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Section I: Visuospatial cognition and body perception

Somatosensation and body perception: the integration of afferent signals in multisensory cognitive processes

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Humans have evolved to interact smoothly with their environment and with others. There are highly complex processes that enable these interactions and many systems are engaged, from the peripheral somatosensory system to a distributed network of cortical regions. This chapter will address the pathway from the peripheral receptors to the brain, including steps where there is the potential for the processing and integration of information, as well as why these have occurred in our evolution. We have a vast system of somatosensory afferents that are distributed over our skin and in our bodies to capture precise signals about our interactions with the world. Somatosensory afference comes from mechanical, thermal, and chemical stimuli, where numerous different types of somatosensory afferent, namely those that respond to mechanoreceptive, thermoreceptive, and/or nociceptive signals respectively, register specific contact and behavior. These signals are persistent and there is considerable integration of this information even before it reaches the brain. Once the input reaches sub-cortical structures and is passed on to the cerebral cortex, there is again a wealth of processes that interact smoothly, to produce the awareness of our body in space and its interactions. These include principal somatosensory targets, such as the primary (S1) and secondary (S2) somatosensory cortices, and the insula. In the integration of information, many other regions are involved, including the activation of a range of cognitive (e.g. attention, memory, learning) and emotional/affective mechanisms, as well as multisensory processing. This chapter will consider the intricacies of these processes, by exploring the sensory origin of body perception.

Key words: Touch, tactile, body, human, perception, temperature, nociception, mechanoreception, afferent

Our skin encompasses the entire body and is our largest sensory organ. It not only holds us together and acts as a barrier, but it receives constant stimulation from the external world and gives us a sense of embodiment. Within our skin and body, we have a vast system of afferents that encode mechanical, thermal, and chemical stimuli and send it to the brain for processing and integration, which have developed for better adaptation to our environment through evolution over millions of years. Our afferent system has evolved to allow us to effortlessly interact with the world and can provide both warning (e.g. pain) and pleasurable (e.g. a gentle caress) information. The somatosensory afferent system can be divided in many ways, such as differences between skin type, skin innervation, or between exteroception and interoception; however, it is highly complex and exhibits large differences between individuals. The chapter will deal mainly with information coming from the skin, but it is important to consider somatosensation from the whole body, which includes the muscles, joints, connective tissue, fascia, viscera, and internal sensing.

In early work, Sherrington described different senses, which included divisions into teloreception (vision, audition), proprioception (body position in space), chemoreception (olfaction, gustation), exteroception (touch, including mechanoreception, thermoreception, and nociception), and interoception (visceral sensing) (Sherrington, 1948). There have been debates to the distinction between exteroception and interoception, and it is clearly a complicated division, but it is generally agreed that exteroception concerns the relationship between the body and the external environment, whereas interoception is the representation of the physiological condition of the body (Craig, 2002). Hence, it is possible that some bodily receptors could be considered both as exteroceptive and interoceptive, such as in affective sensations of pain and pleasure, which can be encoded directly by the skin, but produce emotional responses that impact on homeostatic processes. In this way, sensation refers to the feelings produced about states of the sense organs and nervous system, whereas perception is defined as the interpretation and awareness we gain from the activation of our sensory organs. In the present chapter, the complexity of the somatosensory system will be addressed, with the implications for central processing and its integration with other sensory and cognitive mechanisms.

The sensory origin of body perception

The sensory input from our body comes in the form of many different channels, which are integrated centrally to give our sense of self and bodily perception. The source of these signals is primarily from the skin, but internal sensors in tissue such as muscles, joints, and receptors inside the core of the body, also contribute. Further, our other senses can influence body perception, for example, seeing our body (e.g. looking at our feet to help us walk over rough terrain), hearing our body (e.g. when something touching our skin makes a noise), and even how our body normally smells and tastes, where we may feel different if these inputs change. Although the direct measurement of these processes can be challenging, often due to the complicated nature of our body and environment, there are a number of useful methods to approach these questions. For example, microneurography can be used to measure the activity

in peripheral nerves (for a review, see Ackerley and Watkins, 2022), electrodermal analysis can tell us about emotional responses to touch (Ree et al., 2019; Fedato et al., 2020; see also Chapter 12), electromyography can be used to quantify the use of muscles (Mayo et al., 2018; Ree et al., 2019), and perceptual ratings help us to understand the feelings generated (Ackerley, Saar, et al., 2014; Sailer, Hausmann and Croy, 2020). Below, information from the skin will be first covered in detail, then with consideration of the impact of other sensory inputs.

Somatosensation from the skin

The skin contains numerous specialized receptors to sense mechanical, thermal, and chemical stimuli applied to the body (Figure 1). A recent comprehensive review and analysis of body innervation density stated that there are >1 million fibers in the dorsal roots of the spinal cord in total, which include large-, medium-, and thinly-myelinated fibers to unmyelinated fibers, and it was estimated that a young human adult body has ~230,000 myelinated Aβ mechanoreceptive afferents, although we lose about 5% of our afferents every decade of adulthood (Corniani and Saal, 2020). The capacity of the sensory afferent system is therefore vast; however, the brain processes this input efficiently and effortlessly. The skin itself is highly heterogeneous, where different skin regions have different sensitivities to stimuli, containing several afferent classes, in varying densities.

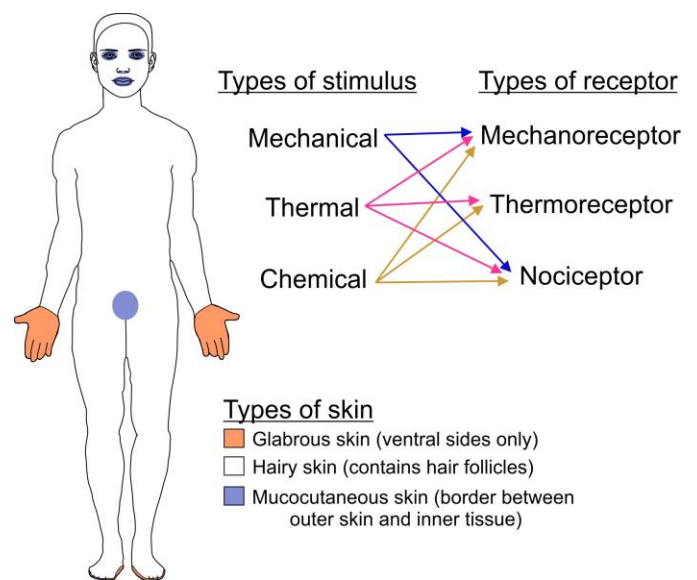


Figure 1: Overview of different skin types, stimuli that impact on the body, and the classes of receptors that can encode this.

