beta activity reflects the mapping of touch in skin-based coordinates. In order to determine whether the brain re-uses tactile-localization mechanisms when a tool is touched we investigated if the oscillatory mechanisms used when localizing touch on a tool are similar to the ones used for localizing touch on the body. We aimed at comparing the reference frame-based neural processing—as reflected in alpha- and beta-band oscillatory activity—during body-based and tool-extended tactile localization.

To this aim, we used EEG to record oscillatory activity while participants performed a cued tactile localization task where contact was applied to either hands or the tips of hand-held rods. We manipulated posture, using the crossed posture where external and anatomical location of touch don't match anymore. Posture of the hands/tool-tips was uncrossed or crossed at participants' body midline, which allowed us to disentangle brain responses related to these different coordinate systems. We found that the scalp distributions of alpha and beta modulation were nearly identical when touch was on the body or on a tool. Only alpha oscillations were modulated by posture, suggesting that they are related to processing of touch in external spatial coordinates. Interestingly, the modulation was identical for mapping touch on the hand or on a tool. Furthermore, source reconstruction of this space-related alpha modulation revealed a similar bilateral network of parieto-occipital regions involved in mapping touch on tools and on hands. These regions have previously been implicated in reference frame transformations during tactile localization.

In conclusion, we found that the brain uses similar oscillatory mechanisms for mapping touch on a hand-held tool and on the body. These results are in line with previous work from our and support the idea of that neural processes devoted to body-related information are being re-used for tool-use. Furthermore, alpha-band modulation followed the position of touch into external space. This is thus the first neural evidence that tactile localization on a hand-held tool involves the use of external spatial coordinates.

Abstract

Numerous studies have suggested that tools become incorporated into a representation of our body. A prominent hypothesis suggests that our brain re-uses body-based computations when we use tools. However, little is known about how this is implemented at the neural level. Here we used the ability to localize touch on both tools and body parts as a case study to fill this gap. Neural oscillations in the alpha (8-13 Hz) and beta (15-25 Hz) frequency bands are involved in mapping touch on the body in distinct reference frames. Alpha activity reflects the mapping of touch in external coordinates, whereas beta activity reflects the mapping of touch in skin-centered coordinates. Here, we aimed at pinpointing the role of these oscillations during tool-extended sensing. We recorded participants' oscillatory activity while tactile stimuli were applied to either hands or the tips of hand-held rods. The posture of the hands/tool-tips was uncrossed or crossed at participants' body midline in order for us to disentangle brain responses related to different coordinate systems. We found that alpha-band activity was modulated similarly across postures when localizing touch on hands and on tools, reflecting the position of touch in external space. Source reconstruction also indicated a similar network of cortical regions involved for tools and hands. Our findings strongly suggest that the brain uses similar oscillatory mechanisms for mapping touch on the body and tools, supporting the idea of neural processes being repurposed for tool-use.

Significance statement

Tool use is one of the defining traits of humankind. Tools allow us to explore our environment and expand our sensorimotor abilities. A prominent hypothesis suggests that our brain re-uses body-based neural processing to swiftly adapt to the use of tools. However, little is known about how this is implemented at the neural level. In the present study we used the ability to map touch on both tools and body parts as a case study to fill this gap. We found that the brain uses similar oscillatory mechanisms for mapping touch on a hand-held tool and on the body. These results provide novel and compelling support to the idea that neural processes devoted to body-related information are repurposed for tool-use.

Introduction

Tools allow us to extend our physical body, therefore amplifying our sensorimotor abilities. It is theorized that tools become incorporated into a neural representation of our body (Head and Holmes, 1911; Maravita and Iriki, 2004; Martel et al., 2016a) as tool use notably alters motor kinematics (Cardinali et al., 2009a; L. Cardinali et al., 2016), representation of body metrics (Cardinali et al., 2011; L. Cardinali et al., 2016; Miller et al., 2014; Sposito et al., 2012), and representation of space around the upper limb (Berti and Frassinetti, 2000; Farnè and Làdavas, 2000). Alongside these studies, Miller et al. (2018) recently found that participants can accurately localize where an object touches the surface of a hand-held tool, thus using the tool as a sensory extension of their body. These behavioral effects prompted the hypothesis that the brain repurposes body-based neural processing to control and sense with a tool. However, evidence for this hypothesis is currently limited (Fabio et al., 2022; A Iriki et al., 1996; Miller et al., 2019a). Here we used tool-extended tactile localization as a case study to investigate the brain repurposing of body-based neural computations during tool use.

Comparing touch localization on hands and tools requires a firm grasp on the underlying neural computations that map touch on the body (Miller et al., 2022). At the level of neural oscillations, touch on the skin leads to a desynchronization of power in two main low-frequency bands: alpha (8-13 Hz) (Cheyne et al., 2003; S. Haegens et al., 2014; Neuper et al., 2006; Salenius et al., 1997; Salmelin and Hari, 1994) and beta (15-25 Hz) (Neuper et al., 2006; Pfurtscheller et al., 2001; Salmelin and Hari, 1994). These frequency bands have been implicated in tactile localization within two types of computational spatial codes (Heed et al., 2015a): Beta activity reflects encoding in anatomical coordinates (Buchholz et al., 2013, 2011; Schubert et al., 2019, 2015), which correspond to the position of touch on the skin; Alpha activity reflects encoding in external coordinates (Buchholz et al., 2013, 2011; Ruzzoli and Soto-Faraco, 2014; Schubert et al., 2019, 2015), which correspond to the position of the touch in the egocentric space around the body.

Typically, the processes behind these spatial codes have been disambiguated by crossing the hands over the body midline: When crossed, the right hand (anatomical coordinates) is located in the left hemisphere (external coordinates), thus creating left-right conflict that affects behavioral performance across several localization tasks (Heed and Azañón, 2014; Shore et al., 2002; Shinya Yamamoto and Kitazawa, 2001b). This conflict is often emphasized by attention cueing paradigms, as mapping touch using external coordinates may require orienting spatial attention (Eardley and van Velzen, 2011b; Heed and Röder, 2010; Schubert et al., 2019).

There is reason to believe that localizing touch on a tool may involve similar neurocomputational mechanisms. At a behavioral level, touch on hand-held tools can be localized

extremely accurately (Luke E. Miller et al., 2018a) and is similarly impaired when the tips of the tools are crossed over the midline while the hands remain uncrossed (Yamamoto et al., 2005; Shinya Yamamoto and Kitazawa, 2001b). Our previous EEG study showed the involvement of alpha activity in tool-extended tactile localization with sources in a network of parieto-frontal areas involved in tactile and spatial processing (Fabio et al., 2022). However, the nature of the reference frame(s) underlying the observed alpha activity remains unclear.

To fill this gap, here we investigated whether the oscillatory mechanisms involved in localizing touch on the body are repurposed when localizing touch on a tool. To determine this, we characterized and compared the reference frames reflected in alpha- and beta-band oscillatory activity, during body-based and tool-extended tactile localization. We used EEG to record oscillatory activity of participants performing a cued tactile localization task on their hands and on hand-held tools while manipulating their posture (crossed vs uncrossed). When tool-tips were crossed over the midline, the hands holding the tools were always uncrossed, allowing us to directly compare tool-based and body-based reference frames.

Materials and methods

Participants

20 right-handed participants (mean age: 24.8 years; range: 18-32 years, 10 males), free of any known sensory, perceptual, or motor disorders, volunteered to participate in the experiment. We chose this sample size in accordance to previous studies about somatosensory oscillations (Haegens et al., 2011; Schubert et al., 2015; Fabio et al., 2022). The experiment was performed in accordance with the ethical standards laid down in the Declaration of Helsinki (2013) and all participants provided written informed consent according to national guidelines of the ethics committee (CPP SUD EST IV RCN: 2010-A01180-39).

Setup

The experiment was divided in two sessions wherein touch was delivered to either the participants' hands (Hand condition) or to hand-held wooden rods (Tool condition); the setup was similar for both conditions. Throughout the experiment, participants sat in an adjustable chair in front of a table. In the Hand condition, they placed their forearm on the table, positioned either in an uncrossed or in a crossed posture (alternated blockwise, order counterbalanced across participants) with each index finger resting on a support at the edge of the table (Fig. 1A). In the Tool condition, participants' arms were placed on adjustable armrests and they hold a 50cm long wooden rod in each hand, either in an

uncrossed or in a crossed posture (alternated blockwise, order counterbalanced across participants). Notably, in the Tool condition, only the tool-tips -but not the hands-crossed their body midline (Fig. 1B)—the overall posture of the upper limb was relatively unchanged when tools were crossed or uncrossed. Depending on the condition, the index fingertips or the tip of each tool rested on a foamed stabilizing support at the edge of the table. When crossed, the rods were raised one above the other in order to avoid their contact during stimulation.

During the localization task, participants fixated on a central cross (2 cm wide) that was displayed on a 16" monitor in front of them and aligned with their body midline. Two solenoids (Mecalectro 8.19-.AB.83; 24 V, supplied with 36 W) were used to contact either index fingers or tool-tips, both with a disc surface of 4 cm to ensure uniform and consistent contact. Behavioral responses were made with a foot pedal (Leptron Footswitch 548561) that was placed underneath the left foot in half of the experiment, and under the right in the other half (alternated condition-wise, order counterbalanced across participants).

We took two approaches to mitigate the presence of auditory feedback from the solenoids. First, noise-cancelling earphones (Bose QuietComfort 20) playing white noise were used to mask the sound created by the solenoids. Further, to avoid any remaining auditory cue, each solenoid had another (decoy) solenoid placed on the opposite side, not in contact with the participants' hands or tools, that were both activated synchronously. All solenoids were mounted on adjustable tripods. Visual feedback was prevented by covering the table with a white cardboard.

Experimental paradigm

Participants performed a tactile spatial discrimination task divided in two sessions depending on the surface stimulated (Hand or Tool). In this task, participants were cued to pay attention to one side of external space. They then had to detect a deviant stimulus (double tap) presented to a hand/tool in this cued side, while ignoring stimuli in the uncued side of space. Importantly, posture was manipulated to disentangle the involvement of different reference frame transformations. Each participant completed both sessions of the experiment on separate days (counterbalanced). Each session started with a practice block of 42 trials in both postures (Uncrossed and Crossed) to ensure they correctly understood and complied with task instructions.

At the beginning of each trial the central cross blinked to indicate the start of the trial. Then one side of the cross briefly turned blue (for 50 ms) to indicate which side of space (left or right, equal probability) participants had to attend to (Fig. 1C). After a variable delay (between 1000–1500 ms; randomly chosen from a uniform distribution), tactile stimulation was applied on participants' right or left finger (Hand session) or on the tip of the right or left rod (Tool session). Note that this was

independent of the cued side. Tactile stimuli were either frequent standard stimuli (solenoid raised once for 50 ms, including rise time and surface contact; probability of 0.75), or rare deviant stimuli (solenoid raised twice in a row for 50 ms separated by a 75 ms gap; probability of 0.25) presented with an equal probability in a random sequence to the left and the right. Participants had to respond as fast and accurately as possible using the foot pedal to rare tactile deviants presented to the cued side (“targets”, probability of 0.125), and to ignore standard stimuli at the attended side, as well as all stimuli presented to the other side. The experiment consisted of two sessions of 10 blocks, half Crossed, half Uncrossed. Each block included 60 standard trials and 20 deviant trials. The analysis included only trials in which standard stimuli were presented and in which, accordingly, no response was required, for a total of 600 trials per sessions. Participants complied with instructions, as evidenced by their high accuracy in each posture and for both surfaces (all>96%).

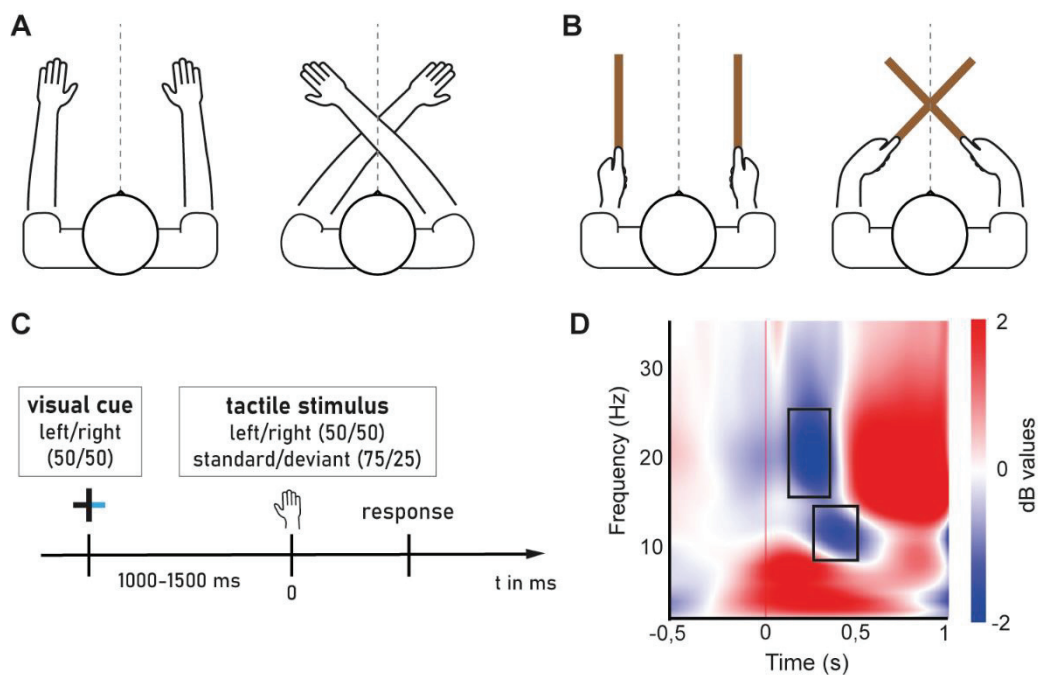


Figure 1. Experimental setup and paradigm

Participants (n=20) performed a tactile detection task for touches applied on two Surfaces: (A) when applied on Hands, participants hold their hands either in an Uncrossed posture (left) or a Crossed posture (right). (B) when applied on Tools, participants hold tools either in an Uncrossed posture (left) or a Crossed posture (right) where only the tool-tips crossed over the body midline (gray dotted line). (C) Trial structure of the tactile discrimination task. Tactile stimulation corresponds to the time zero. (D) Total oscillatory activity of the post-stimulation period over contralateral somatosensory cortex (electrode C3). Modulations are displayed as compared relative to baseline (-500 to -100 ms). Selected time windows for analysis are represented by grey rectangle for each frequency band: 250-500 ms for alpha and 150-350 ms for beta.

EEG recording

EEG data were recorded continuously using a 65 channel ActiCap system (Brain Products). Horizontal and vertical electro-oculograms (EOGs) were recorded using electrodes placed below the left eye, and near the outer canthi of the right eye. Impedance of all electrodes was kept at $<20\text{ k}\Omega$. FCz served as the online reference. EEG and EOG signals were low-pass filtered online at 0.1 Hz, sampled at 2500 Hz, and then saved to disk. Stimulus presentation and behavioral response collection were performed using MatLab on the experimental control computer, which was synchronized and communicated with the EEG data recording system. The trial events were sent to the EEG data recording system via a parallel port.

Pre-processing of the EEG data

EEG signals were preprocessed using the EEGLab Toolbox (Delorme and Makeig, 2004). The preprocessing steps for each participant were as follows: for each session, participants' five blocks in uncrossed posture, followed by their five blocks in crossed posture, were appended into a single dataset. The signal was resampled at 500 Hz and high-pass filtered at 0.1 Hz. Faulty channels were interpolated using a spherical spline. We then epoched data into a time window of 3.5 seconds, 1 second before and 2.5 seconds after the cue and baseline corrected using the period from -500 ms to -100 ms before the cue as baseline. Next, we removed signal artifacts with two steps: first, we removed eye blinks and horizontal eye movements from the signal using independent components analysis (ICA (Delorme and Makeig, 2004)) and a semi-automated algorithm called SASICA (Chaumon et al., 2015). We excluded every trial when participants made a response (whether it was a correct or an incorrect answer) or accidentally released the foot pedal, so that we only kept trials free of any motor activity. We re-epoched the data around the tactile stimulation (time zero), from -1.5 second before to 1 second after, leading to 2.5s epochs, and used the period from -500 ms to -100 ms before the hit for baseline correction. We then manually rejected trials that were contaminated by muscle artefacts or other forms of signal noise. In total, this led to a mean exclusion of 52.6 trials per participant (range: 2–205). Next, we used the EEGLab function *pop_reref* to add FCz (the online reference) back into the dataset and re-referenced the data to the average voltage across the scalp. Finally, for a better signal-to-noise ratio, we swapped the electrodes order of all the trials where the left hand or tool has been touched, so that all trials would now be in reference to the right hand or tool being touched (Buchholz et al., 2013; Schubert et al., 2019).

Time-frequency decomposition

Time-frequency decomposition was performed using the open source toolbox Brainstorm (Tadel et al., 2011) in Matlab. The raw signal of each epoch was decomposed into frequencies between 1–35 Hz (linearly spaced) using Complex Morlet wavelets with a central frequency of 1 Hz and a full-width half maximum of 3 s. These parameters were chosen to ensure that our time-frequency decomposition had good spectral and temporal resolution within the chosen frequency range. Signal was then normalized in decibel (dB) to its ratio with the respective channel mean power during a baseline period ranging from -500 to -100 ms before tactile stimulation, which ensured that no post-stimulus activity contributed to the baseline normalization.

EEG data analysis

Alpha- and beta-band activity were defined here as 8–13 Hz and 15–25 Hz respectively. Based on the observation of the oscillatory temporal dynamics during the time period after the hit (collapsed across all participants and conditions, see Figure 1D), we selected two time windows for analysis for each of our frequency band of interest: 150-350 ms for beta-band, and 250-500 ms for the alpha-band. This is a bias-free method for choosing time windows upon which running the analysis (Cohen, 2014).

Our experimental design had three factors that could be used in our analysis: Surface (Hand or Tool), Posture (Uncrossed or Crossed) and Attention (Unattended or Attended). Our initial analysis included all factors. The main effect of each factor was calculated by averaging the power of each frequency band, as well as the time points within the given time window before comparing the scalp topography of the relevant levels (e.g. Uncrossed vs. Crossed for main effect of Posture) using a cluster-based permutation test ((Maris and Oostenveld, 2007); two-tailed, cluster-level significance threshold of 0.05 and 1000 permutations run). Interaction effects were assessed via subtraction across conditions. For example, take the three-way interaction between Attention, Posture, and Surface. We first calculated the differences between unattended and attended stimulation for each posture separated by surface (e.g. Hand crossed unattended – Hand crossed attended). We then subtracted these differences for each surface before comparing them for each frequency band (average power) in their respective time windows (average time points; CBPT, same parameters). For all two-way interactions (e.g. Attention x Posture) we first collapsed across the unused condition (Surface); we then calculated the difference between levels of the first factor (Unattended – Attended) for each levels of the second factor (Uncrossed, Crossed). In a secondary analysis, we analyzed both surfaces separately.

