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LIMITATIONS OF VIBROTACTILE THRESHOLDS

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Abstract

Thresholds for the perception of vibration at the hand are measured for diagnostic and research purposes but thresholds are limited in what they indicate about tactile perception. This review discusses the conceptual and methodological limitations in using thresholds to understand the information processing systems which underlie the perception of tactile stimuli. It is concluded that future work should advance a model of tactile perception in the hand as active, discriminative, and selective to a range of complex interacting factors.

1. Introduction

The human tactile system is able to extract an extraordinary amount of information about the properties of the physical world from vibrations, systematically process the relevant information, generate perceptions of the properties of objects and surfaces, and guide behaviour.

Feeling the texture of a surface relies on a complex biological system. The physical interaction between the skin and a surface generates vibrations in a repeatable way (Bensmaia and Hollins, 2003). This information about the interaction is captured by neurons in the skin and processed so that the vibrations can be discriminated from one another on the basis of frequency (Cohen and Kirman, 1986) or waveform (Bensmaia and Hollins, 2000). We can observe this processing at a behavioural level in the intuitive ability to discriminate between surface textures across a substantial range of physical scales (Skedung *et al.*, 2013), estimate object and surface properties consistently (LaMotte and Srinivasan, 1991; Morley *et al.*, 1983), and modify behaviour (e.g. grip strength) when interacting with objects (Su *et al.*, 2014; Witney *et al.*, 2004).

The complex and multi-faceted process of tactile perception can be described in a simple model of information processing (Gescheider *et al.*, 2004). Every perceptual system uses specialised cells to systematically transduce energy from the external world into neural signals which carry information, and uses the captured information to guide behaviour. There are therefore two core approaches to looking at a perceptual system: we can describe the function of the physiological structures which capture and process the information – a physiological approach – or we can look at the pattern of behaviour that observers show in response to stimuli and determine what information was used – a psychophysical approach.

The two approaches can be combined by characterising the tactile system as a set of 'Information Processing Channels' (e.g. Verrillo, 1968) with independent neural substrates. This provides a theoretical model of what information is captured by different physiological components of the

perceptual system (Gescheider *et al.*, 2010). In turn, this information determines the responses made by observers.

A goal of behavioural experiments is that the responses of observers allow inferences about the properties of the model. A carefully designed experiment can show how information is processed in the tactile system through the lens of observable and quantifiable behaviour. This approach can be powerful because it looks at the system as a whole, rather than a single small component. Experimental measures from robust behavioural experiments may be obtained quickly, cheaply, and non-invasively, for both research and diagnostic applications.

There is a range of psychophysical measures that can be used to collect data. For example, observers can report feeling a vibration ('Detection'), whether they can feel the difference between vibrations ('Discrimination') or match them to each other ('Matching'), and how much of a particular perceptual property (e.g., intensity) they feel in the vibration ('Magnitude Estimation'). The model of information processing in the tactile system has been focused on vibrotactile thresholds – the minimum amplitude of vibration that generates detection (Verrillo, 1985, 1963).

This overview of the human tactile system concentrates on how psychophysical investigations of vibrotactile thresholds have been integrated with neurophysiology to provide a model of information processing in the tactile system. It is argued that expressing the properties of the tactile system in terms of vibrotactile thresholds is restrictive and ignores the full scope of observations from psychophysics and neurophysiology. It is concluded that the model of information processing based on this foundation is incomplete because it builds in a set of fundamental limitations.

2.   A model of the tactile system

2.1   Vibrotactile thresholds

One of the most powerful methods for understanding a perceptual system is also the most intuitive: examining the relationship between the physical properties of a stimulus and an observer's report of their psychological response (hence 'psycho-physics').

Psychophysical approaches to vibrotaction have focussed primarily on the phenomenon of a 'sensory threshold' – the concept of a minimum amount of stimulus energy necessary to produce a change in sensation. The 'absolute threshold' (the energy required to change the response from 'no sensation' to 'sensation') is most studied, but 'difference thresholds' (the change of energy required to notice a change in the sensation at suprathreshold levels) and thresholds modulated by adaptation or masking follow the same logic. The idea of a threshold for the detection of a stimulus has been ubiquitous in the history of perception research in every modality (Gescheider, 1976; Jones, 1974), and is sometimes thought of as the 'resolution' of the sensory system.