Skin can be generally divided into glabrous skin of the ventral hands and feet, hairy skin, and mucocutaneous skin (e.g., mouth, nose, eyes, genitals). Three main types of stimuli can impact the body, namely of mechanical, thermal, and/or chemical sources, where these are encoded by different types of receptors.

Overall, the skin can be divided into glabrous (non-hairy), hairy, and mucocutaneous skin (Figure 1). The vast majority of the skin (90%) can be classed as hairy skin, as it contains hair follicles. The hairs can be very small and thin (e.g., vellus hairs), or thick and long (e.g., scalp terminal hairs), but this is all defined as hairy skin. Thus, the length and diameter of hairs can differ greatly, as well as hair follicle density, which can vary by more than an order of magnitude across the skin (Szabo, 1967), and vellus hairs account for 80-90% of all hairs (Halata, 1993). It is clear that some skin regions contain many thick, terminal hairs (e.g., scalp, dorsal arms), but there is no significant difference between males and females in hair density itself (Szabo, 1967), only the type of hair differs (i.e., whether it is thick terminal hair or thin vellus hair). It is also noteworthy that the density of hair follicles in human skin is equivalent to that of an similar-sized animal (Schwartz and Rosenblum, 1981). Glabrous skin is defined as the non-hairy skin of the ventral hands and feet, which also has ridges (e.g., fingerprints) that are most obvious on the finger and toe pads. Mucocutaneous skin can almost be classed as a type of border skin, which is the surface between the outer skin and inner bodily tissue. Mucocutaneous skin is often wet (e.g., eyes, mouth, genitals) and needs to be maintained in this state of higher water content. The borders between all skin types are not well-defined, where there is often a smooth transition between skin types, for example, the dorsal sides of the finger tips are classed as hairy skin, but there are virtually no hairs present.

The skin can be divided into at least two layers that are somewhat different in thickness over the skin and estimates of thickness can vary. The epidermis is the top, outer layer of the skin, which also includes the very most outer surface: the stratum corneum. Underneath is the thicker dermis, which is a supporting layer that contains connective tissue. Although the glabrous skin appears to be thicker, the general thickness of the skin is similar across the body, at around 2 mm thick; however, there is regional variation (Figure 2). The hairy skin in general has an epidermis of ~80 μm thickness (Robert *et al.*, 1966; Mogensen *et al.*, 2008), whereas the glabrous skin has a thicker epidermis, where the stratum corneum alone is ~500 μm , and a relatively reduced dermal layer. The overall thickness of the scalp skin is also reduced at ~1.3 mm and the eyelid is very thin at around 0.5 mm (Hwang, 2013), whereas the back has an extremely thick dermis of ~4 mm (Robert *et al.*, 1966) (Figure 2). Depending on the individual, some of the skin on the foot sole can be around ~5 mm thick also, for obvious reasons due to the impact of weight enforced on this skin.

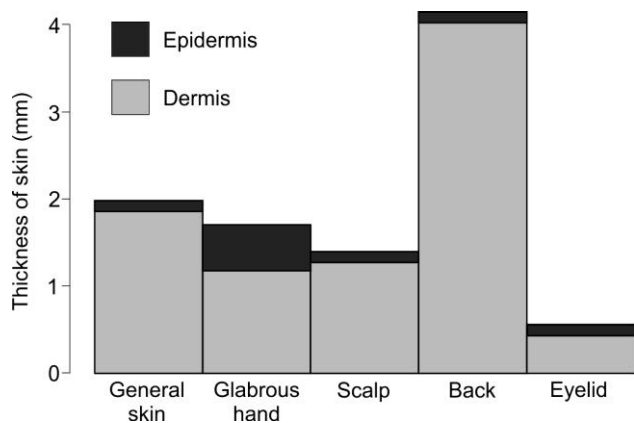


Figure 2: Different thicknesses of skin across the body.

Adapted from Robert *et al.* (1966).

These characteristics of the skin show its high heterogeneity and complexity. This is mirrored in the receptors that are present, which can be generally classified as mechanoreceptive, thermoreceptive, or nociceptive. Although numerous receptors can respond to more than one stimulus type (mechanical/thermal/chemical), they typically show a preference (e.g., peak response) for one type of stimulus. Concerning mechanoreceptors, humans have many different types that are present at different densities across the skin. Low-threshold mechanoreceptive afferents can be generally classed as fast-conducting A β and slowly-conducting C-fiber. Vellus hairs may be innervated by more thinly-myelinated (or unmyelinated) fibers, although this classification cannot be verified, as virtually no recordings from vellus hair afferents (Adriaensen *et al.*, 1983) have been found in microneurography (i.e., peripheral axonal nerve recordings in humans; for an overview of the technique, see Ackerley and Watkins, 2022). There are a number of different

types of A β mechanoreceptive afferent, which can be classed as fast-adapting (i.e., when a mechanical stimulus is applied to the skin, held stationary, then lifted off, there are only responses to the onset and/or offset of touch) or slowly-adapting (i.e., when the same stimulus is applied, there will be clear onset and/or offset responses, as well as firing during the sustained indentation). Four types of A β mechanoreceptive afferent exist in the glabrous skin (Table 1), namely: fast-adapting type I (FA-I, putatively connected to Meissner corpuscles), fast-adapting type II (FA-II, putatively connected to Pacinian corpuscles), slowly-adapting type I (SA-I, putatively connected to Merkel disks), and slowly-adapting type II (SA-II, putatively connected to Ruffini endings) afferents (Vallbo and Johansson, 1984). It is postulated that there are around 17,000 mechanoreceptive afferents in each human hand (Johansson and Vallbo, 1979), which along with the face, is one of the most densely-packed areas of mechanoreceptors. This is why the hands are essential in exploring the world, where we use them for the dexterous manipulation of objects (Johansson and Birznieks, 2004) and to sense a multitude of different textures (Weber *et al.*, 2013), which is encoded precisely with millisecond timing (Johansson and Birznieks, 2004; Mackevicius *et al.*, 2012; Saal *et al.*, 2017) and is essential in our modern-day lives. Further, in line with the development of skillful tool manipulation in humans, studies have shown that the biomechanical context of tool use and tool making has itself influenced the evolution of the human hand (Williams-Hatala *et al.*, 2018). This is important to consider, as the way our body encodes interactions with our world have been highly shaped by our environment and the objects we interact with, whether these be things like tools or other humans.