Source reconstruction

We followed up significant interactions with source reconstruction for each epoch to estimate which brain regions were involved. This was done using the open source toolbox Brainstorm (Tadel et al., 2011). First, a head model was computed using OpenMEEG BEM model (Gramfort et al., 2010). A noise covariance matrix for every participant was computed over a baseline time window of -500 to -100 ms before stimulation. Sources were then estimated using the Standardized low resolution brain electromagnetic tomography (sLORETA(Pascual-Marqui, 2002)) approach with unconstrained dipole orientations across the surface. We then performed time-frequency decomposition on the source files to localize significant power modulations in the alpha-band. The signal at each vertex was decomposed into the mean of frequencies going from 8 to 13 Hz using Complex Morlet wavelets with a central frequency of 1 Hz and a full-width half maximum of 3 s. The signal was then normalized in decibel (dB) to its ratio with the respective channel mean power during a baseline period ranging from -500 to -100 ms before tactile stimulation.

The interaction between Attention and Posture was assessed in a similar manner as previously described. We calculated the difference in alpha power between unattended and attended stimulation for each posture and compared them in the chosen time windows (average time points) using Cluster-based permutation ((Maris and Oostenveld, 2007); two-tailed, cluster-level significance threshold of 0.01 and 1000 permutations run).

Results

Similar oscillatory correlates for tactile localization on hands and tools

The present study investigated whether there were different oscillatory correlates for localizing touch on hands and on tools, with a specific focus on the external remapping of touch. Therefore, the contrasts containing the factor Surface (Hand, Tool) are of particular interest for us. This includes one three-way interaction (Attention x Posture x Surface), two two-way interactions (Attention x Surface, Posture x Surface) and a main effect of Surface. We therefore first determined whether there were statistically significant differences in the oscillatory power of alpha and beta for these contrasts. Significant differences in these contrasts would indicate that tactile-localization modulated oscillatory power differently between the hand and the tool.

Using a cluster-based permutation test (CBPT, α -range = 0.05), we found no significant interactions or main effects with the factor Surface in either the alpha or beta-band (Table 1, CBPT: $p > 0.05$).

Contrasts	Frequency band	p-value
Posture	Alpha	0.316
	Beta	/
Attention	Alpha	0.012
	Beta	0.046
Surface	Alpha	0.276 & 0.346
	Beta	0.164 & 0.359
Posture x Surface	Alpha	/
	Beta	/
Attention x Surface	Alpha	/
	Beta	0.342
Attention x Posture	Alpha	0.006 & 0.049
	Beta	0.194
Attention x Posture x Surface	Alpha	0.242
	Beta	/

Table 1. Contrasts performed on scalp topographies of mean oscillatory power; CBPT, p-value of all clusters found. '/' indicates no cluster with a p-value below 1.

Spatial attention modulates tactile processing according to posture

Given the lack of any statistical differences between oscillations while localizing touch on hands and tools, we next investigated the surface-independent effects of posture on oscillations. A significant effect containing the factor Posture (uncrossed vs. crossed) would suggest processing related to an external reference frame. We did not observe a general main effect of Posture for alpha or beta power (Table 1, CBPT: $p > 0.05$).

We did, however, observe a significant interaction effect between Attention and Posture for power in the alpha band in both hemispheres (left: $p\text{-value}=0.049$ & right: $p\text{-value}=0.006$). The two significant clusters were localized above parieto-occipital channels in their respective hemisphere (Fig. 2A). As can be seen in Figure 2A, touch led to widespread alpha desynchronization across centro-posterior channels, which was increased when attention was directed to the touched side (Main effect of attention: $p < 0.05$, see Table 1). Crucially, we observed that crossing the surface (hand or tool) shifted the topographic distribution of alpha desynchronization, but did so differently for the attended and unattended conditions (lower panels of Figure 2A).

In the beta band, we observed a bilateral decrease of power over central channels that was independent of Posture. We found that the desynchronization of beta was more bilateral in the

Attended condition (Main effect of attention: $p < 0.05$, see Table 1). However, we did not find a significant interaction between Attention and Posture in the beta band (Fig. 2B) and thus do not consider this frequency band in later analyses.

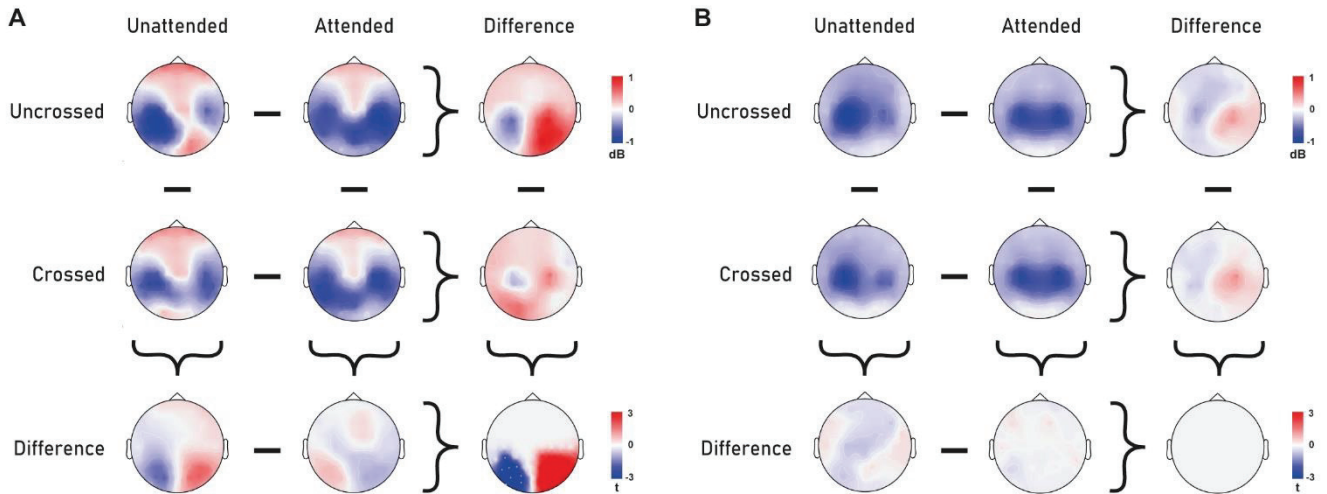


Figure 2. Alpha and beta activity after tactile stimulation

(A) Topographies of alpha-band activity (8–13 Hz, 250 to 500 ms) in uncrossed (1st row) and crossed (2nd row) posture following unattended (1st column) and attended stimuli (2nd column). Difference topographies for attention effects in uncrossed and crossed posture (3rd column), and for posture effects following attended and unattended stimuli (3rd row). Bottom-right corner: topography of the interaction between attention and posture. (B) Topographies of beta-band activity (15–25 Hz, 150 to 300 ms) in uncrossed (1st row) and crossed (2nd row) posture following unattended (1st column) and attended stimuli (2nd column). Difference topographies for attention effects in uncrossed and crossed posture (3rd column), and for posture effects following attended and unattended stimuli (3rd row). Bottom-right corner: topography of the interaction between attention and posture. Data are displayed as if stimuli always occurred on the anatomically right hand or the tool held in the right hand, so that the left hemisphere is contralateral to tactile stimulation in a skin-based reference frame, independent of posture.

Similar topography of alpha desynchronization is observed for hands and tools

We then analyzed each Surface separately, in order to further explore the localization processes for touch on hands and on tools. Visual inspection of the scalp distribution of alpha activity for each Surface reveals a striking resemblance between Hand and Tool (Fig. 3A&B). For each condition, alpha power modulation is almost identical between the two surfaces, with patterns reflecting what we observed when Surfaces were collapsed (Fig. 2A). This underscores the inference that the neural processes underlying localizing touch on each surface are similar.

We then calculated the interaction between Attention and Posture for each surface separately. We found a similar pattern of interaction between hand and tool: For stimulation on the hand, we obtained two clusters, one in each hemisphere (CBPT, left: $p=0.036$ & right: $p=0.074$). We also obtained two clusters with similar distribution when stimulation happened on the tool (CBPT, left: $p=0.195$ & right: $p=0.022$). While not all clusters reached statistical significance for each surface, their overall distribution corresponded well to the interaction between Attention and Posture observed when surfaces were collapsed (Fig. 2A) and therefore displaying a comparable pattern of reference-framed based oscillatory processing.

We next identified the cortical sources underlying this interaction effect for each surface. We observed similar sources for localization on hands and tools: The interaction effect was significant throughout sensorimotor regions, including the primary somatosensory (SI), primary motor cortices (MI) and posterior parietal regions contralateral to the stimulated hand (Fig. 3C, $p=0.046$) and tool (Fig. 3D, $p=0.024$). In the hemisphere ipsilateral to the stimulated hand, cortical sources included the same sensorimotor frontoparietal regions as well as the occipitotemporal cortex (Fig. 3C, $p=0.006$). The interaction effect in the hemisphere ipsilateral to the stimulated tool also spread over the same frontoparietal regions (Fig. 3D, $p=0.006$) but, in contrast with the hand, also included a larger portion of the temporal cortices (Fig. 3D, $p=0.019$). In general, nearly identical sources were found for mapping touch on either hands or tools.

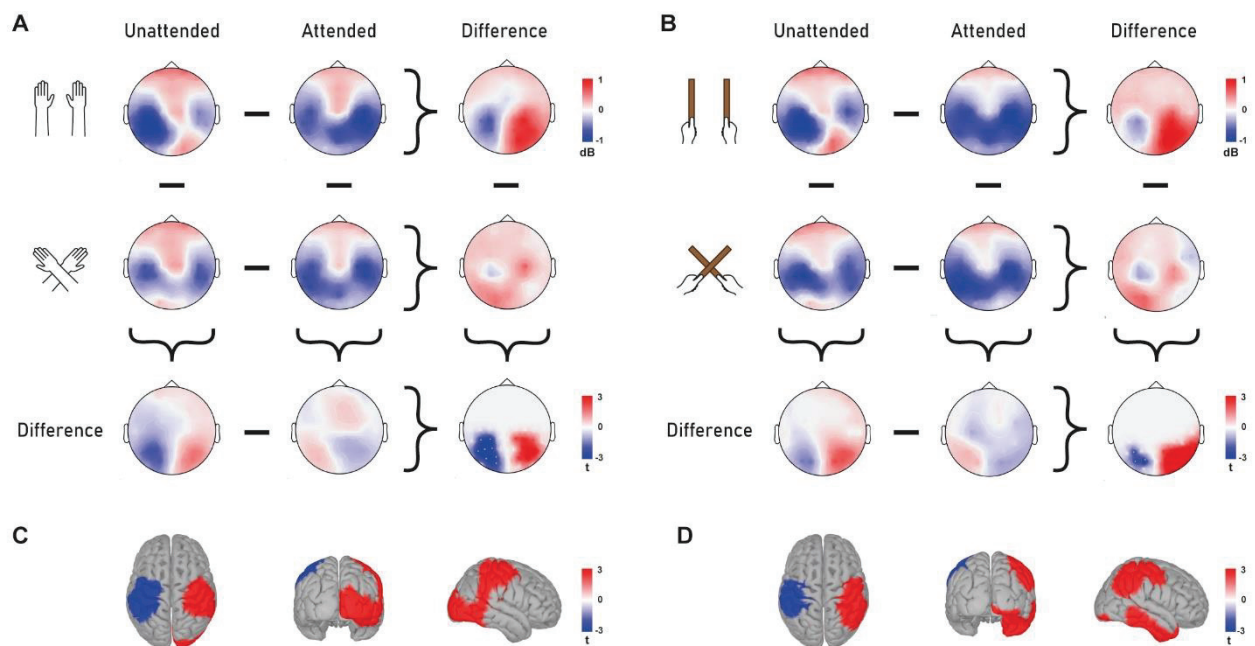


Figure 3. Alpha activity following tactile stimulation on the hand and on the tool

(A) Topographies of alpha-band activity (8–13 Hz, 250 to 500 ms) when tactile stimuli happened on the hand, with uncrossed (1st row) and crossed (2nd row) hands following attended (1st column) and unattended (2nd column) stimuli. Difference topographies for attention effects with uncrossed and crossed hands (3rd column), and for posture effects following attended and unattended stimuli (3rd row). Bottom-right corner: topography of the interaction between attention and posture. (B) Topographies of alpha-band activity (15–25 Hz, 150 to 300 ms) when tactile stimuli happened on the tool, with uncrossed (1st row) and crossed hands (2nd row) following attended (1st column) and unattended (2nd column) stimuli. Difference topographies for attention effects with uncrossed and crossed tools (3rd column), and for posture effects following attended and unattended stimuli (3rd row). Bottom-right corner: topography of the interaction between attention and posture. (C) Source reconstruction of the interaction effect between attention and posture for tactile stimulation on the hand. (D) Source reconstruction of the interaction effect between attention and posture for tactile stimulation on the tool. Data are displayed as if stimuli always occurred on the anatomically right hand or tool held in the right hand, so that the left hemisphere is contralateral to tactile stimulation in a skin-based reference frame, independent of posture.

Discussion

The present study was designed to identify the spatial codes used for localizing tactile stimuli delivered on hand-held tools and to compare them with those typically used when localizing tactile stimuli applied on hands. To this end, we used EEG in a cued tactile localization task whereby we manipulated hand and tool posture (crossed vs. uncrossed). We found a remarkable similarity of alpha and beta power modulation following touch between the two surfaces. Importantly, there was no main effect of posture for either surface, but a significant interaction between attention and posture that was selective for the alpha-band. This effect was also similarly distributed across channels for hand and tool. Furthermore, source localization of this effect for both surfaces revealed that comparable cortical networks were involved. Overall, these findings provide evidence that similar neurocomputational mechanisms are used by the brain to process touch location on the hand and on a hand-held tool. These mechanisms are reflected by alpha activity when manipulating posture, suggesting the use of external coordinates.

Touch on hands and tools rely on shared oscillatory mapping mechanisms

The main result of this study is that localizing touch on hands and tools involves similar oscillatory correlates. Indeed, not only no significant difference was found between oscillatory power of alpha and beta-band between surfaces (see Table 1), but most notably their scalp topographies were almost identical between hand and tool when observed separately (Fig. 3A&B for alpha, beta not shown). These results appear to be consistent with the centuries-old proposal of tool embodiment (Head and Holmes, 1911). Incorporation of a hand-held tool into body representation may indeed consist in repurposing the neural mechanisms that process body-related sensory information for processing information originating from the tool. Until now, neuroscientific evidence for this proposition has been scarce, since the majority of evidence comes from behavioral studies and from paradigms that only measure the effects that tool-use induced on subsequent perceptual or motor measures (Berti and Frassinetti, 2000; Cardinali et al., 2011, 2009a; L. Cardinali et al., 2016; Farnè and Làdavias, 2000; Forsberg et al., 2019; Miller et al., 2014; Sposito et al., 2012). For example, initial evidence of online repurposing comes from Iriki and colleagues' work who measured from macaque monkeys' multisensory postcentral neurons during tool-use and observed an expansion of the visual portion of their receptive field to encompass the tool (A Iriki et al., 1996). At the behavioral level, online remapping of space was observed during tool-use by Berti & Frassinetti (2000), but their neuropsychological approach could not provide indications as to which mechanisms are at play. The

present study overcame this limitation by measuring oscillatory activity underlying reference frame transformations for touch on hands and tools.

Our findings are consistent with previous studies on the neural correlates of tool sensing. We previously recorded EEG activity of human participants during a tactile localization task on a hand-held tool, therefore directly observing online tool-use. We identified a modulation of alpha power dependent of contact location (Fabio et al., 2022), suggesting that it is a signature of tool-extended tactile localization. Consistent with these previous results, here we also found that posture modulated alpha activity dependently of attention: for both surfaces, interaction effects were localized in two parieto-occipital clusters, one in each hemisphere (Fig. 3A&B). We found some differences in the distribution of interaction effect of Attention and Posture between Surfaces. The right occipital cortex was notably activated for the hand, whereas the inferior temporal cortex was activated for the tool. This could be explained by the effect of attention on actively shaping and enhancing spatial representations in the ventral visual pathway (Kay et al., 2015). Besides this difference, the source reconstruction of the alpha modulation was largely comparable between surfaces (Fig. 3 C&D). This new evidence adds to our previous ERP study (Miller et al., 2019a) on tool-extended sensing: touches on the tool and on the arm led to similar stages of cortical processing as well as similar sources involved.

In sum, the remarkable similarity that we found for oscillatory processes for tactile localization on the hand and on the tool suggests that in order to localize a contact happening on a hand-held tool, the human brain repurposes neural mechanisms dedicated to body-related processes to perform the same function with a tool.

Alpha rhythm reflects external spatial coding for touch on hands and tools

Crossing limbs is a well-established method to tease apart localizing processes in external and skin-based coordinates. In this respect, previous electrophysiological studies have linked alpha oscillations to a use of external coordinates and beta to skin-based coordinates (Buchholz et al., 2013, 2011; Ruzzoli and Soto-Faraco, 2014; Schubert et al., 2019). Here, we manipulated hands and tools posture to characterize and compare the cortical oscillations reflecting the crossing effects emerging from hands and tools. This is especially of note for the tool, since only the tool-tips crossed the body midline while the hands stayed in their respective hemisphere (see Fig. 1A). Therefore, any effect observed for crossing when touch is on the tool surface would reflect the remapping of touch on the tool, not the hands.

Consistent with previous findings, we observed that modulation of alpha activity following posture was dependent on attention, which wasn't the case for beta, supporting the involvement of

the alpha band in external processing. Crucially, this modulation of the alpha activity was independent of whether touch localization processes concerned the hands or the tools, as exemplified in the near-identical scalp topographies and significant posterior clusters for both surfaces (Fig. 3A&B). Our previous study (Fabio et al., 2022) also found an involvement of alpha oscillations in the encoding of touch location on tools. While this suggested the encoding of an external spatial code, the paradigm we used did not manipulate posture and was therefore equivocal in these regards. However, the present results indeed support the proposition made in Fabio et al. (2022) that touch on a tool is primarily coded in an external reference frame.

Furthermore, encoding touch localization in external coordinates on the hand and on the tool involves a similar cortical network. Source reconstruction of the alpha coding of external space identified several regions throughout the parietal and frontal cortices in both hemispheres. This included primary somatosensory and motor cortex. Importantly, the posterior parietal sources, also shared by the two surfaces, have previously been implicated in the processing of touch in external space (Avillac et al., 2005; Azañón et al., 2010b; Bremmer et al., 2001; Lloyd et al., 2003). Parietal alpha oscillatory activity indeed appears to play a crucial role in this process (Buchholz et al., 2011; Ruzzoli and Soto-Faraco, 2014; Schubert et al., 2019). To summarize, we found that alpha band indexes the spatial coding of touch in an external reference frame, this effect being independent of whether touch was localized on the hand or a hand-held tool.

Alpha-based coding of external coordinates may depend on attention

Unsurprisingly, we found attention to modulate the overall oscillatory activity of both alpha and beta bands (see Table 1; (Sauseng et al., 2005; van Ede et al., 2011, 2010)). However, it is noteworthy that posture manipulation itself wasn't sufficient to affect oscillatory activities; the modulation of alpha power following the crossing of the hands/tools was dependant on attention. This finding suggests that external spatial of touch was dependent of certain attentional processes. Alpha oscillations have indeed been implicated in tactile spatial attention (Bauer, 2006; Bauer et al., 2012; van Ede et al., 2014, 2011). Post-touch alpha oscillations may thus reflect the orienting of attention in external space (Ossandón et al., 2020).