In a typical vibration detection design, a circular contactor attached to a vibrator is placed in contact with the skin of the hand. The contactor protrudes up through a hole in rigid surface with a gap between the contactor and the surround. The observer rests a skin surface on the contactor and maintains approximately constant pressure. Vibrations of various frequencies and amplitudes are then

delivered, either varying continuously over time (the 'von Bekesy algorithm'; ISO 13091-1:2001) or delivered in controlled intervals (the 'staircase algorithm'; ISO 13091-1:2001). The observer is required to report whether the contactor is vibrating, either verbally or by pressing a button. In most instances this experiment is a variant of a Yes/No detection design, in which the observer reports the presence ("Yes") or absence ("No") of the target. From this design we can specify a minimum level at which the amplitude of the vibration gives rise to perception – the vibrotactile threshold.

Over the last 50 years, these techniques have been instrumental in building understanding of how the tactile system captures different information from a stimulus. Vibrotactile thresholds are also used to assess impaired tactile perception and quantify the severity of the neurological component of the hand-arm vibration syndrome (HAVS), which can present with loss of sensitivity to tactile stimuli (Bovenzi, 1990; Griffin, 1990). These procedures need to be fast and intuitive, even at the cost of accuracy.

Although behavioural tests remain powerful ways to understand a perceptual system, their usefulness depends on the experimental design. Experiments and diagnostic procedures need to be designed so that the results provide clear inferences about the structure and function of the model. Thinking about the system solely in terms of vibrotactile thresholds builds in a set of limitations.

2.2   From thresholds to an information processing model

Thresholds for the detection of vibration are not uniform across the frequency spectrum. Instead, detection is mediated by a set of overlapping broadband filters known as 'information-processing channels', which are selective for different frequency ranges. Originally conceptualised as a 'duplex' model of complementary low- and high-frequency selective channels (Verrillo, 1968; von Békésy, 1939), then 'triplex' (Capraro *et al.*, 1979), there is now understood to be four independent systems in the glabrous skin of the hand which respond differently as a function of the frequency content of the vibration (Gescheider *et al.*, 2010). This psychophysical work has usually labelled the channels as Pacinian (P) and non-Pacinian (NPI, NPII and NPIII). For clarity, however, these channels are referred to throughout this review by their neurophysiological labels: PC, RA, SAI and SAII, respectively.

The channel organisation of vibrotaction has two fundamental properties:
- The channels are independent
- The channels are frequency selective