In hairy skin, the FA-I Meissner afferents are not present, but instead, fast-adapting hair follicle afferents (HFA) and field afferents are present (Vallbo *et al.*, 1995), which are highly sensitive mechanoreceptors (Table 1). Low-threshold mechanoreceptive C-fibers are called C-tactile (CT) afferents (for a review, see Ackerley, 2022) that are intermediate-adapting and are abundant over the arm (Vallbo, Olausson and Wessberg, 1999; Löken *et al.*, 2009; Ackerley, Backlund Wasling, *et al.*, 2014) and face (Nordin, 1990), but are much more sparse on the leg (Edin, 1992; Löken *et al.*, 2022). It is postulated that CTs are also abundant on the torso, but this has never been shown directly. In addition, CTs have occasionally been found on the glabrous skin of the hand (Watkins *et al.*, 2021). Where A β mechanoreceptive afferents have been implicated in the signaling of discriminative touch process, due to their fast conduction velocity, the CT information arrives after a delay, thus they are believed to reinforce gentle contact, such as in pleasant, positive affective touch (McGlone, Wessberg and Olausson, 2014). Interestingly, it is accepted that there is a general decline in the acuity of the mechanosensory system with age (Stevens & Choo, 1996; however, see Skedung *et al.*, 2018 who show that some participants do not decrease much in tactile capacity), although work has shown that touch actually becomes more pleasant with age (Sehlstedt *et al.*, 2016); however, the reason for this is unknown.

Mechanoreceptors primarily encode different types of mechanical event that are applied to the skin (e.g., FA-II afferents encode vibration well, slowly-adapting mechanoreceptors encode pressure well); however, mechanoreceptors can show some sensitivity to thermal and chemical stimuli. Although these have been little-explored, work has shown that SA-IIs may increase their response to cool touch (Konietzny, 1984; also unpublished observations from Ackerley, Backlund Wasling, *et al.*, 2014). Further, SA-Is may have decreased responses to cool touch (Bouvier *et al.*, 2018), but animal work has also shown dynamic SA-I firing increases to cooling (Iggo and Muir, 1969; Duclaux and Kenshalo, 1972). CT afferents have been shown to have decreased firing to mechanical stimulation that is warmer or colder than skin temperature (Ackerley, Backlund Wasling, *et al.*, 2014), although mechanical skin cooling appears to be more complex, where sustained, additional lower-frequency firing can be found (Ackerley *et al.*, 2018). It is also likely that hair follicle afferents show no sensitivity to thermal stimulation of the skin (Ackerley, Backlund Wasling, *et al.*, 2014), but it is clear that when the body is cold, the autonomic nervous system can induce piloerection of hairs, which would lead to afferent activation. Therefore, although mechanoreceptors always encode mechanical events, their responses can be modified by temperature and firing can even be induced with chemicals, such as the sensation of tingling/buzzing induced by sanshool (which also activates thermoreceptors and nociceptors) (Bautista *et al.*, 2008; Lennertz *et al.*, 2010; Cataldo *et al.*, 2021). The complexity of receptor encoding of mixed-modality stimuli again points to the specific adaptation of biological organisms to their environment and the interactions they have.

Main class	Afferent type	Putative receptor	Axon type	Body region	Further information
Low threshold mechanoreceptor	Fast-adapting type 1 (FA-I)	Meissner corpuscles	Myelinated Aβ	Glabrous skin	Signal discriminative aspects of tactile interactions, including form.
	Fast-adapting type 2 (FA-II)	Pacinian corpuscles	Myelinated Aβ	All skin	Highly sensitive to all touch (including remote touch) and signals vibrations well.
	Slowly-adapting type 1 (SA-I)	Merkel disks	Myelinated Aβ	All skin	Signals discriminative aspects of tactile interactions, including pressure.
	Slowly-adapting type 2 (SA-II)	Ruffini endings	Myelinated Aβ	All skin	Usually considered to signal deeper pressure and skin stretch.
	Field afferent	Unknown	Myelinated Aβ	Hairy skin	Very sensitive touch afferents that likely signal minimal-force wetness interactions in hairy skin.
	Hair follicle afferent	Hairs	Myelinated Aβ, thinly myelinated Aδ	Hairy skin	Signals hair movements, from both terminal (thick hairs, myelinated axon) and vellus (fine hairs, thinly-myelinated axon) hairs.
Thermoreceptor	C-tactile (CT), C-low threshold mechanoreceptor, CLTM), type 3	Free nerve ending	Unmyelinated C	All skin*	May signal more sub-conscious and affective aspects of touch. Responds preferentially to slow, gentle, stroking touch delivered at skin temperature.
	Aδ cool	Free nerve ending	Thinly myelinated Aδ	All skin**	Cool-sensitive with a maximum discharge at temperatures around 27°C, believed to be the main neuronal population subserving innocuous cold sensations.
	C-cold, type 2 (C2)	Free nerve ending	Unmyelinated C	All skin**	Cooling, with no sensitivity to touch; can show activity at typical skin temperature and fire down to 0°C. May show paradoxical responses to heating.
Nociceptor	C-warm	Free nerve ending	Unmyelinated C	All skin**	Sensitive to warming, no sensitivity to touch. Subclasses: low threshold warm receptors (LTWR), high threshold warm receptors (HTWR)
	High threshold mechanoreceptor	Free nerve ending?	Myelinated Aβ	All skin**	These have been recently demonstrated in hairy skin (Nagi <i>et al.</i> , 2019). High speed sensing of sharp mechanical pain.
	Aδ nociceptor	Free nerve ending?	Thinly myelinated Aδ	All skin**	Very little evidence of their existence (see Adriaensen <i>et al.</i> , 1983), signals pain.
	C-mechanosensitive (CM), type 1A, polymodal	Free nerve ending	Unmyelinated C	All skin**	Signals noxious touch (CM) and some chemical sensitivity. Subclasses also respond to noxious temperature, namely C-mechano-heat (CMH) and C-mechano-heat-cold (CMHC) nociceptors.
Proprioceptor	C-mechanoinsensitive (CMI or C-MIA), type 1B	Free nerve ending	Unmyelinated C	All skin**	Noxious heat, little mechanical sensitivity within measurable limits. Some chemical sensitivity. Subclasses: C-mechanoinsensitive-heat-insensitive (CMIHI) nociceptors have little thermal sensitivity either, while C-mechanoinsensitive histamine-positive (CMI(His+)), also known as C-pruritic, C-itch) are pruriceptors and sensitive to histamine.
	Primary muscle spindle, type Ia	Annulospiral endings	Myelinated Aα	Muscle	Slowly-adapting response to muscle stretch, with higher dynamic sensitivity, signaling the degree of change in muscle movement.
	Secondary muscle spindle, type II	Flower spray endings	Myelinated Aα	Muscle	Slowly-adapting response to muscle stretch, with lower dynamic sensitivity, signaling the length of the muscle.
	Golgi tendon organ, type Ib	Golgi organ	Myelinated Aα	Tendon	Directly encodes the contraction of the muscle, i.e. muscle tension. Little response to muscle length changes.
Joint receptors		Ruffini, Golgi, Pacini, ?	Myelinated Aα	Joint	Responds well to joint movement, especially at the extremity. Some responses to joint rotation. Little response to mechanical joint pressure.