This involvement of attentional processes in spatial coding was reflected in the scalp topographies and source localization of our interaction effect, which was mostly localized in somatosensory (Bauer et al., 2012; Mima et al., 1998) as well as posterior regions of the cortex, for the hand as well as the tool (Fig.3). This pattern of results is fitting with previous studies about the modulatory effects of attention on tactile ERP (Eimer and Forster, 2003; García-Larrea et al., 1995). In particular, Eimer et al. (2003) suggested that different spatial coordinate systems may be used by

separable attentional control processes with a posterior process operating on the basis of external spatial coordinates, whereas an anterior process is based primarily on anatomically defined spatial codes (Eimer et al., 2003). Since crossing the hands (and hand-held tools) mainly modulate the external coordinates of tactile processing, our tactile spatial localization task likely involved spatial attentional processes taking place in external coordinates. Along these lines, using a similar experimental paradigm, Yue et al. (2009) also found that ERPs to tactile stimuli presented at the tips of tools were modulated by spatial attention (Yue et al., 2009).

To conclude, we found that the brain uses similar oscillatory mechanisms for mapping touch on a hand-held tool and on the body. These results are in line with previous work and support the idea of that neural processes devoted to body-related information are being re-used for tool-use. Furthermore, alpha-band modulation followed the position of touch into external space. This is thus the first neural evidence that tactile localization on a hand-held tool involves the use of external spatial coordinates.

References

- Avillac M, Denève S, Olivier E, Pouget A, Duhamel J-R (2005) Reference frames for representing visual and tactile locations in parietal cortex. *Nature Neuroscience* 8:941–949.
- Azañón E, Longo MR, Soto-Faraco S, Haggard P (2010) The Posterior Parietal Cortex Remaps Touch into External Space. *Current Biology* 20:1304–1309.
- Bauer M (2006) Tactile Spatial Attention Enhances Gamma-Band Activity in Somatosensory Cortex and Reduces Low-Frequency Activity in Parieto-Occipital Areas. *Journal of Neuroscience* 26:490–501.
- Bauer M, Kennett S, Driver J (2012) Attentional selection of location and modality in vision and touch modulates low-frequency activity in associated sensory cortices. *Journal of Neurophysiology* 107:2342–2351.
- Berti A, Frassinetti F (2000) When Far Becomes Near: Remapping of Space by Tool Use. *Journal of Cognitive Neuroscience* 12:415–420.
- Bremner F, Schlack A, Duhamel J-R, Graf W, Fink GR (2001) Space Coding in Primate Posterior Parietal Cortex. *NeuroImage* 14:S46–S51.
- Buchholz VN, Jensen O, Medendorp WP (2011a) Multiple Reference Frames in Cortical Oscillatory Activity during Tactile Remapping for Saccades. *Journal of Neuroscience* 31:16864–16871.

Buchholz VN, Jensen O, Medendorp WP (2011b) Multiple Reference Frames in Cortical Oscillatory Activity during Tactile Remapping for Saccades. *Journal of Neuroscience* 31:16864–16871.

Buchholz VN, Jensen O, Medendorp WP (2013) Parietal Oscillations Code Nonvisual Reach Targets Relative to Gaze and Body. *Journal of Neuroscience* 33:3492–3499.

Cardinali L, Brozzoli C, Finos L, Roy AC, Farnè A (2016) The rules of tool incorporation: Tool morpho-functional & sensori-motor constraints. *Cognition* 149:1–5.

Cardinali L, Brozzoli C, Urquizar C, Salemme R, Roy AC, Farnè A (2011) When action is not enough: Tool-use reveals tactile-dependent access to Body Schema. *Neuropsychologia* 49:3750–3757.

Cardinali L, Frassinetti F, Brozzoli C, Urquizar C, Roy AC, Farnè A (2009) Tool-use induces morphological updating of the body schema. *Current Biology* 19:1157.

Chaumon M, Bishop DVM, Busch NA (2015) A practical guide to the selection of independent components of the electroencephalogram for artifact correction. *Journal of Neuroscience Methods* 250:47–63.

Cheyne D, Gaetz W, Garnero L, Lachaux J-P, Ducorps A, Schwartz D, Varela FJ (2003) Neuromagnetic imaging of cortical oscillations accompanying tactile stimulation. *Cognitive Brain Research* 17:599–611.

Cohen MX (2014) *Analyzing Neural Time Series Data: Theory and Practice*. MIT Press.

Delorme A, Makeig S (2004) EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods* 134:9–21.

Eardley AF, van Velzen J (2011) Event-related potential evidence for the use of external coordinates in the preparation of tactile attention by the early blind: Spatial frameworks in the early blind and sighted. *European Journal of Neuroscience* 33:1897–1907.

Eimer M, Forster B (2003) Modulations of early somatosensory ERP components by transient and sustained spatial attention. *Experimental Brain Research* 151:24–31.

Eimer M, Forster B, Van Velzen J (2003) Anterior and posterior attentional control systems use different spatial reference frames: ERP evidence from covert tactile-spatial orienting. *Psychophysiology* 40:924–933.

Fabio C, Salemme R, Koun E, Farnè A, Miller LE (2022) Alpha Oscillations Are Involved in Localizing Touch on Handheld Tools. *Journal of Cognitive Neuroscience* 34:675–686.

Farnè A, Làdavas E (2000) Dynamic size-change of hand peripersonal space following tool use: *NeuroReport* 11:1645–1649.

- Forsberg A, O'Dowd A, Gherri E (2019) Tool use modulates early stages of visuo-tactile integration in far space: Evidence from event-related potentials. *Biological Psychology* 145:42–54.
- García-Larrea L, Lukaszewicz AC, Mauguière F (1995) Somatosensory responses during selective spatial attention: The N120-to-N140 transition. *Psychophysiology* 32:526–537.
- Gramfort A, Papadopoulos T, Olivi E, Clerc M (2010) OpenMEEG: opensource software for quasistatic bioelectromagnetics. :20.
- Haegens S, Handel BF, Jensen O (2011) Top-Down Controlled Alpha Band Activity in Somatosensory Areas Determines Behavioral Performance in a Discrimination Task. *Journal of Neuroscience* 31:5197–5204.
- Haegens S, Vazquez Y, Zainos A, Alvarez M, Jensen O, Romo R (2014) Thalamocortical rhythms during a vibrotactile detection task. *Proceedings of the National Academy of Sciences* 111:E1797–E1805.
- Head H, Holmes G (1911) Sensory disturbances from cerebral lesions. *Brain* 34:102–254.
- Heed T, Azañón E (2014) Using time to investigate space: a review of tactile temporal order judgments as a window onto spatial processing in touch. *Frontiers in Psychology* 5 Available at: <http://journal.frontiersin.org/article/10.3389/fpsyg.2014.00076/abstract> [Accessed January 15, 2018].
- Heed T, Buchholz VN, Engel AK, Röder B (2015) Tactile remapping: from coordinate transformation to integration in sensorimotor processing. *Trends in Cognitive Sciences* 19:251–258.
- Heed T, Röder B (2010) Common Anatomical and External Coding for Hands and Feet in Tactile Attention: Evidence from Event-related Potentials. *Journal of Cognitive Neuroscience* 22:184–202.
- Iriki A, Tanaka M, Iwamura Y (1996) Coding of modified body schema during tool use by macaque postcentral neurones. *Neuroreport* 7:2325–2330.
- Kay KN, Weiner KS, Grill-Spector K (2015) Attention Reduces Spatial Uncertainty in Human Ventral Temporal Cortex. *Current Biology* 25:595–600.
- Lloyd DM, Shore DI, Spence C, Calvert GA (2003) Multisensory representation of limb position in human premotor cortex. *Nature Neuroscience* 6:17–18.
- Maravita A, Iriki A (2004) Tools for the body (schema). *Trends in Cognitive Sciences* 8:79–86.
- Maris E, Oostenveld R (2007) Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods* 164:177–190.

Martel M, Cardinali L, Roy AC, Farnè A (2016) Tool-use: An open window into body representation and its plasticity. *Cognitive Neuropsychology* 33:82–101.

Miller LE, Fabio C, Azaroual M, Muret D, van Beers RJ, Farnè A, Medendorp WP (2022) A neural surveyor to map touch on the body. *Proc Natl Acad Sci USA* 119:e2102233118.

Miller LE, Fabio C, Ravenda V, Bahmad S, Koun E, Salemme R, Luauté J, Bolognini N, Hayward V, Farnè A (2019) Somatosensory Cortex Efficiently Processes Touch Located Beyond the Body. *Current Biology*:S0960982219313831.

Miller LE, Longo MR, Saygin AP (2014) Tool morphology constrains the effects of tool use on body representations. *Journal of Experimental Psychology: Human Perception and Performance* 40:2143–2153.

Miller LE, Montroni L, Koun E, Salemme R, Hayward V, Farnè A (2018) Sensing with tools extends somatosensory processing beyond the body. *Nature* 561:239–242.

Mima T, Nagamine T, Nakamura K, Shibasaki H (1998) Attention Modulates Both Primary and Second Somatosensory Cortical Activities in Humans: A Magnetoencephalographic Study. *Journal of Neurophysiology* 80:2215–2221.

Neuper C, Wörtz M, Pfurtscheller G (2006) ERD/ERS patterns reflecting sensorimotor activation and deactivation. In: *Progress in Brain Research*, pp 211–222. Elsevier. Available at: <https://linkinghub.elsevier.com/retrieve/pii/S0079612306590144> [Accessed September 4, 2020].

Ossandón JP, König P, Heed T (2020) No Evidence for a Role of Spatially Modulated α -Band Activity in Tactile Remapping and Short-Latency, Overt Orienting Behavior. *J Neurosci* 40:9088–9102.

Pascual-Marqui RD (2002) Standardized low resolution brain electromagnetic. *Clinical Pharmacology*:16.

Pfurtscheller G, Woertz M, Krausz G, Neuper C (2001) Distinction of different fingers by the frequency of stimulus induced beta oscillations in the human EEG. *Neuroscience Letters*:4.

Ruzzoli M, Soto-Faraco S (2014) Alpha Stimulation of the Human Parietal Cortex Attunes Tactile Perception to External Space. *Current Biology* 24:329–332.

Salenius S, Schnitzler A, Salmelin R, Jousmäki V, Hari R (1997) Modulation of Human Cortical Rolandic Rhythms during Natural Sensorimotor Tasks. *NeuroImage* 5:221–228.

Salmelin R, Hari R (1994) Spatiotemporal characteristics of sensorimotor neuromagnetic rhythms related to thumb movement. *Neuroscience* 60:537–550.

Sauseng P, Klimesch W, Stadler W, Schabus M, Doppelmayr M, Hanslmayr S, Gruber WR, Birbaumer N (2005) A shift of visual spatial attention is selectively associated with human EEG alpha activity. *European Journal of Neuroscience* 22:2917–2926.

Schubert JTW, Buchholz VN, Föcker J, Engel AK, Röder B, Heed T (2015a) Oscillatory activity reflects differential use of spatial reference frames by sighted and blind individuals in tactile attention. *NeuroImage* 117:417–428.

Schubert JTW, Buchholz VN, Föcker J, Engel AK, Röder B, Heed T (2015b) Oscillatory activity reflects differential use of spatial reference frames by sighted and blind individuals in tactile attention. *NeuroImage* 117:417–428.

Schubert JTW, Buchholz VN, Föcker J, Engel AK, Röder B, Heed T (2019) Alpha-band oscillations reflect external spatial coding for tactile stimuli in sighted, but not in congenitally blind humans. *Sci Rep* 9:9215.

Shore DI, Spry E, Spence C (2002) Confusing the mind by crossing the hands. *Cognitive Brain Research* 14:153–163.

Sposito A, Bolognini N, Vallar G, Maravita A (2012) Extension of perceived arm length following tool-use: Clues to plasticity of body metrics. *Neuropsychologia* 50:2187–2194.

Tadel F, Baillet S, Mosher JC, Pantazis D, Leahy RM (2011) Brainstorm: A User-Friendly Application for MEG/EEG Analysis. *Computational Intelligence and Neuroscience* 2011:1–13.

van Ede F, de Lange F, Jensen O, Maris E (2011) Orienting Attention to an Upcoming Tactile Event Involves a Spatially and Temporally Specific Modulation of Sensorimotor Alpha- and Beta-Band Oscillations. *Journal of Neuroscience* 31:2016–2024.

van Ede F, Jensen O, Maris E (2010) Tactile expectation modulates pre-stimulus β -band oscillations in human sensorimotor cortex. *NeuroImage* 51:867–876.

van Ede F, Szabenyi S, Maris E (2014) Attentional modulations of somatosensory alpha, beta and gamma oscillations dissociate between anticipation and stimulus processing. *NeuroImage* 97:134–141.

Yamamoto S, Kitazawa S (2001) Sensation at the tips of invisible tools. *Nature neuroscience* 4:979–980.

Yamamoto S, Moizumi S, Kitazawa S (2005) Referral of Tactile Sensation to the Tips of L-Shaped Sticks. *Journal of Neurophysiology* 93:2856–2863.

Yue Z, Bischof G-N, Zhou X, Spence C, Röder B (2009) Spatial attention affects the processing of tactile and visual stimuli presented at the tip of a tool: an event-related potential study. *Exp Brain Res* 193:119–128.

Discussion

Touch is of primary importance when interacting with our environment. It informs us on multiple properties of an object (e.g. texture, shape, size...) that we have come in contact with. This is true whether contact happens directly on our skin or through a hand-held tool. In order to interact with this object, our brain also needs to process its exact location that can guide motor behavior. Localizing touch on the body involves the use of reference frames, which is reflected in the oscillatory activity of the alpha and beta-band: alpha activity reflects the mapping of touch in an external reference frame, whereas beta activity reflects the mapping of touch in an anatomical reference frame. While the neural mechanisms underlying the ability to localize touch on the body have been largely investigated, those underlying tactile localization on a tool have been mostly unexplored. The present thesis hence investigated the neural correlates of tactile localization on a hand-held tool.

In a first event-related potentials study, we combined behaviour, electrophysiology and neuronal modelling to characterize how the human brain localizes touch on a hand-held tool. We found evidence that location information encoded in the tool's vibratory pattern is rapidly extracted and processed (<100 ms post-touch) by somatosensory and parietal cortices. Furthermore, these location-related neural responses were similar to those observed when touch was on the arm. We also found similar cortical sources for localizing touch on each surface, involving primary sensorimotor regions and the PPC.

In the second study, we investigated the oscillatory correlates of tool-extended tactile localization. We identified a modulation of alpha power dependent of contact location on the tool. Moreover, source estimation of this observed alpha modulation showed it originated in a contralateral fronto-parietal network that is known to be involved in tactile localization.

In the third study, we manipulated hand and tool posture (crossed vs. uncrossed) in a cued tactile localization task. We observed that alpha and beta power modulation following touch were remarkably similar between the hand-held tool and the hand. We found a crossing effect selective for the alpha-band that was dependent on attention. This effect was also similarly distributed across channels for hand and tool. Furthermore, source localization of this effect for both surfaces revealed that comparable cortical networks were involved.

Overall, our results provide evidence that similar neurocomputational mechanisms are used by the brain to process touch location on the hand and on a hand-held tool. Oscillatory activity in the alpha range reflects those mechanisms, suggesting the use of external coordinates for tool-extended tactile localization. In this general discussion, the main findings of our different experiments will be

reviewed and integrated with the existing literature. We will discuss the implications of these findings before offering perspectives for future research on this topic and their possible applications.

1. How is touch localized on a hand-held tool ?

1.1. Vibrations encode tactile location on a tool

Touch is not restricted to the boundary of the body, as we can feel a touch happening outside the body, on a hand-held tool (Vaught et al., 1968). We feel the texture of the ground when digging with a shovel, as a surgeon feels the resistance and softness of the tissue they are cutting. A more remarkable example is of a blind person using a cane to probe obstacle in their surroundings. As it happens, touch is not restricted to the tip of the tool but can be felt through its all surface. Miller and colleagues (2018) even found that tactile inputs happening at different location on the surface a hand-held tool were localized by participants with great accuracy, similarly as if they were happening on their own body. The authors even showed that impact location on the tool (in that case a wooden rod) led to specific vibratory pattern, which prompted the suggestion that each location on the surface of the rod is encoded by a vibratory motif (Luke E. Miller et al., 2018b). To directly test this idea at a behavioral and neural level, our first study included a deafferented patient who lost proprioception in their right upper limb. When performing the delayed match-to-sample task while holding the rod in their deafferented hand, their accuracy was of 77% (it was 72% with the rod in the intact hand). These results strongly suggest that the brain uses the vibratory motifs produced when contacting the rod to extract the contact location, and invalidate the idea that contact location might be derived from other information, such as proprioceptive cue.

Pacian corpuscles (PC) produces a high-fidelity neural image of transient and vibratory stimuli transmitted to the hand by objects held in the hand (Johnson, 2001). They have been involved in the perception of distant events through transmitted vibrations when we grasp an object in the hand (Brisben et al., 1999). PC population of the hand are thus likely involved in the ability to localize impact location on a hand-held tool. Indeed, Miller and colleagues (2018) created a simulation of a population of PC afferents of the hand to analyze their response to the mechanical vibrations of a tool. Vibrations led to temporally precise response patterns across the individual afferents and the population response. Using a classifier, the authors accurately decoded impact location from the population spike-timing within approximately 25 ms, therefore demonstrating that PC transduce impact location on the tool (Luke E. Miller et al., 2018b).

1.2. Similar neural mechanisms reflect the processing of touch location on a tool and arm

Since humans can accurately localize touch on a hand-held tool, similarly to when touch happen on the body (Luke E. Miller et al., 2018b), it has been hypothesized that similar processes may be involved when localizing tactile input on the body and on a tool (Luke E. Miller et al., 2018b; Yamamoto et al., 2005; Shinya Yamamoto and Kitazawa, 2001b). We tested this hypothesis across our three studies and provided evidence that tactile localization on the tool indeed shares neural mechanisms with tactile localization on the body.

1.2.1. SEP

The task used in study 1 and 2 was a delayed match-to-sample task designed to exploit repetition suppression effect. Repeating contact location on the tool and on the arm allowed us to characterize the cortical dynamics of touch localization on both surfaces. We recorded SEP as early as 24ms after contact on the tool, which is consistent with the known conduction delays between upper limb nerves and primary somatosensory cortex (Eisen and Elleker, 1980a). Comparison of repetition effect for the tool and for the arm using multivariate analyses showed that statistically similar repetition suppression in the somatosensory system following touch on both surfaces rapidly emerged.

Furthermore, significant location-based repetition suppression effects were identified in a similar time range following contact on both the tool (48 to 108 ms) and the arm (44 to 144 ms). This time range encompass two well-characterized processing stages previously identified for touch on the body: (1) recurrent sensory processing within primary somatosensory (SI) and motor (MI) cortices between 40 and 60 ms after stimulation (Allison et al., 1992a), which has been implicated in spatial processing (Akatsuka et al., 2007b; Cardini et al., 2011b), and (2) feedforward and feedback processing between SI, MI, and posterior parietal regions between 60 and 100 ms after stimulation (Jones et al., 2007b), proposed to contribute to transforming a sensory map into a higher-level spatial representation (Soto-Faraco and Azañón, 2013a). It is also important to note that the suppression effect was too quick to reflect signals related to motor preparation/inhibition, as these generally occurred ~140 ms after touch. Overall, the results of our ERP study suggested that in order to sense with tools, the human brain recruit primary somatosensory dynamics otherwise devoted to the body.