Psychophysical procedures that reveal the thresholds of particular channels have provided substantial evidence for these ideas. Adaptation (Hollins *et al.*, 1990; Verrillo and Gescheider, 1977), and masking (Bolanowski *et al.*, 1988; Gescheider, *et al.*, 1978; Gescheider *et al.*, 1983; Gescheider *et al.*, 1985), have been shown to affect thresholds for perception within frequency ranges associated with particular channels, but not across them. Figure 1 shows how vibrotactile thresholds vary as a function of frequency with different contactor sizes and stimulus exposures, and how this has been reconciled as a four-channel model. See Gescheider and colleagues (2010) for a detailed review of the psychophysical evidence.
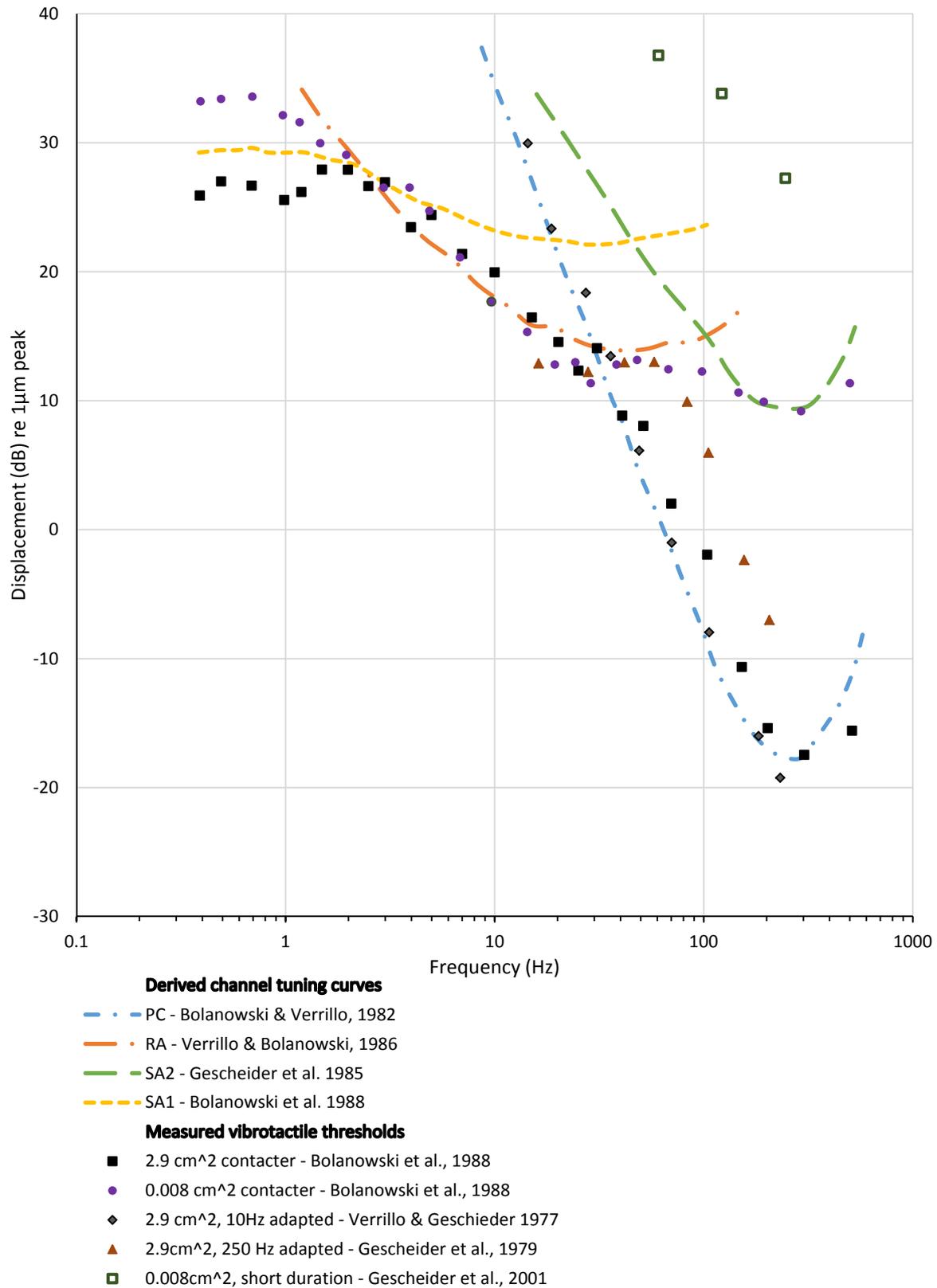
Figure 1. Points show measured vibrotactile thresholds at the thenar eminence as a function of vibration frequency. Dashed lines show psychophysically derived tuning functions of tactile channels. Data adapted from Bolanowski and Verrillo,1982; Bolanowski *et al.*, 1988; Gescheider *et al.*, 2001; Gescheider *et al.*, 1979; Gescheider *et al.*, 1985; Verrillo and Gescheider, 1977; and Verrillo and Bolanowski, 1986.

There is a difference between how the channels are defined and how they are typically expressed in an experimental setting. The channels are defined in terms of the frequency selectivity of their processing regardless of stimulus amplitude, but their properties are almost entirely expressed in terms of the lowest energy to which they are sensitive – their psychophysical threshold for perception of vibration as a function of frequency (Gescheider *et al.*, 2001).

For this reason, questions remain about how the channels mediate perception in response to natural stimuli, which would be expected to excite several or all of the tactile channels (e.g. Gescheider *et al.*, 2004). Most authors argue that perception arises from the integration of these separate systems, although the rules which dictate this integration differ from study to study (Hollins and Bensmaia, 2007; Hollins and Roy, 1996; Roy and Hollins, 1998).

2.3   Neurophysiology of the tactile system

Over time, the information processing channels identified through psychophysical procedures became associated with distinct physiological structures. Each channel is now strongly associated with the properties of particular classes of mechanoreceptors and their afferent nerve fibres (Johansson, 1978; Johansson *et al.* 1982; Johansson and Vallbo, 1979; Johnson, 2001).

Mechanoreceptors are a dedicated class of nerve endings that transduce physical deformation of the skin into electrical impulses. Their precise structures, locations, and neural response characteristics vary substantially across mechanoreceptor types (Johansson *et al.*, 1982) – this variability is what allows different classes of mechanoreceptors to respond selectively to different frequencies of vibration, giving rise to information processing channels that respond selectively to different vibratory inputs. The physiological processes that give rise to frequency selectivity in the channels are illustrated in Figure 2.