Table 1. Proposed division of types of cutaneous mechanoreceptor, thermoreceptor, nociceptor, and muscle proprioceptor.

There is considerable variability within each type, where some types have subclasses. *C-tactile afferents were believed to only be present in hairy skin, but a recent study has shown a sparse projection in glabrous hand skin (Watkins *et al.*, 2021). **The innervation of these afferents in human glabrous skin is unknown from microneurography, but can be inferred from psychophysical tests and animal work. For further reading: mechanoreceptors (Valbo and Johansson, 1984; Valbo *et al.*, 1995; Corniani and Saal, 2020; Ackerley, 2022), thermoreceptors (Konietzny, 1984; Campero *et al.*, 2001; Green, 2004; Schepers and Ringkamp, 2010; Ackerley and Watkins, 2018), nociceptors (Campero, Serra and Ochoa, 1996; Serra *et al.*, 1999; Bostock *et al.*, 2003; Green, 2004; Ackerley and Watkins, 2018; Nagi *et al.*, 2019), and proprioceptors (Matthews, 1972; Hulliger, 1984; Burke, Gandevia and Macefield, 1988; Macefield, 2005).

The skin contains many receptors that primarily encode thermal and noxious stimuli. The thermoreceptive system has received less attention, although it is central in somatosensation: imagine touch without temperature? This is like vision without color. When something touches us, it is always accompanied by the encoding of its temperature. Only a handful studies have looked at pure thermoreceptors, which can be putatively classed into cool Aδ fibers, cold C-fibers, and warm C-fibers, although these classes are debatable, due to a lack of evidence of existence (Konietzny, 1984; Campero *et al.*, 2001; Paricio-Montesinos *et al.*, 2020). It is agreed that C-cold fibers exist and respond to cooling (Konietzny, 1984; Campero *et al.*, 2001, 2009) and the application of menthol (Campero *et al.*, 2009), but are generally not sensitive to touch. However, it could be that they are related to C-mechano-heat-cold (CMHC) nociceptors (Table 1), as C-cold fibers can also paradoxically respond to heating (Campero *et al.*, 2009). It is also noteworthy that the bodily thermal representation is likely very different to the tactile representation. Contrary to the acuity of the hands and face in tactile discrimination, there is a general trend that we sense temperature changes more readily on the upper half of our body. Our face is the most sensitive, especially the lips, where throughout our whole life, we can sense ~0.05°C change in lip temperature (Stevens and Choo, 1998). Temperature sensing on the lower leg is rather poor, especially the toe, which for young adults (<30 years) requires ~2.5°C increase or ~0.5°C decrease in temperature; however, for older adults (>65 years), this rises greatly to ~10°C increase or 3°C decrease in temperature (Stevens and Choo, 1998). Therefore, as well as the general decrease in touch capacity with age, the thermosensory system also has some degradation.

Potentially noxious stimuli, as encoded by nociceptors, has been much more researched, with many publications demonstrating the diversity of C-fiber nociceptors (for overviews, see Bostock *et al.*, 2003; Ackerley and Watkins, 2018). Although humans usually aim to decrease nociceptive input, it is

essential, as it provides a warning that the skin could be damaged. This important source of afference can greatly shape our body perception, as a strong nociceptive input is difficult to ignore and causes negative affect, driving us to do something to alleviate it. There exist many different types of nociceptor, from ultrafast conducting nociceptors (Nagi *et al.*, 2019) through to very slow C-fibers (for a review, see Ackerley & Watkins, 2018) (Table 1). Nociceptors respond to all different types of stimuli, even those that are not particularly noxious, for example, C-mechanosensitive (CM) nociceptors can have low force activation thresholds, similar to low threshold mechanoreceptors, but only respond weakly to gentle touch (Nordin, 1990; Watkins *et al.*, 2017). However, the optimal responses from nociceptors are normally into the painful range (e.g., heating over 42°C, cooling less than 20°C, strong mechanical force).

Overall, it is evident that the skin somatosensory system is highly complex, where many different types of receptors encode bodily interactions, as well as there being large variability at all levels. Even giving someone a hug will activate numerous receptors from all classes, such as all types of low threshold mechanoreceptor, thermoreceptors, nociceptors (mechanoreceptive nociceptors that have lower force activation thresholds), and even muscle proprioceptors (these may fire due to pressure on muscles, as covered below). It is therefore the balance and synergy between the activation of all these different types of somatosensory receptors that shape our bodily perception. For example, lots of input from low threshold mechanoreceptors, with little input from other types, would likely signal a pleasant contact; however, high activation in all classes of receptor would likely be unpleasant (e.g. intense firing, addition of nociception). Further, the balance between the activation of fast-conducting afferents, which give temporally-precise information about actual tactile events, is complemented by the activation of slower afferents (e.g. some thermoreceptors, nociceptors, and CT afferents) that provide 'colour'

to sensations, such as by reinforcing specific aspects of contact (e.g. CTs may reinforce gentle interpersonal interactions).

Internal somatosensory sensing: muscles, joints, and viscera

The division between the outside and inside of the body is rather vague, where there is not a sharp border between external skin and internal tissue. Rather, just like the borders between hairy and glabrous skin, the boundary between external hairy skin and mucocutaneous skin is imprecise. This can be readily seen in the change in skin near mucocutaneous regions (e.g. although our lips seem rather defined, on inspection, there is no sharp border) and felt in that it is difficult to sense exactly where our internal sensation of touch ends (e.g. for rectal sensations, Rogers, 1992). If you concentrate on the border between sensing internal 'touch', such as when food goes down our esophagus, it is not easy to sense the point at which the sensation ends. However, it is clear that we can feel sensations such as pressure and vibration internally, but it is not like feeling external touch; we are aware that it comes from inside the body. Therefore, it is apparent that we can define external contact as touch, but internal sensations are more related to interoception, body schema, and body wellness.