1.2.2. Oscillations

Alpha and beta activity have previously been implicated in tactile spatial processing: alpha seems to reflect the use of external coordinates, whereas beta seems to reflect the use of anatomical

coordinates (Buchholz et al., 2013, 2011; Ruzzoli and Soto-Faraco, 2014; Schubert et al., 2019). In both study 2 and 3, we observed post-touch desynchronization of alpha and beta power following touch on hand-held tool, with temporal distributions consistent with what has been previously shown for touch on the skin (Cheyne et al., 2003; Gaetz and Cheyne, 2006). In study 3, we directly compared the power modulation of each frequency band following touch between the hand and the tool and did not find any significant difference. Moreover, their respective scalp topographies were almost identical between surfaces when observed separately, suggesting that localizing touch on hands and tools involve similar oscillatory correlates.

The repetition effect in study 2 revealed that only alpha activity was involved in localizing touch on the tool. Indeed, this effect was lateralized to the hemisphere contralateral to the stimulation, underscoring its relation to the processing of tactile information. Additionally, no activity was found contralateral to the foot used for the response, ruling out the reflection of motor preparatory activity in the observed alpha effect. Since alpha oscillations are thought to play a prominent role in the coding of external spatial information for touch (Buchholz et al., 2013, 2011; Ruzzoli and Soto-Faraco, 2014; Schubert et al., 2019), we wondered if they play the same role for processing touch on the tool. In order to investigate if the alpha modulation observed in study 2 reflected the use of tactile external coordinates, we manipulated posture of the limbs and of the tools in study 3. Indeed, crossing limbs is a well-established method to tease apart localizing processes in external and anatomical coordinates. This is especially of note for the tool, since only the tool-tips crossed the body midline while the hands stayed in their respective hemispace. Therefore, any effect observed for crossing when touch is on the tool surface would reflect the remapping of touch on the tool, not the hands. We found that posture modulated alpha activity dependently of attention, which wasn't the case for beta. For both surfaces, the alpha modulation was localized in two parieto-occipital clusters, one in each hemisphere. Moreover, the interaction effect between attention and posture was independent of whether touch was localized on the hand or a hand-held tool. Overall, the remarkable similarity that we found for oscillatory processes for tactile localization on the hand and on the tool suggests that in order to localize a contact happening on a hand-held tool, the human brain repurposes neural mechanisms dedicated to body-related processes to perform the same function with a tool. These results support the proposition that touch on a tool is primarily coded in an external reference frame, reflected in the activity of the alpha-band.

1.3. Similar cortical regions localize touch on a tool and arm

We performed source reconstruction on our EEG data in all three studies, in order to identify the cortical sources involved in localizing touch on a hand-held tool. In study 1, we compared the cortical

sources of the repetition suppression effect following touch on the tool and on the arm. For both surface, the earliest stages of shared suppression (52 ms) were confined to primary somatosensory and motor cortices. Activity 80 ms after contact on the rod and arm then spread to nearly identical regions in the PPC. The source localization of the repetition effect in the alpha-band activity observed in study 2 is consistent with the results of study 1. Repeating the location of touch modulated alpha activity in a left-lateralized cortical network that included motor and somatosensory cortices, the premotor cortex, the PPC, and temporal regions. These regions - particularly the PMC and PPC - have been implicated in processing touch in external space (Avillac et al., 2005; Azañón et al., 2010b; Bremmer et al., 2001; Lloyd et al., 2003). Furthermore, the PCC construct higher level spatial representations (Bolognini and Maravita, 2007a; V. N. Buchholz et al., 2011a) and even represent hands and tools within a shared coordinate system (Naito, 2006; Naito et al., 2008b).

Finally, source reconstruction of the interaction effect for alpha observed in study 3 also supported these results. Encoding touch localization in external coordinates on the hand and on the tool involved a similar cortical network. Several regions throughout the parietal and frontal cortices were identified in both hemispheres, including primary somatosensory and motor cortex as well as the PPC. Importantly, parietal alpha oscillatory activity appears to play a crucial role in the processing of touch in external space (Buchholz et al., 2011; Ruzzoli and Soto-Faraco, 2014; Schubert et al., 2019).

To summarize, we found that localizing touches on the tool and on the arm/hand led to similar stages of cortical processing as well as similar oscillatory processes. Alpha band indexes the spatial coding of touch in an external reference frame, this effect being independent of whether touch was localized on the hand or a hand-held tool. Similar cortical sources between surfaces are involved in this process, distributed across a fronto-centro-parietal network. Our results show that tools are fundamental to human behaviour in a previously underappreciated way: they expand the *somatosensory boundaries* of our body at the neural level. Hence, rather than stopping at the skin, our results suggest that somatosensory processing extends beyond the nervous system to include the tools we use.

2. Is the tool incorporated into body representations ?

2.1. Online embodiment

It has been proposed more than a century ago that tools are incorporated into body representation, a phenomenon call tool embodiment (Head and Holmes, 1911). Indeed, tool use induces spatial representational plasticity, which suggests that the incorporation of a hand-held tool into body

representation consists of repurposing the neural mechanisms that process body-related sensory information for processing information originating from the tool. Until now, there has been few neuroscientific evidence for this proposition, since the majority of evidence comes from behavioral studies and from paradigms that only measure the effects that tool-use induced on subsequent perceptual or motor measures (Berti and Frassinetti, 2000; Cardinali et al., 2011, 2009a; L. Cardinali et al., 2016; Farnè and Làdavas, 2000; Forsberg et al., 2019; Miller et al., 2014; Sposito et al., 2012).

Initial evidence of online repurposing comes from Iriki and colleagues' work who measured from macaque monkeys' multisensory postcentral neurons during tool-use and observed an expansion of the visual portion of their receptive field to encompass the tool (A Iriki et al., 1996). At the behavioral level, online remapping of space was observed during tool-use by Berti & Frassinetti (2000), but their neuropsychological approach could not provide indications as to which mechanisms are at play (Berti and Frassinetti, 2000). Our results not only support the idea that the brain repurposes body-related processes to localize touch on a tool, but are also the first evidence to show the neural correlates of tool incorporation online in humans.

2.2. "Active" tool use vs. "Passive" tool use

Previous tool-use studies have found that active wielding (Bruno et al., 2019; L. Cardinali et al., 2016; Galigani et al., 2020) may be necessary for tool embodiment. In the two task we designed, participants never actively wielded the rod, which seems contradictory with this proposition. However, even if no motor movements were made, our tasks required participants to actively treat the rod as a sensory surface, taking sensory input and placing it within a spatial model of the tool. This can be viewed as a form of active use. Moreover, participants of study 1 and 2 often reported adapting their grip on the tool so that it was easier to discriminate between close and far hits. Thus tool-extended sensing can be viewed as an active process and not just a passive pick-up of information.

Consistent with our finding, several other studies have also found that sensory feedback is important for embodiment (Cardinali et al., 2011; Martel et al., 2019; Miller et al., 2017b; Serino et al., 2015). Interestingly, Miller and colleagues (2018) tested the localization performance on a hand-held tool in an active (i.e. self-generated movement) and a passive (i.e. passive reception of impact) setting (Luke E. Miller et al., 2018b). While performance was superior during active sensing, the notably high accuracy during passive sensing suggests that sensory signals, alone, encode a substantial portion of spatial information. Overall, sensing with a hand-held tool appears to be sufficient for tool embodiment, as we have found evidence of the deployment of body related neural processes to sensing with tools.

2.3. Tool representation

Povinelli and colleagues (2010) have suggested that the brain keeps separate representation of the body and the tool, even when actively engaged in tool use. This separation seems indeed necessary in cases where a tool is used as a substitute for the hand in order to pursue actions that would otherwise be hazardous (e.g. cooking) (Povinelli et al., 2010). This idea was supported by the findings of Gallivan et al. (2013). In their fMRI study, participants performed a delayed movement task that required grasp or reach actions towards a single target object. These two different movements were performed using either their hand or reverse tongs, which required opposite operating kinematics compared to when the hand was used alone. They found, first, that areas previously linked to the processing of hand movements and the human body were found to represent actions of the hand alone (and not those of the tool), whereas areas previously linked to the processing of tools and tool-related actions represented actions of the tool alone (and not those of the hand). Second, areas of motor cortex implicated in the generation of movement represented actions performed with both the hand and the tool, but showed distinct activity patterns according to which of these was to be used. Lastly, only areas associated with high-level cognitive and action-related processing showed similar patterns of activity regardless of whether the subjects were about to use the tongs or just their hand. Given that use of the hand and tool required distinct patterns of muscle contractions, this suggests that these higher-level brain regions must be encoding the action itself rather than the movements needed to achieve it. Overall, they showed that tool use is subserved by multiple distributed action-centered neural representations that are both shared with and distinct from those of the hand.

Our own results also support that idea. While we extensively showed that tool-extended localization shares neural processes with tactile localization the body, we also found some processes specific to the tool. Notably, source reconstruction in study 3 highlighted that the inferior temporal cortex was involved in the interaction effect of Attention and Posture only for the tool. This is in line with previous report involving this region in the supramodal representation of manipulable object (Kassuba et al., 2011; Pietrini et al., 2004). Thus, while tactile localization on a hand-held tool re-uses mechanisms devoted to body-related processes, it also seems to involve processes specific to the use of the tool.

3. Implications beyond the present topic

3.1. Alpha as a support for supramodal spatial processes

We found in study 3 that the modulation of alpha power following the crossing of the hands/tools was dependent on attention. This finding suggests that external spatial of touch was dependent, at least in our task, of certain attentional processes. Alpha oscillations have indeed been implicated in tactile spatial attention (Bauer, 2006; Bauer et al., 2012; van Ede et al., 2014, 2011). Post-touch alpha oscillations may thus reflect the orienting of attention in external space (Ossandón et al., 2020), which is involved in the alignment of sensory modalities under a common coordinate system (Ruzzoli and Soto-Faraco, 2014). Indeed, the PMC and PPC are crucial for the reference frame transformations underlying multimodal integration (Avillac et al., 2005; Bolognini and Maravita, 2007a; Bremmer et al., 2001; Graziano and Gross, 1998). Vallar and Maravita have argued that both regions are also important for making the experience of space integrated and unitary across modalities (Vallar and Maravita, 2009). Consistent with this proposal, alpha-band activity has also been implicated in spatial processing of visual (Foster et al., 2017, 2016; Rihs et al., 2007; Samaha et al., 2016) and auditory (Deng et al., 2020; Frey et al., 2014) stimuli. Additionally, attentional selection of location has been shown to modulates low-frequency activity in associated sensory cortices for vision and touch (Bauer et al., 2012; Jones et al., 2010). In the context of these findings, the observed alpha desynchronization during tool extended sensing might reflect a supramodal mechanism for spatial localization.

3.2. What is beta's role?

Beta-band activity was found to be modulated similarly following touch on the tool and on the hand in study 3. The temporal distribution of beta desynchronization in study 2 and 3 was also consistent with what has been previously shown for touch on the skin (Cheyne et al., 2003; Gaetz and Cheyne, 2006). However, contrary to alpha, we did not find any involvement of beta activity in localizing touch on a hand-held tool. We can thus wonder what role beta plays in the processing of touch on the tool? Oscillatory activity in both the alpha and beta frequency range over central and parieto-occipital sensors has been related to the orienting of tactile attention (Haegens et al., 2012; van Ede et al., 2011). Further, beta oscillations has been shown to reflect supramodal, stimulus-specific information during perceptual judgement (Griffiths et al., 2019; Haegens et al., 2017). These report combined to our results points to beta having a similar, supramodal role to alpha, but for non-spatial information related to touch on the tool.

It is interesting to note that we did not find an involvement of beta activity in localizing touch on the hand in study 3. This seems in contradiction with previous reports on the implication of beta in the mapping of touch in skin-centered coordinates (Buchholz et al., 2013; V. N. Buchholz et al., 2011c; Schubert et al., 2015b). However, by manipulating the posture of the hands, we only changed the external coordinates of touch. It is indeed more complicated to isolate the anatomical coordinates of touch, as different position on the body will also have different position in space. Thus our findings do not rule out the involvement of beta in the spatial processing of touch on the body.

4. Perspectives for future research

Contextual cues have been shown to play an important part when localizing a tactile stimulus on the body. For instance, task instructions will influence participants' performance in a tactile localization task (Schubert et al., 2017; Unwalla et al., 2021). This effect of instructions on the use of spatial coordinates has even been reflected in the ERP recording of both sighted and congenitally blind participants (Eardley and van Velzen, 2011a). Furthermore, congenitally blind individuals have also highlighted the relevance of visual information, particularly during development, for reference frame weighting (Röder et al., 2008b, 2004). However, no studies on tool sensing have included congenitally blind participants yet, neither behavioural or with neuro-imaging. If congenitally blind participants exhibit similar neural mechanisms when localizing tactile stimuli on a hand-held tool and on their body, it would further support our hypothesis that the brain repurposes body-related mechanisms to localize touch on the tool. Additionally, recording the EEG data of participants performing the same localization task, but under different instructions (i.e. external vs. anatomical) might allow us to observe the use of anatomical coordinates for localizing touch on the body. Further, it will also inform us if an anatomical reference frame of sort is involved when localizing touch on the tool.

5. Possible applications

Studying the neural processes behind tool-extended tactile localization has practical, real-world implications. Blind individuals often rely on a cane to navigate the world. Our findings and future findings implicating blind participants could help design a new generation of improved cane. Additionally, the use of the white cane requires special training, which could also benefit from further research on tool-extended sensing. Considering the number of visually impaired individuals will double until 2050, it is of primary importance to give them appropriate tools to improve their quality of life.

Another application of such research could be in the domain of prosthetics. A growing movement in bioengineering attempts to design *biomimetic* prosthetic limbs that provide somatosensory feedback to users, with limited—yet, encouraging—success (Bensmaia and Miller, 2014). For a prosthetic device to provide rich perceptual interaction with the world, its wearer must be able to perceive and act upon tactile events across its entire surface. So far, tactile feedback has typically been provided via invasive procedures, such as peripheral nerve stimulation (Valle et al., 2018) and intracortical microstimulation (Flesher et al., 2016). Our findings, as well as previous findings from Miller et al. (2018), suggest that a complementary, non-invasive means to restore sensory feedback would be to design prostheses that possess well designed structural dynamics in response to interactions with touching objects (Luke E. Miller et al., 2018b). Amputees with limb prosthesis can already learn to master the use of their prosthesis using sensory feedback (Tsukamoto, 2000). Identifying the sensorimotor mechanisms for mapping touch on a tool could aid in this use of prosthetic device as extended sensor.

6. Conclusion

The experimental contributions presented in this manuscript supports the idea that the brain re-uses body-related mechanisms to process information received from a hand-held tool. We provide evidence that similar neurocomputational mechanisms are used by the brain to process touch location on the hand and on a hand-held tool. Oscillatory activity in the alpha range reflects those mechanisms, suggesting the use of external coordinates for tool-extended tactile localization. Moreover, a network of fronto-parietal regions implicated in higher-order tactile and spatial processing is involved in processing the location of touch on the tool and on the body.

While the neural correlates of tactile localization on the body have been extensively studied, our work marks the beginning of the investigation of those mechanisms for hand-held tools. Hence, it offers numerous perspectives for future research. Our work also opens perspectives to develop tools used as extended sensors, like prosthetic devices or canes, so that they can be more adapted to their users.

References

- Ackroyd, K., Riddoch, M.J., Humphreys, G.W., Nightingale, S., Townsend, S., 2002. Widening the Sphere of Influence: Using a Tool to Extend Extrapersonal Visual Space in a Patient with Severe Neglect. *Neurocase* 8, 1–12. <https://doi.org/10.1093/neucas/8.1.1>
- Aglioti, S., Beltramello, A., Bonazzi, A., Corbetta, M., 1996. Thumb-pointing in humans after damage to somatic sensory cortex. *Exp Brain Res* 109. <https://doi.org/10.1007/BF00228630>
- Aglioti, S., Smania, N., Peru, A., 1999. Frames of Reference for Mapping Tactile Stimuli in Brain-Damaged Patients. *Journal of Cognitive Neuroscience* 11, 67–79. <https://doi.org/10.1162/089892999563256>
- Akatsuka, K., Wasaka, T., Nakata, H., Kida, T., Hoshiyama, M., Tamura, Y., Kakigi, R., 2007a. Objective examination for two-point stimulation using a somatosensory oddball paradigm: An MEG study. *Clinical Neurophysiology* 118, 403–411. <https://doi.org/10.1016/j.clinph.2006.09.030>
- Akatsuka, K., Wasaka, T., Nakata, H., Kida, T., Kakigi, R., 2007b. The effect of stimulus probability on the somatosensory mismatch field. *Experimental Brain Research* 181, 607–614. <https://doi.org/10.1007/s00221-007-0958-4>
- Allison, T., McCarthy, G., Wood, C.C., 1992a. The relationship between human long-latency somatosensory evoked potentials recorded from the cortical surface and from the scalp. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section* 84, 301–314. [https://doi.org/10.1016/0168-5597\(92\)90082-M](https://doi.org/10.1016/0168-5597(92)90082-M)
- Allison, T., McCarthy, G., Wood, C.C., 1992b. The relationship between human long-latency somatosensory evoked potentials recorded from the cortical surface and from the scalp. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section* 84, 301–314. [https://doi.org/10.1016/0168-5597\(92\)90082-M](https://doi.org/10.1016/0168-5597(92)90082-M)
- Andersen, R.A., Essick, G.K., Siegel, R.M., 1985. Encoding of Spatial Location by Posterior Parietal Neurons. *Science* 230, 456–458. <https://doi.org/10.1126/science.4048942>
- Andersen, R.A., Snyder, L.H., Bradley, D.C., Xing, J., 1997. Multimodal Representation of Space in the Posterior Parietal Cortex and Its Use in Planning Movements. *Annual Review of Neuroscience* 20, 303–330. <https://doi.org/10.1146/annurev.neuro.20.1.303>
- Avillac, M., Denève, S., Olivier, E., Pouget, A., Duhamel, J.-R., 2005. Reference frames for representing visual and tactile locations in parietal cortex. *Nature Neuroscience* 8, 941–949. <https://doi.org/10.1038/nn1480>
- Azañón, E., Camacho, K., Soto-Faraco, S., 2010a. Tactile remapping beyond space: Tactile remapping beyond space. *European Journal of Neuroscience* 31, 1858–1867. <https://doi.org/10.1111/j.1460-9568.2010.07233.x>
- Azañón, E., Longo, M.R., Soto-Faraco, S., Haggard, P., 2010b. The Posterior Parietal Cortex Remaps Touch into External Space. *Current Biology* 20, 1304–1309. <https://doi.org/10.1016/j.cub.2010.05.063>
- Azañón, E., Soto-Faraco, S., 2008. Changing Reference Frames during the Encoding of Tactile Events. *Current Biology* 18, 1044–1049. <https://doi.org/10.1016/j.cub.2008.06.045>

