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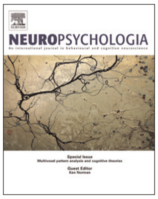

The role of tactile afference in shaping motor behaviour and implications for prosthetic innovation

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ABSTRACT

The present review focusses on how tactile somatosensory afference is encoded and processed, and how this information is interpreted and acted upon in terms of motor control. We relate the fundamental workings of the sensorimotor system to the rehabilitation of amputees using modern prosthetic interventions. Our sense of touch is central to our everyday lives, from allowing us to manipulate objects accurately to giving us a sense of self-embodiment. There are a variety of specialised cutaneous mechanoreceptive afferents, which differ in terms of type and density according to the skin site. In humans, there is a dense innervation of our hands, which is reflected in their vast over-representation in somatosensory and motor cortical areas. We review the accumulated evidence from animal and human studies about the precise interplay between the somatosensory and motor systems, which is highly integrated in many brain areas and often not separable. The glabrous hand skin provides exquisite, discriminative detail about touch, which is useful for refining movements. When these signals are disrupted, such as through injury or amputation, the consequences are considerable. The development of sensory feedback in prosthetics offers a promising avenue for the full integration of a missing body part. Real-time touch feedback from motor intentions aids in grip control and the ability to distinguish different surfaces, even introducing the possibility of pleasure in artificial touch. Thus, our knowledge from fundamental research into sensorimotor interactions should be used to develop more realistic and integrative prostheses.

1. Introduction

Sensorimotor integration is the process where peripheral sensory input is used to update and modulate motor output. We receive a continuous stream of sensory afference from multiple senses, and the present review concentrates on tactile somatosensory input and how this shapes our behaviour. Cutaneous, tactile feedback is particularly pertinent for the fine tuning of dextrous movements involving the hands. The afference from mechanoreceptors in the hands allows us to engage in complex tasks, such as writing or playing a musical instrument. It also provides a wealth of information for exploratory and manipulative tactile interactions with objects, allowing us to distinguish between a multitude of surfaces. Thus, for accurate motor control and exploration of the world, sensorimotor integration is essential. This is achieving by comparing motor behaviour and sensory consequences, with the inclusion of cognitive factors such as prior learning, through internal models. The prediction of the sensory outcome of behaviour, especially in feedforward internal models, is key for smooth and precise interactions with the environment. In clinical conditions where sensory afferent feedback is degraded, patients can become progressively unstable during movements: from fine, dextrous control, to more gross control such as walking. Without precise sensory feedback, problems emerge that can cause accidents and make life difficult.

The question of how to approach sensorimotor integration is like the chicken and the egg: which came first? Sensory and motor systems develop in tandem and it essentially depends on the situation as to how we utilise our capabilities. A tactile stimulus may drive behaviour, for example, contact with a sharp object makes you move your hand away. Conversely, a motor intention may drive the behaviour; you may want to pick up a cup, so make a movement that then provides sensory feedback. Presently, we explore how somatosensory signals are relayed to the brain and processed in tandem with motor intentions, with a view to integrating these signals to advance prosthetics. By definition, the

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term somatosensory refers to any sensory systems providing the brain with information related to the body, including afference from cutaneous, muscle proprioceptive, articular and tendon mechanoreceptors. In the present study, we focus on the cutaneous, tactile system and the term somatosensory will thus be restricted to this sensory channel.

2. Somatosensory pathways

Tactile information is relayed from the periphery to the brain to provide a constant update of object–skin interactions. This is used by the brain to process what is happening on a moment-by-moment basis and shapes how we interact with the external world. Touch is important for controlling how we manipulate objects, but also plays a key role in our social interactions and our well-being. In the following section, we will explore how and where different types of tactile input are relayed to the brain, where these signals are integrated with motor intentions and behaviour.

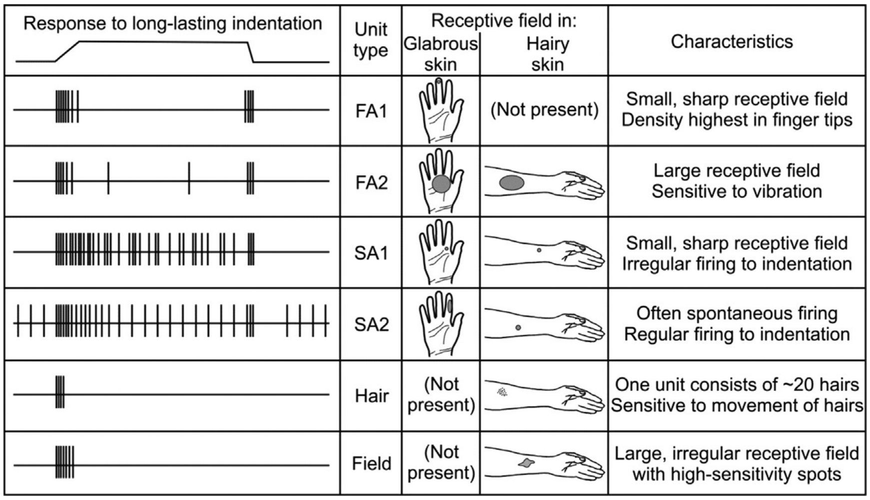
2.1. *From the periphery to the brainstem*