We have numerous receptors encapsulated in our deeper tissue, including in skeletal muscle, joints, and viscera. We gain our sense of self-in-space, proprioception, through four types of sensitive mechanoreceptive afferent: primary muscle spindles (group Ia, situated in the muscle), secondary muscle spindles (group II, situated in the muscle), Golgi tendon organs (group Ib, situated in tendons), and joint receptors (situated in joints) (see Table 1; and for a review, see Macefield, 2005). These proprioceptive afferents have thickly myelinated axons and send information very quickly to the brain. Muscle spindles have the peculiarity of being innervated by a sophisticated, descending, efferent system: the (γ) γ -fusimotor system. This efferent drive can change muscle spindles sensitivity, meaning that the encoding of muscle activity may be influenced by descending factors such as vision, attention, learning, and emotions (for a review on the effects of the γ -drive on muscle afferent firing, see Ribot-Ciscar & Ackerley, 2021). Proprioceptors are important in encoding the position of the body in space, as well as its movement, but they are also activated simply by pressing on muscle. Although tendon and joint receptors are quite insensitive to pressure, muscle spindle afferents will readily respond to pressure applied to the muscle belly. The exquisite sensitivity of muscle afferents is intriguing; they respond to rather gentle touch, including light tapping, pressure, and a range of vibration applied to the skin over muscle receptive field, and will even respond to more remote stimuli, such as via tendon manipulation or more remote vibration (Macefield, 2005). This implies that the input from muscle afferents during tactile interactions, even passive ones, can provide information about bodily contact. In a similar way, cutaneous afferents have also been shown to respond well to body movements, where it has been demonstrated that mechanoreceptive afferents, particularly type IIs, are tuned to joint orientation (Aimonetti *et al.*, 2007).

We also have receptors that have thinly-myelinated axons (group III, A δ fibers, mainly mechanosensitive) and are unmyelinated (group IV, C-fibers, mainly metabosensitive) in our skeletal muscle, which send information more slowly to the brain and can signal mechanical, thermal, and chemical changes in our muscles. Where muscle and joint proprioceptive afferents likely contribute at least to some direct awareness of the body in space (Macefield, Gandevia and Burke, 1990; Macefield, 2005), the group III and IV fibers are tentatively classed as nociceptors. They can signal neuromuscular fatigue and pain, as they are optimally activated through exercise contraction-induced mechanical, thermal, and metabolic stimuli (McCord and Kaufman, 2009; Amann *et al.*, 2020). Thus, where proprioceptors can be classed as more exteroceptive, group III and IV muscle afferents are more interoceptive, as their direct stimulation can cause cardiovascular reflex adjustments. The majority of group III and IV muscle afferents are chemosensitive (around half), while around a third respond to mechanical stimulation, and a third to thermal stimuli (Jankowski *et al.*, 2013).

There are receptors deep in our bodies that contribute to our visceral sense of interception and internal sensing. Much less is known about these, as it is extremely challenging to conduct microneurography recordings from internal sources (cf. Dunham *et al.*, 2018; Ottaviani *et al.*, 2020). However, it is clear that we can receive mechanical, thermal, and nociceptive afferent information from our internal bodies. One type of mechanoreceptor, the Pacinian corpuscle (FA-II afferent in the skin) is found throughout the entire body, from the internal

organs and nerves of the torso and pelvis, to within the connective tissue of joints, and in blood vessels (Roberts, 1959), although these Pacini end-organs can be of considerably different size and shape (Sheehan, 1933). Mechanosensing is important in our body, but especially in the gut, where we have other myelinated afferents (unencapsulated fibers, Merkel-like enterochromaffin cells) and unmyelinated afferents that capture specialized and non-specialized sensory signals in the gut (Sheehan, 1933; Mercado-Perez and Beyder, 2022), which often can be linked to visceral affective sensations, such as fullness after a meal and in painful pathologies. Although there is a lot to learn about human internal sensing and what it contributes to body representations, it cannot be overlooked, as it has evolved to give us an integrated sense of self and is essential in our well-being.

Central processing and integration of somatosensory signals

Once a peripheral receptor has been activated, the signal is transmitted towards the central nervous system, where somatosensory signals are forwarded mainly to the parietal lobe. Although this pathway is simplified in textbooks, there is incredible complexity at all levels, with divergence and convergence of afference well before the information enters the brain. Below is an overview of this complex system and the potential points at which information changes along the afferent pathway.

Classic central pathways activated by somatosensory afference

Our sense of tactile awareness is mainly subserved by myelinated A β mechanoreceptive afferents, which is part of the so-called, 'discriminative touch pathway' (McGlone, Wessberg and Olsson, 2014). The canonical view is that these afferents constitute a direct route or 'labelled-line' for touch information to be transmitted very quickly to the brain. Typically, the afference enters the spinal cord via the dorsal root, then ascends ipsilaterally up the dorsal columns in a topographically-organized fashion. The input from the main body is relayed by the cuneate (input from the upper body) or gracile (input from the lower body) parts of the dorsal column nuclei (DCN), then the signals cross the midline (decussation) to synapse in the thalamus, and then on to primary (S1) and secondary (S2) somatosensory cortical areas. These responses shape our reactions about touch and how we explore our world with millisecond precision. On the other hand, more slowly-conducting information in the anterolateral system takes a different route. C-fiber input is typically seen as entering the spinal cord, then ascending 1-2 vertebral levels to make ipsilateral synapses in the dorsal horn. Secondary neurons at this site project over the midline (decussation) and the information ascends via lamina I of the dorsal horn, through the spinothalamic tract, to synapse in the ventral posterior thalamus, and then on to cortical areas such as the insular cortex, S1, and cingulate cortex. However, this canonical textbook view is far from the actual complexity of this pathway: the ascending information is not simply relayed, rather, there is the potential for processing and interaction at each step.