- Azañón, E., Soto-Faraco, S., 2007. Alleviating the ‘crossed-hands’ deficit by seeing uncrossed rubber hands. *Exp Brain Res* 182, 537–548. <https://doi.org/10.1007/s00221-007-1011-3>
- Azañón, E., Stenner, M.-P., Cardini, F., Haggard, P., 2015. Dynamic Tuning of Tactile Localization to Body Posture. *Current Biology* 25, 512–517. <https://doi.org/10.1016/j.cub.2014.12.038>
- Badde, S., Heed, T., 2016. Towards explaining spatial touch perception: Weighted integration of multiple location codes. *Cognitive Neuropsychology* 33, 26–47. <https://doi.org/10.1080/02643294.2016.1168791>
- Badde, S., Heed, T., Röder, B., 2014. Processing load impairs coordinate integration for the localization of touch. *Atten Percept Psychophys* 76, 1136–1150. <https://doi.org/10.3758/s13414-013-0590-2>
- Badde, S., Röder, B., Heed, T., 2015. Flexibly weighted integration of tactile reference frames. *Neuropsychologia* 70, 367–374. <https://doi.org/10.1016/j.neuropsychologia.2014.10.001>
- Bartolomeo, P., Perri, R., Gainotti, G., 2004. The influence of limb crossing on left tactile extinction. *Journal of Neurology, Neurosurgery, and Psychiatry* 49–55.
- Bauer, M., 2006. Tactile Spatial Attention Enhances Gamma-Band Activity in Somatosensory Cortex and Reduces Low-Frequency Activity in Parieto-Occipital Areas. *Journal of Neuroscience* 26, 490–501. <https://doi.org/10.1523/JNEUROSCI.5228-04.2006>
- Bauer, M., Kennett, S., Driver, J., 2012. Attentional selection of location and modality in vision and touch modulates low-frequency activity in associated sensory cortices. *Journal of Neurophysiology* 107, 2342–2351. <https://doi.org/10.1152/jn.00973.2011>
- Bell, J., Bolanowski, S., Holmes, M.H., 1994. The structure and function of pacinian corpuscles: A review. *Progress in Neurobiology* 42, 79–128. [https://doi.org/10.1016/0301-0082\(94\)90022-1](https://doi.org/10.1016/0301-0082(94)90022-1)
- Belmonte, C., Viana, F., 2008. Molecular and cellular limits to somatosensory specificity. *Molecular Pain* 4, 14. <https://doi.org/10.1186/1744-8069-4-14>
- Bender, M.B., 1952. Disorders in perception; with particular reference to the phenomena of extinction and displacement, Disorders in perception; with particular reference to the phenomena of extinction and displacement. Charles C. Thomas, Oxford, England.
- Bensmaia, S.J., Miller, L.E., 2014. Restoring sensorimotor function through intracortical interfaces: Progress and looming challenges. *Nature Reviews Neuroscience* 15, 313–325. <https://doi.org/10.1038/nrn3724>
- Berlucchi, G., Aglioti, S.M., 2010. The body in the brain revisited. *Exp Brain Res* 200, 25–35. <https://doi.org/10.1007/s00221-009-1970-7>
- Berti, A., Frassinetti, F., 2000. When Far Becomes Near: Remapping of Space by Tool Use. *Journal of Cognitive Neuroscience* 12, 415–420. <https://doi.org/10.1162/089892900562237>
- Bisiach, E., Vallar, G., 2000. Unilateral neglect in humans, in: *Handbook of Neuropsychology: Sect 1: Introduction, Sect 2: Attention, Vol. 1, 2nd Ed, Handbook of Neuropsychology*. Elsevier Science Publishers B.V., Amsterdam, Netherlands, pp. 459–502.
- Bloesch, E.K., Davoli, C.C., Roth, N., Brockmole, J.R., Abrams, R.A., 2012. Watch this! Observed tool use affects perceived distance. *Psychon Bull Rev* 19, 177–183. <https://doi.org/10.3758/s13423-011-0200-z>

- Blohm, G., Alikhanian, H., Gaetz, W., Goltz, H.C., DeSouza, J.F., Cheyne, D.O., Crawford, J.D., 2018. Neuromagnetic signatures of the spatiotemporal transformation for manual pointing (preprint). *Neuroscience*. <https://doi.org/10.1101/253328>
- Bolognini, N., Maravita, A., 2007a. Proprioceptive Alignment of Visual and Somatosensory Maps in the Posterior Parietal Cortex. *Current Biology* 17, 1890–1895. <https://doi.org/10.1016/j.cub.2007.09.057>
- Bolognini, N., Maravita, A., 2007b. Proprioceptive Alignment of Visual and Somatosensory Maps in the Posterior Parietal Cortex. *Current Biology* 17, 1890–1895. <https://doi.org/10.1016/j.cub.2007.09.057>
- Brecht, M., 2017. The Body Model Theory of Somatosensory Cortex. *Neuron* 94, 985–992. <https://doi.org/10.1016/j.neuron.2017.05.018>
- Bremmer, F., Schlack, A., Duhamel, J.-R., Graf, W., Fink, G.R., 2001. Space Coding in Primate Posterior Parietal Cortex. *NeuroImage* 14, S46–S51. <https://doi.org/10.1006/nimg.2001.0817>
- Brisben, A.J., Hsiao, S.S., Johnson, K.O., 1999. Detection of Vibration Transmitted Through an Object Grasped in the Hand. *Journal of Neurophysiology* 81, 1548–1558. <https://doi.org/10.1152/jn.1999.81.4.1548>
- Bruno, V., Carpinella, I., Rabuffetti, M., De Giuli, L., Sinigaglia, C., Garbarini, F., Ferrarin, M., 2019. How Tool-Use Shapes Body Metric Representation: Evidence From Motor Training With and Without Robotic Assistance. *Front. Hum. Neurosci.* 13, 299. <https://doi.org/10.3389/fnhum.2019.00299>
- Buchholz, V.N., Jensen, O., Medendorp, W.P., 2013. Parietal Oscillations Code Nonvisual Reach Targets Relative to Gaze and Body. *Journal of Neuroscience* 33, 3492–3499. <https://doi.org/10.1523/JNEUROSCI.3208-12.2013>
- Buchholz, V. N., Jensen, O., Medendorp, W.P., 2011a. Multiple Reference Frames in Cortical Oscillatory Activity during Tactile Remapping for Saccades. *Journal of Neuroscience* 31, 16864–16871. <https://doi.org/10.1523/JNEUROSCI.3404-11.2011>
- Buchholz, Verena N, Jensen, O., Medendorp, W.P., 2011. Multiple reference frames in cortical oscillatory activity during tactile remapping for saccades. *The Journal of neuroscience : the official journal of the Society for Neuroscience* 31, 16864–71. <https://doi.org/10.1523/JNEUROSCI.3404-11.2011>
- Buchholz, V. N., Jensen, O., Medendorp, W.P., 2011b. Multiple Reference Frames in Cortical Oscillatory Activity during Tactile Remapping for Saccades. *Journal of Neuroscience* 31, 16864–16871. <https://doi.org/10.1523/JNEUROSCI.3404-11.2011>
- Buchholz, V. N., Jensen, O., Medendorp, W.P., 2011c. Multiple Reference Frames in Cortical Oscillatory Activity during Tactile Remapping for Saccades. *Journal of Neuroscience* 31, 16864–16871. <https://doi.org/10.1523/JNEUROSCI.3404-11.2011>
- Burton, G., 1993. Non-Neural extensions of Haptic Sensitivity. *Ecological Psychology* 5, 105–124.
- Cadieux, M.L., Shore, D.I., 2013. Response Demands and Blindfolding in the Crossed-Hands Deficit: An Exploration of Reference Frame Conflict. *Multisensory Research* 26, 465–482. <https://doi.org/10.1163/22134808-00002423>

- Canzoneri, E., Ferrè, E.R., Haggard, P., 2014. Combining proprioception and touch to compute spatial information. *Exp Brain Res* 232, 1259–1266. <https://doi.org/10.1007/s00221-014-3842-z>
- Canzoneri, E., Ubaldi, S., Rastelli, V., Finisguerra, A., Bassolino, M., Serino, A., 2013. Tool-use reshapes the boundaries of body and peripersonal space representations. *Experimental Brain Research* 228, 25–42. <https://doi.org/10.1007/s00221-013-3532-2>
- Cardinali, L., Brozzoli, C., Finos, L., Roy, A.C., Farnè, A., 2016. The rules of tool incorporation: Tool morpho-functional & sensori-motor constraints. *Cognition* 149, 1–5. <https://doi.org/10.1016/j.cognition.2016.01.001>
- Cardinali, Lucilla, Brozzoli, C., Luauté, J., Roy, A.C., Farnè, A., 2016. Proprioception Is Necessary for Body Schema Plasticity: Evidence from a Deafferented Patient. *Frontiers in Human Neuroscience* 10. <https://doi.org/10.3389/fnhum.2016.00272>
- Cardinali, L., Brozzoli, C., Urquizar, C., Salemme, R., Roy, A.C., Farnè, A., 2011. When action is not enough: Tool-use reveals tactile-dependent access to Body Schema. *Neuropsychologia* 49, 3750–3757. <https://doi.org/10.1016/j.neuropsychologia.2011.09.033>
- Cardinali, L., Frassinetti, F., Brozzoli, C., Urquizar, C., Roy, A.C., Farnè, A., 2009a. Tool-use induces morphological updating of the body schema. *Current Biology* 19, 1157. <https://doi.org/10.1016/j.cub.2009.06.048>
- Cardinali, L., Frassinetti, F., Brozzoli, C., Urquizar, C., Roy, A.C., Farnè, A., 2009b. Tool-use induces morphological updating of the body schema. *Current Biology* 19, 1157. <https://doi.org/10.1016/j.cub.2009.06.048>
- Cardinali, L., Jacobs, S., Brozzoli, C., Frassinetti, F., Roy, A.C., Farnè, A., 2012. Grab an object with a tool and change your body: tool-use-dependent changes of body representation for action. *Exp Brain Res* 218, 259–271. <https://doi.org/10.1007/s00221-012-3028-5>
- Cardini, F., Longo, M.R., Haggard, P., 2011a. Vision of the Body Modulates Somatosensory Intracortical Inhibition. *Cerebral Cortex* 21, 2014–2022. <https://doi.org/10.1093/cercor/bhq267>
- Cardini, F., Longo, M.R., Haggard, P., 2011b. Vision of the Body Modulates Somatosensory Intracortical Inhibition. *Cerebral Cortex* 21, 2014–2022. <https://doi.org/10.1093/cercor/bhq267>
- Carello, C., Fitzpatrick, P., Turvey, M.T., 1992. Haptic probing: Perceiving the length of a probe and the distance of a surface probed. *Perception & Psychophysics* 51, 580–598. <https://doi.org/10.3758/BF03211655>
- Cauler, L.J., Kulics, A.T., 1991. The neural basis of the behaviorally relevant N1 component of the somatosensory-evoked potential in SI cortex of awake monkeys: evidence that backward cortical projections signal conscious touch sensation. *Experimental Brain Research* 84, 607–619. <https://doi.org/10.1007/BF00230973>
- Chaumon, M., Bishop, D.V.M., Busch, N.A., 2015. A practical guide to the selection of independent components of the electroencephalogram for artifact correction. *Journal of Neuroscience Methods* 250, 47–63. <https://doi.org/10.1016/j.jneumeth.2015.02.025>
- Cheyne, D., Gaetz, W., Garnero, L., Lachaux, J.-P., Ducorps, A., Schwartz, D., Varela, F.J., 2003. Neuromagnetic imaging of cortical oscillations accompanying tactile stimulation. *Cognitive Brain Research* 17, 599–611. [https://doi.org/10.1016/S0926-6410\(03\)00173-3](https://doi.org/10.1016/S0926-6410(03)00173-3)

- Chiel, H.J., Beer, R.D., 1997. The brain has a body: Adaptive behavior emerges from interactions of nervous system, body and environment. *Trends in Neurosciences* 20, 553–557. [https://doi.org/10.1016/S0166-2236\(97\)01149-1](https://doi.org/10.1016/S0166-2236(97)01149-1)
- Clark, A., 2008. *Supersizing the mind: Embodiment, action, and cognitive extension*. Oxford University Press, New York.
- Cohen, M.X., 2014. *Analyzing Neural Time Series Data: Theory and Practice*. MIT Press.
- Cohen, Y.E., Andersen, R.A., 2002. A common reference frame for movement plans in the posterior parietal cortex. *Nature Reviews Neuroscience* 3, 553. <https://doi.org/10.1038/nrn873>
- Colby, C.L., 1998. Action-Oriented Spatial Reference Frames in Cortex. *Neuron* 20, 15–24. [https://doi.org/10.1016/S0896-6273\(00\)80429-8](https://doi.org/10.1016/S0896-6273(00)80429-8)
- Committeri, G., Galati, G., Paradis, A.-L., Pizzamiglio, L., Berthoz, A., LeBihan, D., 2004. Reference Frames for Spatial Cognition: Different Brain Areas are Involved in Viewer-, Object-, and Landmark-Centered Judgments About Object Location. *Journal of Cognitive Neuroscience* 16, 1517–1535. <https://doi.org/10.1162/0898929042568550>
- Committeri, G., Pitzalis, S., Galati, G., Patria, F., Pelle, G., Sabatini, U., Castriota-Scanderbeg, A., Piccardi, L., Guariglia, C., Pizzamiglio, L., 2007. Neural bases of personal and extrapersonal neglect in humans. *Brain* 130, 431–441. <https://doi.org/10.1093/brain/awl265>
- Costantini, M., Frassinetti, F., Maini, M., Ambrosini, E., Gallese, V., Sinigaglia, C., 2014. When a laser pen becomes a stick: remapping of space by tool-use observation in hemispatial neglect. *Exp Brain Res* 232, 3233–3241. <https://doi.org/10.1007/s00221-014-4012-z>
- Crollen, V., Lazzouni, L., Rezk, M., Bellemare, A., Lepore, F., Collignon, O., 2017. Visual Experience Shapes the Neural Networks Remapping Touch into External Space. *J. Neurosci.* 37, 10097–10103. <https://doi.org/10.1523/JNEUROSCI.1213-17.2017>
- de Haan, B., Karnath, H.-O., Driver, J., 2012. Mechanisms and anatomy of unilateral extinction after brain injury. *Neuropsychologia, Special Issue: Spatial Neglect and Attention* 50, 1045–1053. <https://doi.org/10.1016/j.neuropsychologia.2012.02.015>
- de Vignemont, F., 2010. Body schema and body image—Pros and cons. *Neuropsychologia* 48, 669–680. <https://doi.org/10.1016/j.neuropsychologia.2009.09.022>
- de Vignemont, F., Ehrsson, H.H., Haggard, P., 2005. Bodily Illusions Modulate Tactile Perception. *Current Biology* 15, 1286–1290. <https://doi.org/10.1016/j.cub.2005.06.067>
- Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods* 134, 9–21. <https://doi.org/10.1016/j.jneumeth.2003.10.009>
- Deng, Y., Choi, I., Shinn-Cunningham, B., 2020. Topographic specificity of alpha power during auditory spatial attention. *NeuroImage* 207, 116360. <https://doi.org/10.1016/j.neuroimage.2019.116360>
- di Pellegrino, G., Làdavas, E., Farné, A., 1997. Seeing where your hands are. *Nature* 388, 730–730. <https://doi.org/10.1038/41921>
- Driver, J., Spence, C., 1998. Attention and the crossmodal construction of space. *Trends in Cognitive Sciences* 2, 254–262. [https://doi.org/10.1016/S1364-6613\(98\)01188-7](https://doi.org/10.1016/S1364-6613(98)01188-7)

- Duhamel, J.-R., Bremmer, F., Ben Hamed, S., Graf, W., 1997. Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature* 389, 845–848. <https://doi.org/10.1038/39865>
- Eardley, A.F., van Velzen, J., 2011a. Event-related potential evidence for the use of external coordinates in the preparation of tactile attention by the early blind: Spatial frameworks in the early blind and sighted. *European Journal of Neuroscience* 33, 1897–1907. <https://doi.org/10.1111/j.1460-9568.2011.07672.x>
- Eardley, A.F., van Velzen, J., 2011b. Event-related potential evidence for the use of external coordinates in the preparation of tactile attention by the early blind: Spatial frameworks in the early blind and sighted. *European Journal of Neuroscience* 33, 1897–1907. <https://doi.org/10.1111/j.1460-9568.2011.07672.x>
- Eimer, M., Forster, B., 2003. Modulations of early somatosensory ERP components by transient and sustained spatial attention. *Experimental Brain Research* 151, 24–31. <https://doi.org/10.1007/s00221-003-1437-1>
- Eimer, M., Forster, B., Van Velzen, J., 2003. Anterior and posterior attentional control systems use different spatial reference frames: ERP evidence from covert tactile-spatial orienting. *Psychophysiology* 40, 924–933. <https://doi.org/10.1111/1469-8986.00110>
- Eisen, A., Elleker, G., 1980a. Sensory nerve stimulation and evoked cerebral potentials. *Neurology* 30, 1097–1097. <https://doi.org/10.1212/WNL.30.10.1097>
- Eisen, A., Elleker, G., 1980b. Sensory nerve stimulation and evoked cerebral potentials. *Neurology* 30, 1097–1105.
- Elithorn, A., Piercy, M.F., Crosskey, M.A., 1952. SOME MECHANISMS OF TACTILE LOCALIZATION REVEALED BY A STUDY OF LEUCOTOMIZED PATIENTS. *J Neurol Neurosurg Psychiatry* 15, 272–282.
- Fabio, C., Salemme, R., Koun, E., Farnè, A., Miller, L.E., 2022. Alpha Oscillations Are Involved in Localizing Touch on Handheld Tools. *Journal of Cognitive Neuroscience* 34, 675–686. https://doi.org/10.1162/jocn_a_01820
- Farnè, A., Bonifazi, S., Làdavas, E., 2005. The role played by tool-use and tool-length on the Plastic Elongation of peri-hand space: a single case study. *Cognitive Neuropsychology* 22, 408–418. <https://doi.org/10.1080/02643290442000112>
- Farnè, A., Làdavas, E., 2000. Dynamic size-change of hand peripersonal space following tool use: *NeuroReport* 11, 1645–1649. <https://doi.org/10.1097/00001756-200006050-00010>
- Farnè, A., Serino, A., Làdavas, E., 2007. Dynamic Size-Change of Peri-Hand Space Following Tool-Use: Determinants and Spatial Characteristics Revealed Through Cross-Modal Extinction. *Cortex* 43, 436–443. [https://doi.org/10.1016/S0010-9452\(08\)70468-4](https://doi.org/10.1016/S0010-9452(08)70468-4)
- Feurra, M., Paulus, W., Walsh, V., Kanai, R., 2011. Frequency Specific Modulation of Human Somatosensory Cortex. *Frontiers in Psychology* 2. <https://doi.org/10.3389/fpsyg.2011.00013>
- Filimon, F., 2010. Human Cortical Control of Hand Movements: Parietofrontal Networks for Reaching, Grasping, and Pointing. *Neuroscientist* 16, 388–407. <https://doi.org/10.1177/1073858410375468>