Based on the information-processing model, a psychophysical experiment allows inferences about which mechanoreceptors are responding to a particular stimulus. By assuming that the most sensitive channel mediates perception at the lowest amplitude of a particular vibratory stimulus (Gescheider *et al.*, 2004), psychophysically determined vibrotactile thresholds identify the most sensitive mechanoreceptors in specific frequency ranges. Given the complex interacting factors that influence the firing of the afferents in the skin, however, this assumption may be simplistic.
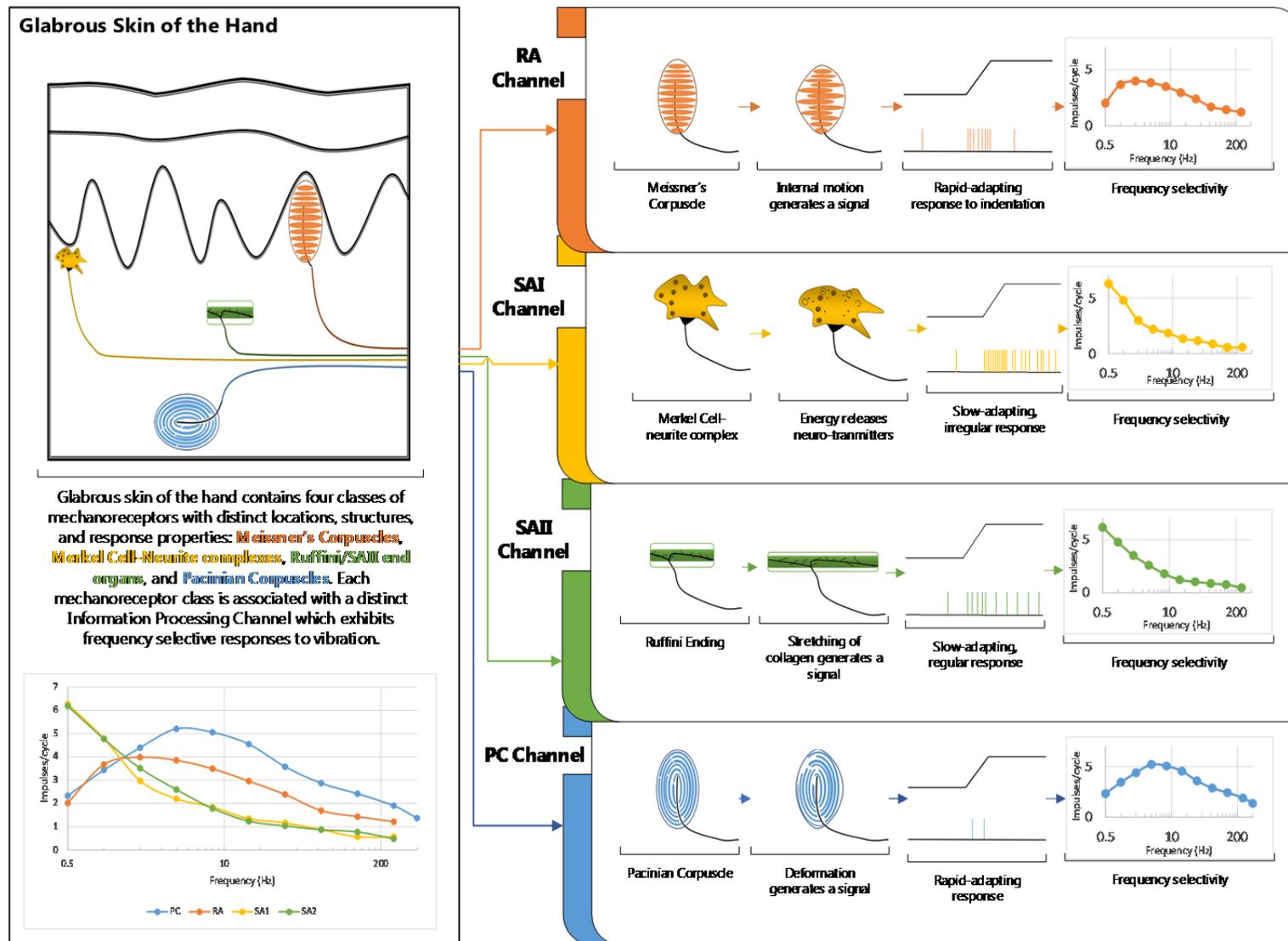
Figure 2. Summary of the physiological responses to vibration in mechanoreceptors and afferent neurons in the glabrous skin of the hand. Variation in the structure, location, and neural response cause the channels to respond selectively to particular frequencies. Frequency selectivity data was adapted from Johansson *et al.*, 1982.