There are multiple points where ascending information transmission becomes more complex. Even the peripheral nerve afferent is highly complex. The receptor end is very sensitive to stimulation, but the axon and dorsal root ganglion (DRG) cell body are also electrically excitable (Devor, 1999; Ackerley and Watkins, 2018). It has even been postulated that the DRG neuron serves as a source of afferent input, as some DRG cells are able to fire repetitively (Devor, 1999). For afferent fibers that ascend directly up the spinal cord (e.g. A β mechanoreceptive afferents), the principle branch of the axon ascends in the dorsal column; however, collateral branches of the entering axon also terminate in the spinal cord locally, or within a few segments, adding to the potential for interactions (for an in-depth overview, see Abaira & Ginty, 2013). Small-diameter afferents have an even more complex termination pattern, with a high degree of interaction, where different dorsal horn interneurons play a key role in integrating information and there are neurons that project these signals from the vast majority of the whole dorsal horn (layers I-V). The information, which can come from a number of afferent types, is then sent via the dorsal columns, the spinothalamic tract, or the spinothalamic tract (Abaira and Ginty, 2013).

For signals that reach the DCN, each ascending main afferent contacts ~1700 DCN neurons and each one receives input from ~300 afferents (Johansson and Flanagan, 2009). The synaptic interruption in the DCN provides a processing step for ascending information. A single DCN neuron can have a similar receptive field and response properties to other DCN neurons, yet each individual neuron responds to a unique combination of convergent input, where it has been demonstrated that tactile and object features have already

been computed, making their activity more similar to cortical responses than peripheral nerve input (Jörntell *et al.*, 2014; Suresh *et al.*, 2021).

The vast majority of all sensory afference is relayed to the cortex via the thalamus, notably apart from olfactory signals. Some postural information is sent to the cerebellum, via the spinocerebellar tracts, and sympathetic afferents terminate in medullary nuclei and the hypothalamus, before entering cortical areas. The thalamic nuclei are thought to be the gateway to the brain, where incoming signals are relayed to cortical areas; however, the thalamus is a potential source of large integration of both incoming afference and for reciprocal exchange between cortical areas via cortico-thalamo-cortical connections (Cappe *et al.*, 2009). The circuitry of the thalamic nuclei will not be covered presently, but, in brief, specific areas have been identified that are associated with somatosensory input, such as the ventral posterolateral (VPL) nucleus of the thalamus for tactile bodily inputs, the ventral posteromedial nucleus for facial input, and the posterior part of the ventromedial nucleus (VMpo) and the basal part of the ventromedial nucleus (VMb) that are involved in affective and visceral sensing (for a review on interoceptive pathways, see Craig, 2002). Studies have demonstrated that thalamic responses, like in the DCN, resemble more the firing patterns of somatosensory cortical neurons than the peripheral code, where tactile feature extraction has been demonstrated in VPL (Vazquez, Salinas and Romo, 2013). Thus, the responses of neurons, both in the DCN and thalamus, are similar to somatosensory cortical activity, but they are not identical: there is processing and extraction of pertinent information in these sub-cortical structures.

After passing through the sub-cortical nuclei, somatosensory afference is mainly sent to the parietal lobe, where Brodmann area (BA) 3 of the S1 receives a vast input from the thalamus (Kaas *et al.*, 1984); however, mechanoreceptive, thermoreceptive, and nociceptive information are all represented in the S1, S2, and insula (Davis *et al.*, 1998; Stancák *et al.*, 2006; Rolls, Grabenhorst and Parris, 2008; Peltz *et al.*, 2011; Mancini *et al.*, 2012; Panchuelo *et al.*, 2020). There are multiple, precise body representations in S1 (Kaas *et al.*, 1979; Sánchez-Panchuelo *et al.*, 2013), but somatotopical relations are less evident in the S2 and insula. There is a wealth of research on tactile responses in S1, which will not be covered in-depth here, but it is clear that the human S1 responds to a broad spectrum of mechanosensory input, from vibration to pressure, and all types of tactile discrimination, yet it is also evident that activity in both the S1 and thalamus is highly related to the period of sensory activation, thus the processing of the direct somatosensory signal (Romo and Rossi-Pool, 2020). Therefore, it is believed that the S1 is the main tactile awareness detection center that then drives other areas in the parietal and frontal lobes to act and make decisions (Romo *et al.*, 1998). However, S1 does not function alone and has, amongst others, dense connections with the primary motor cortex (M1), S2, and insula.

The wide activation of cortical areas in 'quantal touch' (the basic, elementary sensation provoked from stimulating a single afferent) been demonstrated using a unique approach to stimulate a single mechanoreceptive afferent and measure the resulting the cortical activity, i.e. using single unit intraneural microstimulation with brain imaging (Trullsson *et al.*, 2001; Sanchez Panchuelo *et al.*, 2016; O'Neill *et al.*, 2019). This approach uses microneurography to identify and record from single A β mechanoreceptive afferents, then the same peripheral neuronal axon is electrically stimulated using very low current pulses. It is possible to gain a 'quantal' percept of a tactile sensation, where it is believed that the activity in one mechanoreceptor can be felt as a specific point on the skin, for example, an FA-I afferent feel like a small point of vibration, whereas an SA-I feels like a small point of pressure (Vallbo *et al.*, 1984; Torebjörk, Vallbo and Ochoa, 1987; Watkins *et al.*, 2022). Although it is clear that this percept is likely evoked by the activity of many thousands of neurons, there is conservation along the somatosensory path and the selective artificial stimulation of one mechanoreceptive afferent activates a network of cortical areas. This was demonstrated to a high degree at 7 Tesla (T) functional magnetic resonance imaging (fMRI), where single unit intraneural microstimulation gave rise to a small area of contralateral S1 being activated, which was in correspondence with a larger area activated at the same cortical region by point-vibration at the skin receptive field site of the afferent. Further, activity to single unit intraneural microstimulation was also found bilaterally in the S2, M1, premotor cortex, insula, and posterior parietal cortex, as well as in contralateral prefrontal cortex and in the ipsilateral S1 (Sanchez Panchuelo *et al.*, 2016). It is noteworthy that the M1 was co-activated during this pure tactile input, demonstrating the common, yet lesser-reported finding of S1/M1 synchrony, whether the source is motor or somatosensory. However, due to

the close anatomical proximity of S1 and M1, as well as the strong links between somatosensation and movement, this co-dependence is to be expected. Further, many of the activations from intraneural microstimulation were bilateral, even S1, showing the integrated nature of bodily touch processing. These findings show the need for constant interplay between movement and its feedback, which is especially important in complex manipulations, such as in tool use, and points to why these functions are difficult to separate.