- Flesher, S.N., Collinger, J.L., Foldes, S.T., Weiss, J.M., Downey, J.E., Tyler-Kabara, E.C., Bensmaia, S.J., Schwartz, A.B., Boninger, M.L., Gaunt, R.A., 2016. Intracortical microstimulation of human somatosensory cortex. *Science Translational Medicine* 8.
- Fogassi, L., Gallese, V., di Pellegrino, G., Fadiga, L., Gentilucci, M., Luppino, G., Matelli, M., Pedotti, A., Rizzolatti, G., 1992. Space coding by premotor cortex. *Exp Brain Res* 89, 686–690. <https://doi.org/10.1007/BF00229894>
- Forsberg, A., O’Dowd, A., Gherri, E., 2019. Tool use modulates early stages of visuo-tactile integration in far space: Evidence from event-related potentials. *Biological Psychology* 145, 42–54. <https://doi.org/10.1016/j.biopsycho.2019.03.020>
- Foster, J.J., Bsaies, E.M., Jaffe, R.J., Awh, E., 2017. Alpha-Band Activity Reveals Spontaneous Representations of Spatial Position in Visual Working Memory. *Current Biology* 27, 3216–3223.e6. <https://doi.org/10.1016/j.cub.2017.09.031>
- Foster, J.J., Sutterer, D.W., Serences, J.T., Vogel, E.K., Awh, E., 2016. The topography of alpha-band activity tracks the content of spatial working memory. *Journal of Neurophysiology* 115, 168–177. <https://doi.org/10.1152/jn.00860.2015>
- Frey, J.N., Mainy, N., Lachaux, J.-P., Muller, N., Bertrand, O., Weisz, N., 2014. Selective Modulation of Auditory Cortical Alpha Activity in an Audiovisual Spatial Attention Task. *Journal of Neuroscience* 34, 6634–6639. <https://doi.org/10.1523/JNEUROSCI.4813-13.2014>
- Frissen, I., Yao, H.-Y., Guastavino, C., Hayward, V., 2022. Humans sense by touch the location of objects that roll in handheld containers. *Quarterly Journal of Experimental Psychology* 174702182210864. <https://doi.org/10.1177/17470218221086458>
- Gaetz, W., Cheyne, D., 2006. Localization of sensorimotor cortical rhythms induced by tactile stimulation using spatially filtered MEG. *NeuroImage* 30, 899–908. <https://doi.org/10.1016/j.neuroimage.2005.10.009>
- Galigani, M., Castellani, N., Donno, B., Franza, M., Zuber, C., Allet, L., Garbarini, F., Bassolino, M., 2020. Effect of tool-use observation on metric body representation and peripersonal space. *Neuropsychologia* 148, 107622. <https://doi.org/10.1016/j.neuropsychologia.2020.107622>
- Gallace, A., Soto-Faraco, S., Dalton, P., Kreukniet, B., Spence, C., 2008. Response requirements modulate tactile spatial congruency effects. *Exp Brain Res* 191, 171–186. <https://doi.org/10.1007/s00221-008-1510-x>
- García-Larrea, L., Lukaszewicz, A.C., Mauguière, F., 1995. Somatosensory responses during selective spatial attention: The N120-to-N140 transition. *Psychophysiology* 32, 526–537. <https://doi.org/10.1111/j.1469-8986.1995.tb01229.x>
- Giudice, N.A., Klatzky, R.L., Bennett, C.R., Loomis, J.M., 2013. Perception of 3-D location based on vision, touch, and extended touch. *Exp Brain Res* 224, 141–153. <https://doi.org/10.1007/s00221-012-3295-1>
- Giurgola, S., Pisoni, A., Maravita, A., Vallar, G., Bolognini, N., 2019. Somatosensory cortical representation of the body size. *Human Brain Mapping* 40, 3534–3547. <https://doi.org/10.1002/hbm.24614>
- Gramfort, A., Papadopoulos, T., Olivi, E., Clerc, M., 2010. OpenMEEG: opensource software for quasistatic bioelectromagnetics 20.

- Graziano, M.S., Gross, C.G., 1998. Spatial maps for the control of movement. *Current Opinion in Neurobiology* 8, 195–201. [https://doi.org/10.1016/S0959-4388\(98\)80140-2](https://doi.org/10.1016/S0959-4388(98)80140-2)
- Griffiths, B.J., Mayhew, S.D., Mullinger, K.J., Jorge, J., Charest, I., Wimber, M., Hanslmayr, S., 2019. Alpha/beta power decreases track the fidelity of stimulus-specific information. *eLife* 8, e49562. <https://doi.org/10.7554/eLife.49562>
- Grill-Spector, K., Henson, R., Martin, A., 2006. Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences* 10, 14–23. <https://doi.org/10.1016/j.tics.2005.11.006>
- Groh, J.M., Sparks, D.L., 1996. Saccades to somatosensory targets. III. eye-position-dependent somatosensory activity in primate superior colliculus. *Journal of Neurophysiology* 75, 439–453. <https://doi.org/10.1152/jn.1996.75.1.439>
- Haegens, Saskia, Cousijn, H., Wallis, G., Harrison, P.J., Nobre, A.C., 2014. Inter- and intra-individual variability in alpha peak frequency. *NeuroImage* 92, 46–55. <https://doi.org/10.1016/j.neuroimage.2014.01.049>
- Haegens, S., Handel, B.F., Jensen, O., 2011. Top-Down Controlled Alpha Band Activity in Somatosensory Areas Determines Behavioral Performance in a Discrimination Task. *Journal of Neuroscience* 31, 5197–5204. <https://doi.org/10.1523/JNEUROSCI.5199-10.2011>
- Haegens, S., Luther, L., Jensen, O., 2012. Somatosensory Anticipatory Alpha Activity Increases to Suppress Distracting Input. *Journal of Cognitive Neuroscience* 24, 677–685. https://doi.org/10.1162/jocn_a_00164
- Haegens, S., Vazquez, Y., Zainos, A., Alvarez, M., Jensen, O., Romo, R., 2014. Thalamocortical rhythms during a vibrotactile detection task. *Proceedings of the National Academy of Sciences* 111, E1797–E1805. <https://doi.org/10.1073/pnas.1405516111>
- Haegens, S., Vergara, J., Rossi-Pool, R., Lemus, L., Romo, R., 2017. Beta oscillations reflect supramodal information during perceptual judgment. *Proc Natl Acad Sci USA* 114, 13810–13815. <https://doi.org/10.1073/pnas.1714633115>
- Harrar, V., Harris, L.R., 2009. Eye position affects the perceived location of touch. *Exp Brain Res* 198, 403–410. <https://doi.org/10.1007/s00221-009-1884-4>
- Head, H., Holmes, G., 1911. Sensory disturbances from cerebral lesions. *Brain* 34, 102–254. <https://doi.org/10.1093/brain/34.2-3.102>
- Heed, T., Azañón, E., 2014. Using time to investigate space: a review of tactile temporal order judgments as a window onto spatial processing in touch. *Frontiers in Psychology* 5. <https://doi.org/10.3389/fpsyg.2014.00076>
- Heed, T., Backhaus, J., Röder, B., 2012. Integration of hand and finger location in external spatial coordinates for tactile localization. *Journal of Experimental Psychology: Human Perception and Performance* 38, 386–401. <https://doi.org/10.1037/a0024059>
- Heed, T., Buchholz, V.N., Engel, A.K., Röder, B., 2015a. Tactile remapping: from coordinate transformation to integration in sensorimotor processing. *Trends in Cognitive Sciences* 19, 251–258. <https://doi.org/10.1016/j.tics.2015.03.001>

- Heed, T., Möller, J., Röder, B., 2015b. Movement Induces the Use of External Spatial Coordinates for Tactile Localization in Congenitally Blind Humans. *Multisensory Research* 28, 173–194. <https://doi.org/10.1163/22134808-00002485>
- Heed, T., Röder, B., 2010. Common Anatomical and External Coding for Hands and Feet in Tactile Attention: Evidence from Event-related Potentials. *Journal of Cognitive Neuroscience* 22, 184–202. <https://doi.org/10.1162/jocn.2008.21168>
- Heilman, K.M., Valenstein, E., 1979. Mechanisms underlying hemispatial neglect. *Annals of Neurology* 5, 166–170. <https://doi.org/10.1002/ana.410050210>
- Hensel, H., 1973. Cutaneous Thermoreceptors, in: Albe-Fessard, D., Andres, K.H., Bates, J.A.V., Besson, J.M., Brown, A.G., Burgess, P.R., Darian-Smith, I., v. Düring, M., Gordon, G., Hensel, H., Jones, E., Libet, B., Oscarsson, O., Perl, E.R., Pompeiano, O., Powell, T.P.S., Réthelyi, M., Schmidt, R.F., Semmes, J., Skoglund, S., Szentágothai, J., Towe, A.L., Wall, P.D., Werner, G., Whitsel, B.L., Zotterman, Y., Iggo, A. (Eds.), *Somatosensory System, Handbook of Sensory Physiology*. Springer, Berlin, Heidelberg, pp. 79–110. https://doi.org/10.1007/978-3-642-65438-1_4
- Hermosillo, R., Ritterband-Rosenbaum, A., van Donkelaar, P., 2011. Predicting Future Sensorimotor States Influences Current Temporal Decision Making. *Journal of Neuroscience* 31, 10019–10022. <https://doi.org/10.1523/JNEUROSCI.0037-11.2011>
- Hillis, A.E., Chang, S., Heidler-Gary, J., Newhart, M., Kleinman, J.T., Davis, C., Barker, P.B., Aldrich, E., Ken, L., 2006. Neural Correlates of Modality-specific Spatial Extinction. *Journal of Cognitive Neuroscience* 18, 1889–1898. <https://doi.org/10.1162/jocn.2006.18.11.1889>
- Ho, C., Spence, C., 2007. Head orientation biases tactile localization. *Brain Research* 1144, 136–141. <https://doi.org/10.1016/j.brainres.2007.01.091>
- Holmes, N.P., Sanabria, D., Calvert, G.A., Spence, C., 2007. Tool-Use: Capturing Multisensory Spatial Attention or Extending Multisensory Peripersonal Space? *Cortex* 43, 469–489. [https://doi.org/10.1016/S0010-9452\(08\)70471-4](https://doi.org/10.1016/S0010-9452(08)70471-4)
- Hsiao, S., Yau, J., 2008. Neural basis of haptic perception, in: Grunwald, M. (Ed.), *Human Haptic Perception: Basics and Applications*. Birkhäuser Basel, Basel, pp. 103–112. https://doi.org/10.1007/978-3-7643-7612-3_8
- Imamizu, H., Kuroda, T., Miyauchi, S., Yoshioka, T., Kawato, M., 2003. Modular organization of internal models of tools in the human cerebellum. *Proc. Natl. Acad. Sci. U.S.A.* 100, 5461–5466. <https://doi.org/10.1073/pnas.0835746100>
- Imamizu, H., Miyauchi, S., Tamada, T., Sasaki, Y., Takano, R., Pütz, B., Yoshioka, T., Kawato, M., 2000. Human cerebellar activity representing acquired internal model of a new tool. *Nature* 403, 192–195.
- Iriki, A., Tanaka, M., Iwamura, Y., 1996. Coding of modified body schema during tool use by macaque postcentral neurones. *Neuroreport* 7, 2325–2330. <https://doi.org/10.1097/00001756-199610020-00010>
- Iriki, Atsushi, Tanaka, M., Iwamura, Y., 1996. Coding of modified body schema during tool use by macaque postcentral neurones. *Neuroreport* 7, 2325–2330. <https://doi.org/10.1097/00001756-199610020-00010>

- Japyassú, H.F., Laland, K.N., 2017. Extended spider cognition. *Animal Cognition* 20, 375–395. <https://doi.org/10.1007/s10071-017-1069-7>
- Jenkins, W.M., Merzenich, M.M., 1987. Chapter 21 Reorganization of neocortical representations after brain injury: a neurophysiological model of the bases of recovery from stroke, in: Seil, F.J., Herbert, E., Carlson, B.M. (Eds.), *Progress in Brain Research, Neural Regeneration*. Elsevier, pp. 249–266. [https://doi.org/10.1016/S0079-6123\(08\)61829-4](https://doi.org/10.1016/S0079-6123(08)61829-4)
- Johansson, Roland S., Flanagan, J.R., 2009. Coding and use of tactile signals from the fingertips in object manipulation tasks. *Nat Rev Neurosci* 10, 345–359. <https://doi.org/10.1038/nrn2621>
- Johansson, Roland S., Flanagan, J.R., 2009. Coding and use of tactile signals from the fingertips in object manipulation tasks. *Nature Reviews Neuroscience* 10, 14–20. <https://doi.org/10.1038/nrn2621>
- Johansson, R.S., Westling, G., 1984. Roles of glabrous skin receptors and sensorimotor memory in automatic control of precision grip when lifting rougher or more slippery objects. *Exp Brain Res* 56, 550–564. <https://doi.org/10.1007/BF00237997>
- Johnson, K.O., 2001. The roles and functions of cutaneous mechanoreceptors. *Current Opinion in Neurobiology* 11, 455–461. [https://doi.org/10.1016/S0959-4388\(00\)00234-8](https://doi.org/10.1016/S0959-4388(00)00234-8)
- Johnson-Frey, S.H., 2004. The neural bases of complex tool use in humans. *Trends in Cognitive Sciences* 8, 71–78. <https://doi.org/10.1016/j.tics.2003.12.002>
- Jones, S.R., Kerr, C.E., Wan, Q., Pritchett, D.L., Hamalainen, M., Moore, C.I., 2010. Cued Spatial Attention Drives Functionally Relevant Modulation of the Mu Rhythm in Primary Somatosensory Cortex. *Journal of Neuroscience* 30, 13760–13765. <https://doi.org/10.1523/JNEUROSCI.2969-10.2010>
- Jones, S.R., Pritchett, D.L., Stufflebeam, S.M., Hamalainen, M., Moore, C.I., 2007a. Neural Correlates of Tactile Detection: A Combined Magnetoencephalography and Biophysically Based Computational Modeling Study. *Journal of Neuroscience* 27, 10751–10764. <https://doi.org/10.1523/jneurosci.0482-07.2007>
- Jones, S.R., Pritchett, D.L., Stufflebeam, S.M., Hamalainen, M., Moore, C.I., 2007b. Neural Correlates of Tactile Detection: A Combined Magnetoencephalography and Biophysically Based Computational Modeling Study. *Journal of Neuroscience* 27, 10751–10764. <https://doi.org/10.1523/JNEUROSCI.0482-07.2007>
- Jörntell, H., Bengtsson, F., Geborek, P., Spanne, A., Terekhov, A.V., Hayward, V., 2014a. Segregation of Tactile Input Features in Neurons of the Cuneate Nucleus. *Neuron* 83, 1444–1452. <https://doi.org/10.1016/j.neuron.2014.07.038>
- Jörntell, H., Bengtsson, F., Geborek, P., Spanne, A., Terekhov, A. V., Hayward, V., 2014b. Segregation of tactile input features in neurons of the cuneate nucleus. *Neuron* 83, 1444–1452. <https://doi.org/10.1016/j.neuron.2014.07.038>
- Kassuba, T., Klinge, C., Hölig, C., Menz, M.M., Ptito, M., Röder, B., Siebner, H.R., 2011. The left fusiform gyrus hosts trisensory representations of manipulable objects. *NeuroImage* 56, 1566–1577. <https://doi.org/10.1016/j.neuroimage.2011.02.032>
- Kay, K.N., Weiner, K.S., Grill-Spector, K., 2015. Attention Reduces Spatial Uncertainty in Human Ventral Temporal Cortex. *Current Biology* 25, 595–600. <https://doi.org/10.1016/j.cub.2014.12.050>

- Kekoni, J., Hämäläinen, H., Saarinen, M., Gröhn, J., Reinikainen, K., Lehtokoski, A., Näätänen, R., 1997. Rate effect and mismatch responses in the somatosensory system: ERP-recordings in humans. *Biological Psychology* 46, 125–142. [https://doi.org/10.1016/S0301-0511\(97\)05249-6](https://doi.org/10.1016/S0301-0511(97)05249-6)
- Kerkhoff, G., 2001. Spatial hemineglect in humans. *Progress in Neurobiology* 63, 1–27. [https://doi.org/10.1016/S0301-0082\(00\)00028-9](https://doi.org/10.1016/S0301-0082(00)00028-9)
- Kilteni, K., Ehrsson, H.H., 2017. Sensorimotor predictions and tool use: Hand-held tools attenuate self-touch. *Cognition* 165, 1–9. <https://doi.org/10.1016/j.cognition.2017.04.005>
- Kitazawa, S., 2002. Where conscious sensation takes place. *Consciousness and Cognition* 11, 475–477. [https://doi.org/10.1016/S1053-8100\(02\)00031-4](https://doi.org/10.1016/S1053-8100(02)00031-4)
- Klatzky, R.L., Lederman, S.J., 1999. Tactile roughness perception with a rigid link interposed between skin and surface. *Perception & Psychophysics* 61, 591–607. <https://doi.org/10.3758/BF03205532>
- Kóbor, I., Füredi, L., Kovács, G., Spence, C., Vidnyánszky, Z., 2006. Back-to-front: Improved tactile discrimination performance in the space you cannot see. *Neuroscience Letters* 400, 163–167. <https://doi.org/10.1016/j.neulet.2006.02.037>
- Lackner, J.R., 1988. Some proprioceptive influences on the perceptual representation of body shape and orientation. *Brain* 111, 281–297. <https://doi.org/10.1093/brain/111.2.281>
- Làdavvas, E., Farnè, A., Carletti, M., Zeloni, G., 1994. Neglect determined by the relative location of responses. *Brain* 117, 705–714. <https://doi.org/10.1093/brain/117.4.705>
- LaMotte, R.H., 2000. Softness Discrimination With a Tool. *Journal of Neurophysiology* 83, 1777–1786. <https://doi.org/10.1152/jn.2000.83.4.1777>
- Li, L., Rutlin, M., Abraira, V.E., Cassidy, C., Kus, L., Gong, S., Jankowski, M.P., Luo, W., Heintz, N., Koerber, H.R., Woodbury, C.J., Ginty, D.D., 2011. The Functional Organization of Cutaneous Low-Threshold Mechanosensory Neurons. *Cell* 147, 1615–1627. <https://doi.org/10.1016/j.cell.2011.11.027>
- Lloyd, D.M., Shore, D.I., Spence, C., Calvert, G.A., 2003. Multisensory representation of limb position in human premotor cortex. *Nature Neuroscience* 6, 17–18. <https://doi.org/10.1038/nn991>
- Loewenstein, W.R., Mendelson, M., 1965. Components of receptor adaptation in a Pacinian corpuscle. *J Physiol* 177, 377–397.
- Longo, M.R., Azañón, E., Haggard, P., 2010. More than skin deep: Body representation beyond primary somatosensory cortex. *Neuropsychologia* 48, 655–668. <https://doi.org/10.1016/j.neuropsychologia.2009.08.022>
- Longo, M.R., Lourenco, S.F., 2006. On the nature of near space: Effects of tool use and the transition to far space. *Neuropsychologia* 44, 977–981. <https://doi.org/10.1016/j.neuropsychologia.2005.09.003>
- Loutit, A.J., Vickery, R.M., Potas, J.R., 2021. Functional organization and connectivity of the dorsal column nuclei complex reveals a sensorimotor integration and distribution hub. *J Comp Neurol* 529, 187–220. <https://doi.org/10.1002/cne.24942>