3. Limitations of vibrotactile thresholds in building an information processing model

3.1 The 'high threshold' assumption and vulnerability to response bias

The idea of a psychophysical threshold as a set value that differentiates between events that are always not observed ("No" responses) and events that are always observed ("Yes" responses), known as the High Threshold model, is fallacious (Green and Swets, 1966; Macmillan and Creelman, 1991). Instead, what we see is an increasing probability of a yes response as the amplitude of the stimulus increases – resulting in a situation in which some missed targets are of higher amplitude than some observed targets. This probabilistic processing reflects the noise in any biological system. Detecting a low-energy target depends on differentiating between normal background activity (noise) and a very small increase in this signal generated by the presence of a weak stimulus (signal + noise). The decision is made by establishing a criterion value above which a signal is probably a target, generating a 'Yes' response, and below which it is probably a blank, generating a 'No' response. This is the fundamental idea behind signal detection theory (Green and Swets, 1966; Swets and Green, 1963).

Classical detection designs get around this problem by adopting an arbitrary percentage correct at which the observer is considered to reliably observe the stimulus – typically 75%. Vibrotactile detection thresholds therefore do not reveal the limits, or resolution, of a sensory system. Even with the same observer in identical experimental conditions, the vibrotactile threshold will vary as a function of what level of activation corresponds to a 'criterion' value.

A number of factors influence the placement of the criterion (e.g. Darian-Smith *et al.*, 1980; Hellström, 1985; LaMotte and Mountcastle, 1975; Poulton, 1989; Treisman, 1964). By causing observers to adopt different criteria, the same amplitude stimuli can generate different 'thresholds' (Green and Swets, 1966; Macmillan and Creelman, 1991; Morioka and Griffin, 2002).

A measured vibrotactile threshold is not a constant value. Instead, it is the product of a particular participant, stimulus, experimental design, and response criterion. This is one reason for the intra- and inter-subject variability observed in vibrotactile thresholds (Aaserud *et al.*, 1990). The variability can impede some research. The popular Yes/No detection designs tend to overestimate the energy needed to produce a response in the system, whereas two-alternative forced-choice (2AFC) procedures, which can negate response bias, show substantially lower apparent thresholds (Morioka and Griffin, 2002).

This variability also places a limit on the accuracy of vibrotactile thresholds as a diagnostic tool. Before a small change in a threshold can be assumed to have medical significance it must be understood what proportion of variability in subject responses can be attributed to the physiological effects of a medical condition and what proportion to a change in response bias or some other factor.

3.2 The role of active perception in normal touch

The tactile system in the hands is primarily engaged in active perception of the world (Gibson, 1962; Lederman and Klatzky, 1987). In order to perceive a surface or object, the skin of the hand must be

placed into contact with it. During texture discriminations, observers move their hand in a stereotyped way to extract relevant information (Lederman and Klatzky, 1993; Lederman *et al.*, 1982). Lateral movement of the skin across a surface generates vibrations with frequencies that are dependent on the spatial properties of the surface (Bensmaia and Hollins, 2003). These vibrations contain information from 'active touch' that can be adjusted to maximise the availability of the relevant information for the appropriate information processing channels.

Discrimination paradigms can be designed to access specific property differences between stimuli, rather than just presence or absence. The vibrations delivered during experiments on vibrotactile detection are not assessing the information content of the system, merely the presence or absence of any information. This abstraction of a single aspect of vibrotactile sensation has been useful for the identification of the 'information-processing channels', but limits the degree to which we can observe the function of the channel in the context of normal touch.

3.3   The ecological validity of vibrotactile thresholds

The difference between the normal function of the channels and the abstracted isolation of their vibrotactile thresholds plays into a broader point about ecological validity – the extent to which experimental findings can be generalised to normal life.

Tactile perception in the hand and fingers is arguably primarily discriminative; it is concerned with rich data extraction about the properties of objects rather than the detection of vibration. Natural tactile stimuli will to give rise to activity in several or all of the four channels, and perception will be the result of the integration of the information they have captured (e.g. Gescheider *et al.*, 2010). This seems especially likely given that stereotyped exploratory procedures (Lederman and Klatzky, 1993) modulate the information available to the system, and are likely to increase the information available to the system rather than limit it to near-threshold energies.