The S2 is very much implicated in the processing of more complicated aspects of touch, such as form, orientation, and pattern. Where S1 is closely related to somatosensory discrimination, S2 encodes task performance and influences decision making, which is associated with knowledge of both present and past tactile events (Romo *et al.*, 2002). There is often a contralateral predominance in S1 activity to touch, but both S2 cortices often respond, which is similarly seen with the insula (Olausson *et al.*, 2002). Concerning the insula, this structure has been more implicated in the processing of homeostatic and affective stimuli, such as the perception of gentle touch, temperature, and pain in the posterior insula (Craig *et al.*, 2000; Craig, 2002; Olausson *et al.*, 2002). However, the insula is activated during all tactile interactions (Morrison, 2016). Other somatosensory association areas over parietal regions, such as Brodmann area (BA) 5 and 7, are typically also activated during somatosensory interactions (Ackerley *et al.*, 2012), but these have been less-studied as compared to the main areas and respond in the integration of somatosensory signals with other processes. Somatosensory association cortex is involved in multisensory, motor, and vestibular processing, where the more caudal areas, going towards visual cortex, have more been implicated in the integration of somatosensory and visual signals (Iwamura, 2003).

Overall, it is evident that for each step of information being encoded peripherally and sent to be integrated centrally, there is the potential for complexity, where signals are filtered, processed, and integrated to better adapt the information and extract relevant features. This is highlighted in a rare group of people who have sensory neuronopathy, losing large myelinated somatosensory fiber function below the level around their head. They have no fast-feedback from touch or movements, although they can complete some sensorimotor tasks, with the aid of slowly-conducting fiber input, vision, and their residual motor memory (Cole and Sedgwick, 1992). This shows that damage to the afferent pathway can be compensated by other mechanisms. This complexity continues well into the cortex, where primary targets for somatosensory information represent stimulus characteristics well, but other activated areas, as covered below, are more implicated in the integration and understanding of what the input means to us.

Integration of somatosensory signals with other senses and with internal mechanisms

As mentioned above, somatosensory stimuli can activate a widespread network of brain areas, including areas in all lobes, sub-cortical structures, and the cerebellum. However, these additional regions often involve more specific tasks, such as the engagement of cognitive and emotional mechanisms, which are well-ingrained into everyday life and have thus evolved in complex ways to be co-activated at different levels. Concerning multisensory integration, there are senses that are heavily interlinked, such as taste and smell, yet touch is impacted by all our senses. Vision, audition, and proprioception are inherently highly associated with touch, and how we explore something tactually can be influenced by smell and even taste, such as when we eat something, the food has specific gustatory and olfactory qualities, but you also feel its texture. Touch is also very important in vestibular mechanisms, such as when you reach out to help balance, which becomes particularly evident with aging.

Internal central mechanisms may engage the more typically-activated somatosensory areas, for example, S1 that can respond to visual input, which includes seeing touch of objects and between humans. The discovery of mirror neurons in the motor system, which respond during a self-action and on the observations of another's action (for a review, see Rizzolatti & Craighero, 2004), has opened up many lines of research concerning the internal representations of others. The mere exposure of watching touch interactions between humans (i.e. vicarious touch) readily activates the S1, S2, and insula, as well as other parietal-opercular areas (Blakemore *et al.*, 2005; McCabe *et al.*, 2008; Keysers, Kaas and Gazzola, 2010; Ebisch *et al.*, 2011; Morrison, Björnsdotter and Olausson, 2011; Bolognini *et al.*, 2014), although the specific network may depend on the exact situation. For example, there are differences in the somatosensory brain activity found during active self-touch and passive touch

delivered at the same skin, where strong activity is provoked in self-touch in S1, but also that self-touch activates somatosensory association areas, including the precuneus (Ackerley *et al.*, 2012). These findings demonstrate that networks exist to distinguish between self-touch and interpersonal- or object-touch, which include how we can cancel feedback from our own movements in a context-dependent manner (Blakemore, Wolpert and Frith, 1998; Ackerley *et al.*, 2012). Further, it highlights the importance of our ability to actively manipulate tools and their incorporation into our body schema (Miller *et al.*, 2018, 2019), which has also been implicated in the expansion of the precuneus in our evolutionary development (Bruner *et al.*, 2017).

In evolutionary terms, our social interactions have heavily shaped our development (Dunbar, 2010). This includes the propensity for touch, such as in grooming, to strengthen social bonds and conspecific relationships. Direct interactions with others and the development of our complex social network is underpinned by verbal and non-verbal communication, but in the case of touch, it is hypothesized that CT afferents form a basis to help reinforce and reward gentle interpersonal contact (Löken *et al.*, 2009; Vallbo, Olsson and Wessberg, 2009; Olsson *et al.*, 2010; Ackerley, Backlund Wasling, *et al.*, 2014). CT-optimal touch has been shown to activate the insula well (Olsson *et al.*, 2002; Morrison, 2016). Some studies have found activity in the superior temporal sulcus (STS) during affective touch stimulation, although it is likely that this area is more involved in the integration of touch with information from the other senses and ongoing integrative processes (Morrison, 2016). However, the premotor cortex and STS are often recruited during the observation of social touch, often more than when the person views an object being touched. The STS and surrounding cortical regions have been implicated in processing biological motion and the movements involved in social situations (Deen *et al.*, 2015), as well as being activated in multisensory motion processing (Beauchamp *et al.*, 2008), thus encode higher level aspects about our everyday and inter-personal interactions. There is a clear importance of social context in our lives, which is heavily engrained in our contact with others. This is also reflected in processing the meaning of touch, where social significance can also impact on central processing (Gazzola *et al.*, 2012).

The prefrontal cortex is often activated during situations of somatosensory comparison, where working memory is engaged, such as in the discrimination between two tactile tasks (Romo *et al.*, 1999). There are clear attentional and context-dependent mechanisms that modulate activity in primary somatosensory areas, where information from various brain structures concerning memory, attention, motivation, and emotion, will shape responses (Romo and Salinas, 2001). For example, task-dependent activity during a vibrotactile attention paradigm has shown many different cortical areas that can respond to help the task at hand, including regions in the frontal eye fields, premotor cortex, superior temporal sulcus, and supplementary motor area (Burton, Sinclair and McLaren, 2008). Another study found that sensory stimuli that change and capture our attention and awareness recruit multimodal mechanisms, such as the additional activation of the temporoparietal junction, inferior frontal gyrus, cingulate, and supplementary motor areas (Downar *et al.*, 2000). The recruitment of such diverse and distributed networks demonstrates the complex involvement of numerous cortical areas in the full processing of somatosensory stimuli, in line with the needs for the current situation, enabling us to act in appropriate ways.