- Ludwig, C.J.H., Gilchrist, I.D., 2002. Stimulus-driven and goal-driven control over visual selection. *Journal of Experimental Psychology: Human Perception and Performance* 28, 902–912. <https://doi.org/10.1037/0096-1523.28.4.902>
- Lungarella, M., Sporns, O., 2006. Mapping information flow in sensorimotor networks. *PLoS Computational Biology* 2, 1301–1312. <https://doi.org/10.1371/journal.pcbi.0020144>
- Luppino, G., Murata, A., Govoni, P., Matelli, M., 1999. Largely segregated parietofrontal connections linking rostral intraparietal cortex (areas AIP and VIP) and the ventral premotor cortex (areas F5 and F4). *Exp Brain Res* 128, 181–187. <https://doi.org/10.1007/s002210050833>
- Macefield, V.G., Häger-Ross, C., Johansson, R.S., 1996. Control of grip force during restraint of an object held between finger and thumb: responses of cutaneous afferents from the digits. *Exp Brain Res* 108, 155–171. <https://doi.org/10.1007/BF00242913>
- Maij, F., Seegelke, C., Medendorp, W.P., Heed, T., 2020. External location of touch is constructed post-hoc based on limb choice. *eLife* 9, e57804. <https://doi.org/10.7554/eLife.57804>
- Maij, F., Wing, A.M., Medendorp, W.P., 2017. Afferent motor feedback determines the perceived location of tactile stimuli in the external space presented to the moving arm. *Journal of Neurophysiology* 118, 187–193. <https://doi.org/10.1152/jn.00286.2016>
- Mancini, F., Longo, M.R., Iannetti, G.D., Haggard, P., 2011. A supramodal representation of the body surface. *Neuropsychologia* 49, 1194–1201. <https://doi.org/10.1016/j.neuropsychologia.2010.12.040>
- Maravita, A., 2002. Active Tool Use with the Contralesional Hand Can Reduce Cross-modal Extinction of Touch on that Hand. *Neurocase* 8, 411–416. <https://doi.org/10.1093/neucas/8.6.411>
- Maravita, A., Husain, M., Clarke, K., Driver, J., 2001. Reaching with a tool extends visual–tactile interactions into far space: evidence from cross-modal extinction. *Neuropsychologia* 39, 580–585. [https://doi.org/10.1016/S0028-3932\(00\)00150-0](https://doi.org/10.1016/S0028-3932(00)00150-0)
- Maravita, A., Iriki, A., 2004. Tools for the body (schema). *Trends in Cognitive Sciences* 8, 79–86. <https://doi.org/10.1016/j.tics.2003.12.008>
- Maria, R., Panchuelo, S., Ackerley, R., Glover, P.M., Bowtell, R.W., Wessberg, J., Francis, S.T., Mcglone, F., 2016. Mapping quantal touch using 7 Tesla functional magnetic resonance imaging and single-unit intraneural microstimulation. *eLife* 1–19. <https://doi.org/10.7554/eLife.12812>
- Maris, E., Oostenveld, R., 2007. Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods* 164, 177–190. <https://doi.org/10.1016/j.jneumeth.2007.03.024>
- Martel, M., Cardinali, L., Bertonati, G., Jouffrais, C., Finos, L., Farnè, A., Roy, A.C., 2019. Somatosensory-guided tool use modifies arm representation for action. *Sci Rep* 9, 5517. <https://doi.org/10.1038/s41598-019-41928-1>
- Martel, M., Cardinali, L., Roy, A.C., Farnè, A., 2016a. Tool-use: An open window into body representation and its plasticity. *Cognitive Neuropsychology* 33, 82–101. <https://doi.org/10.1080/02643294.2016.1167678>
- Martel, M., Cardinali, L., Roy, A.C., Farnè, A., 2016b. Tool-use: An open window into body representation and its plasticity. *Cognitive Neuropsychology* 33, 82–101. <https://doi.org/10.1080/02643294.2016.1167678>

- Medina, J., Coslett, H.B., 2010. From maps to form to space: Touch and the body schema. *Neuropsychologia* 48, 645–654. <https://doi.org/10.1016/j.neuropsychologia.2009.08.017>
- Medina, J., McCloskey, M., Coslett, H.B., Rapp, B., 2014. Somatotopic representation of location: Evidence from the Simon effect. *Journal of Experimental Psychology: Human Perception and Performance* 40, 2131–2142. <https://doi.org/10.1037/a0037975>
- Medina, J., Theodoropoulos, N., Liu, Y., Reyes, P.G., Gherri, E., 2019. External coding and salience in the tactile Simon effect. *Acta Psychologica* 198, 102874. <https://doi.org/10.1016/j.actpsy.2019.102874>
- Mendelson, M., Loewenstein, W.R., 1964. Mechanisms of Receptor Adaptation. *Science* 144, 554–555. <https://doi.org/10.1126/science.144.3618.554>
- Merzenich, M.M., Kaas, J.H., Wall, J., Nelson, R.J., Sur, M., Felleman, D., 1983. Topographic reorganization of somatosensory cortical areas 3b and 1 in adult monkeys following restricted deafferentation. *Neuroscience* 8, 33–55. [https://doi.org/10.1016/0306-4522\(83\)90024-6](https://doi.org/10.1016/0306-4522(83)90024-6)
- Miller, L.E., Cawley-Bennett, A., Longo, M.R., Saygin, A.P., 2017a. The recalibration of tactile perception during tool use is body-part specific. *Experimental Brain Research* 235, 2917–2926. <https://doi.org/10.1007/s00221-017-5028-y>
- Miller, L.E., Cawley-Bennett, A., Longo, M.R., Saygin, A.P., 2017b. The recalibration of tactile perception during tool use is body-part specific. *Experimental Brain Research* 235, 2917–2926. <https://doi.org/10.1007/s00221-017-5028-y>
- Miller, L.E., Fabio, C., Azaroual, M., Muret, D., van Beers, R.J., Farnè, A., Medendorp, W.P., 2022. A neural surveyor to map touch on the body. *Proc Natl Acad Sci USA* 119, e2102233118. <https://doi.org/10.1073/pnas.2102233118>
- Miller, L.E., Fabio, C., Ravenda, V., Bahmad, S., Koun, E., Salemme, R., Luauté, J., Bolognini, N., Hayward, V., Farnè, A., 2019a. Somatosensory Cortex Efficiently Processes Touch Located Beyond the Body. *Current Biology* S0960982219313831. <https://doi.org/10.1016/j.cub.2019.10.043>
- Miller, L.E., Longo, M.R., Saygin, A.P., 2019b. Tool Use Modulates Somatosensory Cortical Processing in Humans. *Journal of Cognitive Neuroscience* 31, 1782–1795. https://doi.org/10.1162/jocn_a_01452
- Miller, L.E., Longo, M.R., Saygin, A.P., 2014. Tool morphology constrains the effects of tool use on body representations. *Journal of Experimental Psychology: Human Perception and Performance* 40, 2143–2153. <https://doi.org/10.1037/a0037777>
- Miller, Luke E., Montroni, L., Koun, E., Salemme, R., Hayward, V., Farnè, A., 2018a. Sensing with tools extends somatosensory processing beyond the body. *Nature* 561, 239–242. <https://doi.org/10.1038/s41586-018-0460-0>
- Miller, Luke E., Montroni, L., Koun, E., Salemme, R., Hayward, V., Farnè, A., 2018. Sensing with tools extends somatosensory processing beyond the body. *Nature* 561, 239–242. <https://doi.org/10.1038/s41586-018-0460-0>
- Miller, Luke E., Montroni, L., Koun, E., Salemme, R., Hayward, V., Farnè, A., 2018b. Sensing with tools extends somatosensory processing beyond the body. *Nature* 561, 239–242. <https://doi.org/10.1038/s41586-018-0460-0>

- Mima, T., Nagamine, T., Nakamura, K., Shibasaki, H., 1998. Attention Modulates Both Primary and Second Somatosensory Cortical Activities in Humans: A Magnetoencephalographic Study. *Journal of Neurophysiology* 80, 2215–2221. <https://doi.org/10.1152/jn.1998.80.4.2215>
- Näätänen, R., 1995. The mismatch negativity: a powerful tool for cognitive neuroscience. *Ear Hear* 16, 6–18.
- Näätänen, R., Paavilainen, P., Rinne, T., Alho, K., 2007. The mismatch negativity (MMN) in basic research of central auditory processing: A review. *Clinical Neurophysiology* 118, 2544–2590. <https://doi.org/10.1016/j.clinph.2007.04.026>
- Naito, E., 2006. Somatic Sensation of Hand-Object Interactive Movement Is Associated with Activity in the Left Inferior Parietal Cortex. *Journal of Neuroscience* 26, 3783–3790. <https://doi.org/10.1523/JNEUROSCI.4835-05.2006>
- Naito, E., Ehrsson, H.H., 2006. Somatic sensation of hand-object interactive movement is associated with activity in the left inferior parietal cortex. *Journal of Neuroscience* 26, 3783–3790. <https://doi.org/10.1523/JNEUROSCI.4835-05.2006>
- Naito, E., Scheperjans, F., Eickhoff, S.B., Amunts, K., Roland, P.E., Zilles, K., Ehrsson, H.H., 2008a. Human superior parietal lobule is involved in somatic perception of bimanual interaction with an external object. *Journal of Neurophysiology* 99, 695–703. <https://doi.org/10.1152/jn.00529.2007>
- Naito, E., Scheperjans, F., Eickhoff, S.B., Amunts, K., Roland, P.E., Zilles, K., Ehrsson, H.H., 2008b. Human Superior Parietal Lobule Is Involved in Somatic Perception of Bimanual Interaction With an External Object. *Journal of Neurophysiology* 99, 695–703. <https://doi.org/10.1152/jn.00529.2007>
- Nakata, H., Inui, K., Nishihira, Y., Hatta, A., Sakamoto, M., Kida, T., Wasaka, T., Kakigi, R., 2004. Effects of a go/nogo task on event-related potentials following somatosensory stimulation. *Clinical Neurophysiology* 115, 361–368. <https://doi.org/10.1016/j.clinph.2003.09.013>
- Neuper, C., Wörtz, M., Pfurtscheller, G., 2006. ERD/ERS patterns reflecting sensorimotor activation and deactivation, in: *Progress in Brain Research*. Elsevier, pp. 211–222. [https://doi.org/10.1016/S0079-6123\(06\)59014-4](https://doi.org/10.1016/S0079-6123(06)59014-4)
- Nou M., Sato K., Shimokawa F., Ishizuka H., 2020. How does Kitchen Knife Cause Different Sensation? *Transactions of Japan Society of Kansei Engineering* 19, 301–307. <https://doi.org/10.5057/jjske.TJSKE-D-20-00012>
- Orlov, T., Makin, T.R., Zohary, E., 2010. Topographic Representation of the Human Body in the Occipitotemporal Cortex. *Neuron* 68, 586–600. <https://doi.org/10.1016/j.neuron.2010.09.032>
- Ossandón, J.P., König, P., Heed, T., 2020. No Evidence for a Role of Spatially Modulated α -Band Activity in Tactile Remapping and Short-Latency, Overt Orienting Behavior. *J. Neurosci.* 40, 9088–9102. <https://doi.org/10.1523/JNEUROSCI.0581-19.2020>
- Overvliet, K.E., Azañón, E., Soto-Faraco, S., 2011a. Somatosensory saccades reveal the timing of tactile spatial remapping. *Neuropsychologia* 49, 3046–3052. <https://doi.org/10.1016/j.neuropsychologia.2011.07.005>

- Overvliet, K.E., Azañón, E., Soto-Faraco, S., 2011b. Somatosensory saccades reveal the timing of tactile spatial remapping. *Neuropsychologia* 49, 3046–3052. <https://doi.org/10.1016/j.neuropsychologia.2011.07.005>
- Pagel, B., Heed, T., Röder, B., 2009. Change of reference frame for tactile localization during child development: Reference frame for tactile localization in children. *Developmental Science* 12, 929–937. <https://doi.org/10.1111/j.1467-7687.2009.00845.x>
- Pantev, C., Ross, B., Fujioka, T., Trainor, L.J., Schulte, M., Schulz, M., 2003. Music and Learning-Induced Cortical Plasticity. *Annals of the New York Academy of Sciences* 999, 438–450. <https://doi.org/10.1196/annals.1284.054>
- Pascual-Marqui, R.D., 2002. Standardized low resolution brain electromagnetic. *Clinical Pharmacology* 16.
- Peck, A.J., Jeffers, R.G., Carello, C., Turvey, M.T., 1996. Haptically Perceiving the Length of One Rod by Means of Another. *Ecological Psychology* 8, 237–258. https://doi.org/10.1207/s15326969eco0803_3
- Peeters, R., Simone, L., Nelissen, K., Fabbri-Destro, M., Vanduffel, W., Rizzolatti, G., Orban, G.A., 2009. The Representation of Tool Use in Humans and Monkeys: Common and Uniquely Human Features. *Journal of Neuroscience* 29, 11523–11539. <https://doi.org/10.1523/JNEUROSCI.2040-09.2009>
- Pegna, A.J., Petit, L., Caldara-Schnetzer, A.-S., Khateb, A., Annoni, J.-M., Sztajzel, R., Landis, T., 2001. So near yet so far: Neglect in far or near space depends on tool use. *Annals of Neurology* 50, 820–822. <https://doi.org/10.1002/ana.10058>
- Penfield, W., Boldrey, E., 1937. SOMATIC MOTOR AND SENSORY REPRESENTATION IN THE CEREBRAL CORTEX OF MAN AS STUDIED BY ELECTRICAL STIMULATION. *Brain* 60, 389–443. <https://doi.org/10.1093/brain/60.4.389>
- Penfield, W., Rasmussen, T., 1950. The cerebral cortex of man; a clinical study of localization of function, The cerebral cortex of man; a clinical study of localization of function. Macmillan, Oxford, England.
- Pesaran, B., Nelson, M.J., Andersen, R.A., 2006. Dorsal Premotor Neurons Encode the Relative Position of the Hand, Eye, and Goal during Reach Planning. *Neuron* 51, 125–134. <https://doi.org/10.1016/j.neuron.2006.05.025>
- Pfurtscheller, G., Woertz, M., Krausz, G., Neuper, C., 2001. Distinction of different fingers by the frequency of stimulus induced beta oscillations in the human EEG. *Neuroscience Letters* 4.
- Pietrini, P., Furey, M.L., Ricciardi, E., Gobbin, M.I., Wu, W.-H.C., Cohen, L., Guazzelli, M., Haxby, J.V., 2004. Beyond sensory images: Object-based representation in the human ventral pathway. *Proceedings of the National Academy of Sciences* 101, 5658–5663. <https://doi.org/10.1073/pnas.0400707101>
- Pouget, A., 2002. Multisensory spatial representations in eye-centered coordinates for reaching. *Cognition* 83, B1–B11. [https://doi.org/10.1016/S0010-0277\(01\)00163-9](https://doi.org/10.1016/S0010-0277(01)00163-9)
- Povinelli, D.J., Reaux, J.E., Frey, S.H., 2010. Chimpanzees' context-dependent tool use provides evidence for separable representations of hand and tool even during active use within

- peripersonal space. *Neuropsychologia* 48, 243–247.
<https://doi.org/10.1016/j.neuropsychologia.2009.09.010>
- Rasmusson, D.D., Turnbull, B.G., 1983. Immediate effects of digit amputation on SI cortex in the raccoon: Unmasking of inhibitory fields. *Brain Research* 288, 368–370.
[https://doi.org/10.1016/0006-8993\(83\)90120-8](https://doi.org/10.1016/0006-8993(83)90120-8)
- Rihs, T.A., Michel, C.M., Thut, G., 2007. Mechanisms of selective inhibition in visual spatial attention are indexed by β -band EEG synchronization. *Eur J Neurosci* 25, 603–610.
<https://doi.org/10.1111/j.1460-9568.2007.05278.x>
- Roberts, R.D., Wing, A.M., Durkin, J., Humphreys, G.W., 2003. Effects Of Posture On Tactile Temporal Order Judgements.
- Röder, B., Föcker, J., Hötting, K., Spence, C., 2008a. Spatial coordinate systems for tactile spatial attention depend on developmental vision: evidence from event-related potentials in sighted and congenitally blind adult humans. *European Journal of Neuroscience* 28, 475–483.
<https://doi.org/10.1111/j.1460-9568.2008.06352.x>
- Röder, B., Föcker, J., Hötting, K., Spence, C., 2008b. Spatial coordinate systems for tactile spatial attention depend on developmental vision: evidence from event-related potentials in sighted and congenitally blind adult humans. *European Journal of Neuroscience* 28, 475–483.
<https://doi.org/10.1111/j.1460-9568.2008.06352.x>
- Röder, B., Rösler, F., Spence, C., 2004. Early Vision Impairs Tactile Perception in the Blind. *Current Biology* 14, 121–124. <https://doi.org/10.1016/j.cub.2003.12.054>
- Romano, D., Uberti, E., Caggiano, P., Cocchini, G., Maravita, A., 2019. Different tool training induces specific effects on body metric representation. *Exp Brain Res* 237, 493–501.
<https://doi.org/10.1007/s00221-018-5405-1>
- Ronga, I., Galigani, M., Bruno, V., Castellani, N., Rossi Sebastiano, A., Valentini, E., Fossataro, C., Neppi-Modona, M., Garbarini, F., 2021. Seeming confines: Electrophysiological evidence of peripersonal space remapping following tool-use in humans. *Cortex* 144, 133–150.
<https://doi.org/10.1016/j.cortex.2021.08.004>
- Rothwell, J.C., 1987. Proprioceptors in Muscle, Joint and Skin, in: Rothwell, J.C. (Ed.), *Control of Human Voluntary Movement*. Springer US, Boston, MA, pp. 74–104. https://doi.org/10.1007/978-1-4684-7688-0_4
- Ruzzoli, M., Soto-Faraco, S., 2014. Alpha Stimulation of the Human Parietal Cortex Attunes Tactile Perception to External Space. *Current Biology* 24, 329–332.
<https://doi.org/10.1016/j.cub.2013.12.029>
- Saal, H.P., Delhay, B.P., Rayhaun, B.C., Bensmaia, S.J., 2017. Simulating tactile signals from the whole hand with millisecond precision. *Proceedings of the National Academy of Sciences* 114, E5693–E5702. <https://doi.org/10.1073/pnas.1704856114>
- Saig, A., Gordon, G., Assa, E., Arieli, A., Ahissar, E., 2012. Motor-Sensory Confluence in Tactile Perception. *Journal of Neuroscience* 32, 14022–14032.
<https://doi.org/10.1523/JNEUROSCI.2432-12.2012>