The glabrous skin of the hand can be considered to be performing a function analogous to the fovea in vision: it contains high relative receptor density compared to the periphery, hyper-acuity, high receptor diversity, over-representation in the brain, and demonstrates stereotyped information-seeking behaviours – exploratory procedures and eye movements respectively. Some researchers also consider the fingers a 'fovea' for pain (Mancini *et al.*, 2013). Like the fovea, the glabrous skin of the hand is specialised for high information content discrimination, rather than low level detection.

Vibrotactile threshold procedures, in order to isolate the channels from one another, only access the lowest level of activity in the channels – a signal of whether there is a stimulus present at all. Discrimination procedures, on the other hand, are structured for looking at the content of information in the channels.

3.4   Mechanoreceptors display complex selectivity

Although the information processing channels for tactile perception might be characterised by their selectivity for the frequency content of vibration, they also display marked selectivity to a wide variety of other stimulus parameters. These parameters include: the static force of the contactor (Brisben *et al.*, 1999; Craig and Sherrick, 1969; Harada and Griffin, 1991; Lamoré and Keemink, 1988; Maeda

and Griffin, 1994), contact area (Lamoré and Keemink, 1988; Maeda and Griffin, 1994; Verrillo, 1985), stimulus duration (Gescheider and Joelson, 1983; Verrillo, 1965), skin temperature (Bolanowski *et al.*, 1988), skin indentation (Whitehouse and Griffin, 2002), active or passive movement (Yıldız *et al.*, 2015), pressure distribution (Srinivasan and LaMotte, 1991) body location (Forta *et al.*, 2012) and surface topography (Skedung *et al.*, 2013). Untangling the effects of these factors on thresholds is challenging because they interact with one another. For example, introducing a surround limits the effective surface area of stimulation, but also alters factors like static force, skin indentation and pressure distribution (e.g. Verrillo, 1985).

An alternative perspective on the information processing channels and their sensitivity to various parameters is to consider the channels as having discrete 'functions' (e.g. Johnson, 2001). Although this viewpoint illustrates the role of selectivity in tactile perception, it may underestimate the integration of different channels as a 'team effort' to provide diverse information about objects (e.g. Saal and Bensmaia, 2014).

3.5   Neural thresholds versus psychophysical thresholds

In neurology, all neurons display some level of baseline activity ('noise') regardless of stimulation, and react to stimulation in a probabilistic and idiosyncratic way (Doya, 2007). Although it is possible to assign neural thresholds in terms of the number of spikes per second or per stimulus cycle (Bolanowski *et al.*, 1988), which may correlate with measured psychophysical thresholds (Bolanowski *et al.*, 1988), the significance of a specific number or rate of spikes is unclear given that some studies have found that even the first impulse of a tactile generated signal is sufficient for fine grained discrimination (Mackevicius *et al.*, 2012).

3.6   The implications of neural coding strategies

To an extent, the basic channel structure assumes that the underlying physiology of the channels employs a 'rate code'. A rate code is a neural coding scheme in which the activation level of a channel is reflected by its overall number (or change in number) of impulses. In a rate code, increases in the amplitude of a vibratory stimulus result in increases in the mechanoreceptor response rate, and at some level this activity crosses a threshold for perception, at which point the vibration is felt.

Neurophysiological research has shown that the channels employ a range of codes to capture information about a stimulus (Bensmaia, 2008; Cohen and Vierk, 1993; Harvey *et al.*, 2013; Hollins and Bensmaia, 2007; Weber *et al.*, 2013). The PC and RA channels appear to code primarily temporally (Muniak et al., 2007), so a single channel's spike pattern over time contains information about the frequency of the vibration. This activity interacts with amplitude, such that increases in amplitude will produce non-linear changes in the response of the neuron as a function of frequency.

The implications of changes in neural responses that reflect both the pattern of indentation over time and the amplitude of that indentation have yet to be related to changes in vibrotactile thresholds. This may also suggest that vibrotactile thresholds do not reflect the full function of the tactile channels.

4. Conclusions

The concept of information-processing channels processing vibratory inputs is central to our understanding of human tactile perception. The basic properties of the channels and the evidence for their existence comes from a long traditional of psychophysical research, and this remains a powerful tool for investigating the properties of the human tactile system.

Psychophysically, the frequency selectivity of the channels is expressed in terms of the minimum amplitude of vibration necessary to elicit a sensation – a vibrotactile threshold – as a function of frequency. This model of tactile perception is limited to low energy stimuli unrepresentative of the normal neurophysiological response of the channels. This model of tactile perception could be complemented with psychophysical evidence of tactile perception in the hand performing active, discriminative perception and differentially sensitive for a range of complex interacting factors.

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