We have learned a great deal about the human touch system from the technique of microneurography: *in vivo*, axonal nerve recordings from single afferents in awake humans (Vallbo and Hagbarth, 1968; Vallbo et al., 2004). This has provided a wealth of information about the functioning of the peripheral tactile system across the body, including responses from the skin of the hands, arms, face, legs and feet. A single mechanoreceptive afferent can encode many aspects of a tactile stimulus, such as pressure, vibration and force (Johnson, 2001; Knibestöl and Vallbo, 1980; Knibestöl, 1973, 1975; Ribot-Ciscar et al., 1989; Vallbo and Johansson, 1984), as well as more complex facets such as texture and features (Connor et al., 1990; Phillips et al., 1992; Pruszynski and Johansson, 2014; Saal et al., 2009; Weber et al., 2013).

There are many different types of mechanoreceptive afferent in human skin, and these can be classified based on a number of criteria, including whether the mechanoreceptor ending sits in glabrous (non-hairy) or hairy skin, whether it has a fast-conducting myelinated axon (30–75 m/s) or a slowly-conducting unmyelinated axon (~1 m/s), and its adaptation properties to a sustained tactile indentation (slow-, intermediate- or fast-adaptation). In the glabrous skin of the ventral hands and feet, there are four main types of mechanoreceptive afferent, namely, fast-adapting type 1 (FA1, Meissner corpuscles), slowly-adapting type 1 (SA1, Merkel discs), fast-adapting type 2 (FA2, Pacinian corpuscles) and slowly-adapting type 2 (SA2, Ruffini endings) mechanoreceptive afferents (Fig. 1). There are around 17,000 of these myelinated mechanoreceptors in the human hand, where FA1s account for 43%, SA1s for 25%, FA2s for 13%, and SA2s for 19% (Johansson and Vallbo, 1979). The type 1 mechanoreceptive afferents are characterised by having small, point-like receptive fields, whereas the type 2 afferents have larger, more diffuse receptive fields. The large number of mechanoreceptors allows for high discrimination of tactile surfaces with the hands, and particularly the finger tips, where the FA1s are clustered. There have been numerous microneurographical recordings from SA2s from the glabrous hand in humans (Vallbo and Johansson, 1984), although histological work shows their presence, yet scarcity (Miller et al., 1958; Paré et al., 2003; Chikenji et al., 2010, 2011). The microneurography recordings may over-estimate the numbers of SA2s, as there is an innate sampling bias from spontaneously active units, which the SA2s very often are (see Fig. 1).

Hairy skin, which covers the vast majority of the body, also contains SA1, SA2 and FA2 mechanoreceptive afferents, as well as myelinated hair afferents and field afferents (Vallbo et al., 1995) (Fig. 1), and unmyelinated C low-threshold mechanoreceptors (CLTMs in animals), so called C-tactile (CT) afferents in humans (Vallbo et al., 1993, 1999). The tactile information typically used in sensorimotor integration comes from the fast-conducting, myelinated afferents, which provide the brain with high spatial and temporal resolution information about discriminative touch e.g. what, when and where. CT afferents convey gentle touch; however, there is a delay of >1.5 s before the touch information is processed in the brain, due to the slow conduction along the unmyelinated axon (Ackerley et al., 2013). These afferents are hypothesised to signal hedonic information about touch such as pleasantness, which is less useful for precise sensorimotor integration, although likely plays a role in the control and motivation of behaviour, such as driving the need to seek pleasurable, interactive social touch (McGlone et al., 2014).

Most research has focussed on investigating touch on the glabrous skin of the hands, partly due to its key role in our everyday lives. The precise responses from these mechanoreceptive afferents have been shown to play an essential role in the prehension needed for the dynamic balance between grip and load forces (Johansson and Westling, 1987; Westling and Johansson, 1987), for example when lifting slippery objects (Johansson and



Response to long-lasting indentation	Unit type	Receptive field in: Glabrous skin	Receptive field in: Hairy skin	Characteristics
	FA1		(Not present)	Small, sharp receptive field Density highest in finger tips
	FA2			Large receptive field Sensitive to vibration
	SA1			Small, sharp receptive field Irregular firing to indentation
	SA2			Often spontaneous firing Regular firing to indentation
	Hair	(Not present)		One unit consists of ~20 hairs Sensitive to movement of hairs
	Field	(Not present)		Large, irregular receptive field with high-sensitivity spots

Fig. 1. Differences between cutaneous myelinated mechanoreceptive afferents that signal discriminative aspects of touch. The response to a long-lasting tactile indentation stimulus demonstrates the differences between fast-adapting (FA) and slowly-adapting (SA) afferents. The representative size of the afferent's receptive field (type 1 or type 2) is shown in glabrous and/or hairy skin, with notable further characteristics.

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