- Salenius, S., Schnitzler, A., Salmelin, R., Jousmäki, V., Hari, R., 1997. Modulation of Human Cortical Rolandic Rhythms during Natural Sensorimotor Tasks. *NeuroImage* 5, 221–228. <https://doi.org/10.1006/nimg.1997.0261>
- Salmelin, R., Hari, R., 1994. Spatiotemporal characteristics of sensorimotor neuromagnetic rhythms related to thumb movement. *Neuroscience* 60, 537–550. [https://doi.org/10.1016/0306-4522\(94\)90263-1](https://doi.org/10.1016/0306-4522(94)90263-1)
- Samaha, J., Sprague, T.C., Postle, B.R., 2016. Decoding and Reconstructing the Focus of Spatial Attention from the Topography of Alpha-band Oscillations. *Journal of Cognitive Neuroscience* 28, 1090–1097. https://doi.org/10.1162/jocn_a_00955
- Sambo, C.F., Forster, B., 2009. An ERP Investigation on Visuotactile Interactions in Peripersonal and Extrapersonal Space: Evidence for the Spatial Rule. *Journal of Cognitive Neuroscience* 21, 1550–1559. <https://doi.org/10.1162/jocn.2009.21109>
- Sambo, C.F., Torta, D.M., Gallace, A., Liang, M., Moseley, G.L., Iannetti, G.D., 2013. The temporal order judgement of tactile and nociceptive stimuli is impaired by crossing the hands over the body midline. *PAIN* 154, 242–247. <https://doi.org/10.1016/j.pain.2012.10.010>
- Sauseng, P., Klimesch, W., Stadler, W., Schabus, M., Doppelmayr, M., Hanslmayr, S., Gruber, W.R., Birbaumer, N., 2005. A shift of visual spatial attention is selectively associated with human EEG alpha activity. *European Journal of Neuroscience* 22, 2917–2926. <https://doi.org/10.1111/j.1460-9568.2005.04482.x>
- Schaefer, M., Rothenmund, Y., Heinze, H.-J., Rotte, M., 2004. Short-term plasticity of the primary somatosensory cortex during tool use: *NeuroReport* 15, 1293–1297. <https://doi.org/10.1097/01.wnr.0000129573.36301.db>
- Schendan, H.E., Kutas, M., 2003. Time course of processes and representations supporting visual object identification and memory. *Journal of Cognitive Neuroscience* 15, 111–135. <https://doi.org/10.1162/089892903321107864>
- Schicke, T., Roder, B., 2006. Spatial remapping of touch: Confusion of perceived stimulus order across hand and foot. *Proceedings of the National Academy of Sciences* 103, 11808–11813. <https://doi.org/10.1073/pnas.0601486103>
- Schubert, J.T.W., Badde, S., Röder, B., Heed, T., 2017. Task demands affect spatial reference frame weighting during tactile localization in sighted and congenitally blind adults. *PLoS ONE* 12. <https://doi.org/10.1371/journal.pone.0189067>
- Schubert, J.T.W., Buchholz, V.N., Föcker, J., Engel, A.K., Röder, B., Heed, T., 2019. Alpha-band oscillations reflect external spatial coding for tactile stimuli in sighted, but not in congenitally blind humans. *Sci Rep* 9, 9215. <https://doi.org/10.1038/s41598-019-45634-w>
- Schubert, J.T.W., Buchholz, V.N., Föcker, J., Engel, A.K., Röder, B., Heed, T., 2015a. Oscillatory activity reflects differential use of spatial reference frames by sighted and blind individuals in tactile attention. *NeuroImage* 117, 417–428. <https://doi.org/10.1016/j.neuroimage.2015.05.068>
- Schubert, J.T.W., Buchholz, V.N., Föcker, J., Engel, A.K., Röder, B., Heed, T., 2015b. Oscillatory activity reflects differential use of spatial reference frames by sighted and blind individuals in tactile attention. *NeuroImage* 117, 417–428. <https://doi.org/10.1016/j.neuroimage.2015.05.068>

- Schwenkreis, P., El Tom, S., Ragert, P., Pleger, B., Tegenthoff, M., Dinse, H.R., 2007. Assessment of sensorimotor cortical representation asymmetries and motor skills in violin players. *European Journal of Neuroscience* 26, 3291–3302. <https://doi.org/10.1111/j.1460-9568.2007.05894.x>
- Schwoebel, J., Coslett, H.B., 2005. Evidence for Multiple, Distinct Representations of the Human Body. *Journal of Cognitive Neuroscience* 17, 543–553. <https://doi.org/10.1162/0898929053467587>
- Seed, A., Byrne, R., 2010. Animal tool-use. *Curr Biol* 20, R1032–1039. <https://doi.org/10.1016/j.cub.2010.09.042>
- Serino, A., Bassolino, M., Farnè, A., Làdavas, E., 2007. Extended Multisensory Space in Blind Cane Users. *Psychological Science* 18, 642–648. <https://doi.org/10.1111/j.1467-9280.2007.01952.x>
- Serino, A., Canzoneri, E., Marzolla, M., di Pellegrino, G., Magosso, E., 2015. Extending peripersonal space representation without tool-use: evidence from a combined behavioral-computational approach. *Front. Behav. Neurosci.* 9. <https://doi.org/10.3389/fnbeh.2015.00004>
- Serino, A., Haggard, P., 2010. Touch and the body. *Neuroscience & Biobehavioral Reviews* 34, 224–236. <https://doi.org/10.1016/j.neubiorev.2009.04.004>
- Shen, G., Smyk, N.J., Meltzoff, A.N., Marshall, P.J., 2018. Neuropsychology of human body parts: Exploring categorical boundaries of tactile perception using somatosensory mismatch responses. *Journal of Cognitive Neuroscience* 30, 1858–1869. https://doi.org/10.1162/jocn_a_01313
- Shinozaki, N., Yabe, H., Sutoh, T., Hiruma, T., Kaneko, S., 1998. Somatosensory automatic responses to deviant stimuli. *Cognitive Brain Research* 7, 165–171. [https://doi.org/10.1016/S0926-6410\(98\)00020-2](https://doi.org/10.1016/S0926-6410(98)00020-2)
- Shore, D.I., Gray, K., Spry, E., Spence, C., 2005. Spatial Modulation of Tactile Temporal-Order Judgments. *Perception* 34, 1251–1262. <https://doi.org/10.1068/p3313>
- Shore, D.I., Spry, E., Spence, C., 2002. Confusing the mind by crossing the hands. *Cognitive Brain Research* 14, 153–163. [https://doi.org/10.1016/S0926-6410\(02\)00070-8](https://doi.org/10.1016/S0926-6410(02)00070-8)
- Shumaker, R.W., Walkup, K.R., Beck, B.B., 2011. *Animal Tool Behavior: The Use and Manufacture of Tools by Animals*. JHU Press.
- Simon, J.R., 1969. Reactions toward the source of stimulation. *Journal of Experimental Psychology* 81, 174–176. <https://doi.org/10.1037/h0027448>
- Simoncelli, E.P., Olshausen, B.A., 2001. Natural Image Statistics and Neural Representation. *Annual Review of Neuroscience* 24, 1193–1216. <https://doi.org/10.1146/annurev.neuro.24.1.1193>
- Smania, N., Aglioti, S., 1995. Sensory and spatial components of somaesthetic deficits following right brain damage. *Neurology* 45, 1725–1730. <https://doi.org/10.1212/WNL.45.9.1725>
- Soechtin, J.F., Flanders, M., 1992. Moving in three-dimensional space: frames of reference, vectors, and coordinate systems. *Annual review of neuroscience* 15, 167–191.
- Soto-Faraco, S., Azañón, E., 2013a. Electrophysiological correlates of tactile remapping. *Neuropsychologia* 51, 1584–1594. <https://doi.org/10.1016/j.neuropsychologia.2013.04.012>
- Soto-Faraco, S., Azañón, E., 2013b. Electrophysiological correlates of tactile remapping. *Neuropsychologia* 51, 1584–1594. <https://doi.org/10.1016/j.neuropsychologia.2013.04.012>

- Soto-Faraco, S., Ronald, A., Spence, C., 2004. Tactile selective attention and body posture: Assessing the multisensory contributions of vision and proprioception. *Perception & Psychophysics* 66, 1077–1094. <https://doi.org/10.3758/BF03196837>
- Sposito, A., Bolognini, N., Vallar, G., Maravita, A., 2012. Extension of perceived arm length following tool-use: Clues to plasticity of body metrics. *Neuropsychologia* 50, 2187–2194. <https://doi.org/10.1016/j.neuropsychologia.2012.05.022>
- Sposito, A.V., Bolognini, N., Vallar, G., Posteraro, L., Maravita, A., 2010. The spatial encoding of body parts in patients with neglect and neurologically unimpaired participants. *Neuropsychologia* 48, 334–340. <https://doi.org/10.1016/j.neuropsychologia.2009.09.026>
- Strömmer, J.M., Tarkka, I.M., Astikainen, P., 2014. Somatosensory mismatch response in young and elderly adults. *Frontiers in Aging Neuroscience* 6, 1–9. <https://doi.org/10.3389/fnagi.2014.00293>
- Sur, M., Merzenich, M.M., Kaas, J.H., 1980. Magnification, receptive-field area, and “hypercolumn” size in areas 3b and 1 of somatosensory cortex in owl monkeys. *Journal of Neurophysiology* 44, 295–311. <https://doi.org/10.1152/jn.1980.44.2.295>
- Tadel, F., Baillet, S., Mosher, J.C., Pantazis, D., Leahy, R.M., 2011. Brainstorm: A User-Friendly Application for MEG/EEG Analysis. *Computational Intelligence and Neuroscience* 2011, 1–13. <https://doi.org/10.1155/2011/879716>
- Takahashi, T., Kansaku, K., Wada, M., Shibuya, S., Kitazawa, S., 2013. Neural Correlates of Tactile Temporal-Order Judgment in Humans: an fMRI Study. *Cerebral Cortex* 23, 1952–1964. <https://doi.org/10.1093/cercor/bhs179>
- Tales, A., Newton, P., Troscianko, T., Butler, S., 1999. Mismatch negativity in the visual modality. *NeuroReport* 10, 3363–3367.
- Tamè, L., Azañón, E., Longo, M.R., 2019. A Conceptual Model of Tactile Processing across Body Features of Size, Shape, Side, and Spatial Location. *Frontiers in Psychology* 10. <https://doi.org/10.3389/fpsyg.2019.00291>
- Tamè, L., Braun, C., Lingnau, A., Schwarzbach, J., Demarchi, G., Li Hegner, Y., Farnè, A., Pavani, F., 2012. The Contribution of Primary and Secondary Somatosensory Cortices to the Representation of Body Parts and Body Sides: An fMRI Adaptation Study. *Journal of Cognitive Neuroscience* 24, 2306–2320. https://doi.org/10.1162/jocn_a_00272
- Tamè, L., Farnè, A., Pavani, F., 2011. Spatial coding of touch at the fingers: Insights from double simultaneous stimulation within and between hands. *Neuroscience Letters* 487, 78–82. <https://doi.org/10.1016/j.neulet.2010.09.078>
- Tamè, L., Pavani, F., Papadelis, C., Farnè, A., Braun, C., 2015. Early integration of bilateral touch in the primary somatosensory cortex. *Human Brain Mapping* 36, 1506–1523. <https://doi.org/10.1002/hbm.22719>
- Taylor-Clarke, M., Jacobsen, P., Haggard, P., 2004. Keeping the world a constant size: object constancy in human touch. *Nat Neurosci* 7, 219–220. <https://doi.org/10.1038/nn1199>
- Tinazzi, M., Ferrari, G., Zampini, M., Aglioti, S.M., 2000. Neuropsychological evidence that somatic stimuli are spatially coded according to multiple frames of reference in a stroke patient with

- tactile extinction. *Neuroscience Letters* 287, 133–136. [https://doi.org/10.1016/S0304-3940\(00\)01157-5](https://doi.org/10.1016/S0304-3940(00)01157-5)
- Tsukamoto, Y., 2000. Pinpointing of an Upper Limb Prosthesis. *JPO: Journal of Prosthetics and Orthotics* 12, 5–6.
- Tuthill, J.C., Azim, E., 2018. Proprioception. *Current Biology* 28, R194–R203. <https://doi.org/10.1016/j.cub.2018.01.064>
- Umiltà, M., Escola, L., Intskirveli, I., Grammont, F., Rochat, M., Caruana, F., Jezzini, A., Gallese, V., Rizzolatti, G., 2008. When pliers become fingers in the monkey motor system. *Proceedings of the National Academy of Sciences* 105, 2209–2213.
- Umiltà, M.A., Escola, L., Intskirveli, I., Grammont, F., Rochat, M., Caruana, F., Jezzini, A., Gallese, V., Rizzolatti, G., 2008. When pliers become fingers in the monkey motor system. *Proceedings of the National Academy of Sciences* 105, 2209–2213. <https://doi.org/10.1073/pnas.0705985105>
- Unwalla, K., Goldreich, D., Shore, D.I., 2021. Exploring Reference Frame Integration Using Response Demands in a Tactile Temporal-Order Judgement Task. *Multisens. Res.* 34, 807–838. <https://doi.org/10.1163/22134808-bja10057>
- Vallar, G., 1993. The anatomical basis of spatial hemineglect in humans, in: *Unilateral Neglect: Clinical and Experimental Studies, Brain Damage, Behaviour & Cognition Series*. Lawrence Erlbaum Associates, Inc, Hillsdale, NJ, US, pp. 27–59.
- Vallar, G., Maravita, A., 2009. Personal and Extrapersonal Spatial Perception, in: Berntson, G.G., Cacioppo, J.T. (Eds.), *Handbook of Neuroscience for the Behavioral Sciences*. John Wiley & Sons, Inc., Hoboken, NJ, USA, p. neubb001016. <https://doi.org/10.1002/9780470478509.neubb001016>
- Vallar, G., Perani, D., 1987. The Anatomy of Spatial Neglect in Humans, in: Jeannerod, M. (Ed.), *Advances in Psychology, Neurophysiological and Neuropsychological Aspects of Spatial Neglect*. North-Holland, pp. 235–258. [https://doi.org/10.1016/S0166-4115\(08\)61716-1](https://doi.org/10.1016/S0166-4115(08)61716-1)
- Vallar, G., Rusconi, M.L., Bignamini, L., Geminiani, G., Perani, D., 1994. Anatomical correlates of visual and tactile extinction in humans: a clinical CT scan study. *Journal of Neurology, Neurosurgery & Psychiatry* 57, 464–470. <https://doi.org/10.1136/jnnp.57.4.464>
- Vallbo, A.B., Johansson, R.S., 1984. Properties of cutaneous mechanoreceptors in the human hand related to touch sensation. *Human Neurobiology* 3–14.
- Valle, G., Mazzoni, A., Iberite, F., D’Anna, E., Strauss, I., Granata, G., Controzzi, M., Clemente, F., Rognini, G., Cipriani, C., Stieglitz, T., Petrini, F.M., Rossini, P.M., Micera, S., 2018. Biomimetic Intra-neural Sensory Feedback Enhances Sensation Naturalness, Tactile Sensitivity, and Manual Dexterity in a Bidirectional Prosthesis. *Neuron* 100, 37–45. <https://doi.org/10.1016/j.neuron.2018.08.033>
- van Ede, F., Chekroud, S.R., Stokes, M.G., Nobre, A.C., 2019. Concurrent visual and motor selection during visual working memory guided action. *Nature Neuroscience* 22, 477–483. <https://doi.org/10.1038/s41593-018-0335-6>
- van Ede, F., de Lange, F., Jensen, O., Maris, E., 2011. Orienting Attention to an Upcoming Tactile Event Involves a Spatially and Temporally Specific Modulation of Sensorimotor Alpha- and Beta-Band

- Oscillations. *Journal of Neuroscience* 31, 2016–2024. <https://doi.org/10.1523/JNEUROSCI.5630-10.2011>
- van Ede, F., Jensen, O., Maris, E., 2010. Tactile expectation modulates pre-stimulus β -band oscillations in human sensorimotor cortex. *NeuroImage* 51, 867–876. <https://doi.org/10.1016/j.neuroimage.2010.02.053>
- van Ede, F., Szebényi, S., Maris, E., 2014. Attentional modulations of somatosensory alpha, beta and gamma oscillations dissociate between anticipation and stimulus processing. *NeuroImage* 97, 134–141. <https://doi.org/10.1016/j.neuroimage.2014.04.047>
- Van Pelt, S., Toni, I., Diedrichsen, J., Medendorp, W.P., 2010. Repetition Suppression Dissociates Spatial Frames of Reference in Human Saccade Generation. *Journal of Neurophysiology* 104, 1239–48. <https://doi.org/10.1152/jn.00393.2010>
- Vaught, G.M., Simpson, W.E., Ryder, R., 1968. Feeling with a stick. *Perceptual and Motor Skills* 26, 848–848. <https://doi.org/10.2466/pms.1968.26.3.848>
- Vazquez, Y., Salinas, E., Romo, R., 2013. Transformation of the neural code for tactile detection from thalamus to cortex. *Proceedings of the National Academy of Sciences* 110, E2635–E2644. <https://doi.org/10.1073/pnas.1309728110>
- Wada, M., Takano, K., Ikegami, S., Ora, H., Spence, C., Kansaku, K., 2012. Spatio-Temporal Updating in the Left Posterior Parietal Cortex. *PLoS ONE* 7, e39800. <https://doi.org/10.1371/journal.pone.0039800>
- Watanabe, J., Nakatani, M., Ando, H., Tachi, S., 2009. Haptic localizations for onset and offset of vibrotactile stimuli are dissociated. *Exp Brain Res* 193, 483–489. <https://doi.org/10.1007/s00221-009-1711-y>
- Weinstein, S., 1968. Intensive and Extensive Aspects of Tactile Sensitivity as a Function of Body Part, Sex and Laterality. *The Skin Senses* 195–218.
- Witt, J.K., Proffitt, D.R., Epstein, W., 2005. Tool Use Affects Perceived Distance, But Only When You Intend to Use It. *Journal of Experimental Psychology: Human Perception and Performance* 31, 880–888. <https://doi.org/10.1037/0096-1523.31.5.880>
- Yamamoto, Shinya, Kitazawa, S., 2001a. Reversal of subjective temporal order due to arm crossing. *Nat Neurosci* 4, 759–765. <https://doi.org/10.1038/89559>
- Yamamoto, Shinya, Kitazawa, S., 2001b. Sensation at the tips of invisible tools. *Nature neuroscience* 4, 979–980.
- Yamamoto, S., Kitazawa, S., 2001. Sensation at the tips of invisible tools. *Nature neuroscience* 4, 979–980. <https://doi.org/10.1038/neuro721>
- Yamamoto, S., Moizumi, S., Kitazawa, S., 2005. Referral of Tactile Sensation to the Tips of L-Shaped Sticks. *Journal of Neurophysiology* 93, 2856–2863. <https://doi.org/10.1152/jn.01015.2004>
- Yoshioka, T., Bensmaïa, S.J., Craig, J.C., Hsiao, S.S., 2007. Texture perception through direct and indirect touch: An analysis of perceptual space for tactile textures in two modes of exploration. *Somatosensory & Motor Research* 24, 53–70. <https://doi.org/10.1080/08990220701318163>
- Young, R.W., 2003. Evolution of the human hand : the role of throwing and clubbing. *Journal of Anatomy*. <https://doi.org/10.1046/j.1469-7580.2003.00144.x>. Copyright

- Yue, Z., Bischof, G.-N., Zhou, X., Spence, C., Röder, B., 2009. Spatial attention affects the processing of tactile and visual stimuli presented at the tip of a tool: an event-related potential study. *Exp Brain Res* 193, 119–128. <https://doi.org/10.1007/s00221-008-1599-y>
- Zeharia, N., Hertz, U., Flash, T., Amedi, A., 2012. Negative blood oxygenation level dependent homunculus and somatotopic information in primary motor cortex and supplementary motor area. *Proceedings of the National Academy of Sciences* 109, 18565–18570. <https://doi.org/10.1073/pnas.1119125109>