Frontal areas, including the orbitofrontal cortex, are recruited in the affective evaluation of touch, as in pleasantness processing (Rolls, Grabenhorst, and Parris 2008; Rolls *et al.* 2003). The OFC is also known to be activated by other senses in a similar fashion, for example, in the processing of gustatory pleasantness and even in bodily pain (Francis *et al.*, 1999; Rolls *et al.*, 2003; Rolls, Grabenhorst and Parris, 2008), thus represents a multisensory area for the evaluation of reward, be it for positive or negative reinforcement. The cingulate cortex has also been implicated in similar affective processing of stimuli from different senses and is subject to cognitive modulation (Francis *et al.*, 1999; Rolls *et al.*, 2003; McCabe *et al.*, 2008). Overall, these higher-order brain areas are clearly modulated in different ways, depending on the task at hand and the behavioral situation, where decision-making and orientation towards goals play a large role in determining the processing.

One further central area that makes a major contribution to somatosensory integration is the cerebellum and the pre-cerebellar nuclei (e.g., pons, inferior olive). The cerebro-cerebellar projection is one of the major pathways of the brain, linking many cerebral cortical regions, especially somatosensory, motor, and visual areas, with the cerebellar cortex. There is considerable integration in the cerebellum, where the afferent input greatly

outnumbers the efferent output (ratio 40:1, Brodal, 1992). The cerebellum is highly involved in the modulation and regulation of behavior, and in the acquisition of new skills, where timing and learning are important. Concerning touch and interactions with the environment, the cerebellum is believed to be important in generating feed-forward sensory prediction for the consequences of behavior. Thus, there is the ongoing comparison of motor output with sensory input and whether this matches or there is any error, where tactile pathways play a central role in shaping this (Blakemore, Wolpert and Frith, 2000; Bower, 2011; Schäfer and Hoebeek, 2018).

The point at which information becomes truly 'multisensory' is difficult to identify, as the brain is heavily interconnected, thus is it likely that somatosensory signals are influenced very early by the other senses, as well as by ongoing cognitive and emotional mechanisms, as outlined above. However, there are specific situations where somatosensory information is highly co-processed with other sensory information. For example, in the case of tactile motion, as well as the STS that is involved in biological motion perception, area V5/MT, which plays a key role in visual motion perception, is activated when the skin is stroked (Hagen *et al.*, 2002). However, a further study using vibrotactile stimulation of the skin found responses only in MST, where these were as strong as in S1 (Beauchamp *et al.*, 2007). Further, in touch-audition interactions, sounds can modulate how touch is perceived, as clearly found in the classic parchment illusion and roughness perception (Jousmäki and Hari, 1998; Guest *et al.*, 2002).

In addition to any processing of incoming somatosensory information, the brain needs to act on that information. The mechanisms of this will not be covered presently, although it is noteworthy that the brain can directly adapt its own input, depending on the circumstances. As mentioned above, proprioceptive muscle afferents are innervated by the descending γ -fusimotor efferent system, which can directly modify muscle spindle sensitivity to better adapt actions to the behavioral situation. This has been shown for cognitive mechanisms, such as attention and learning, as well as the impact of emotion (for a review see Ribot-Ciscar & Ackerley, 2021). There has even been shown to be a direct influence of vision on muscle afferent firing. A recent study has shown that when participants did not see their foot move, muscle spindle firing was slightly increased, as compared to when participants had congruent proprioceptive and visual information (Ackerley *et al.*, 2019). This demonstrates a weighting of information, where proprioceptive signals may be augmented from a central command when visual feedback is not available. In another study, it was shown that when muscle afference feedback from a moving hand was coupled with incongruent visual information, proprioceptive sensitivity was reduced to resolve such bisensory discrepancy (Jones, Wessberg and Vallbo, 2001). In all, the descending γ -fusimotor drive shows the influence of the brain on our own sensory feedback, where there are feed-forward processes that enable the rapid and efficient adaptation to an external situation, which helps us prepare responsive and appropriate action. This process is ongoing and is updated continually, showing the complex, intricate nature of our interactions with our environment.

Conclusion and future perspectives

In all, this chapter has examined the sensory origin of bodily perception, in looking at the different types of somatosensory afference that is received and processed by the brain, and why these have been selected in evolutionary terms to help us encode interactions with our environment. It highlights the complexity throughout this process, where even at the receptor level, there can be an integration of signals (e.g., the encoding of mechanical and thermal signals by mechanoreceptors). Somatosensory processes clearly involve multisensory integration, as well as being influenced by ongoing cognitive and emotional/affective mechanisms. In the case of touch especially, vision is a key component in humans, where we are driven by the dominance of visual inputs, and it is evident that these interact with somatosensory areas to understand our contact with the environment (e.g., texture perception) and with others (e.g., social significance). However, our tactile sense provides us with the means to do many complex tasks, such as object manipulation, which has greatly shaped who we are. The progression from early occasional tool use, many millions of years ago, to the habitual incorporation of tools in our lives, through to these tools now being obligatory, highlights how touch and our need to manipulate and explore things in our world has modified our own bodies over time (Shea, 2017). Rather, we now possess 'prosthetic capacities' that allow us to treat tools as an extension of our own bodies (Miller *et al.*, 2018, see also Chapter 3), which have been shaped by biological and environmental influences

(Bruner, 2021). It seems that humans can integrate external objects, likely even other people, into body schema, meaning that these external entities can become temporarily integrated into our self.

There are many avenues yet to explore in bodily perception and it is of interest to use increasingly sophisticated techniques, such as high-field fMRI, to probe mechanisms in humans precisely, especially sub-cortical structures. It is also of interest to investigate the relevance of the expansion of the human parietal cortex (Bruner, Battaglia-Mayer and Caminiti, 2022), especially in comparison with other animals and their differences in object manipulation capacities and social structures. Further, it is of importance to define tasks and protocols to unravel the exact processes underlying cognitive influences on somatosensation, where open science and the availability of data will mean access to a vast amount of information that can be used to gain further, meaningful insights into somatosensory processes, with increased power to enable the reliable generalization of findings. This would advance our understanding of bodily perception, both on a fundamental level, but also in combating somatosensory diseases.

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