University of Southampton

Faculty of Engineering and Physical Sciences

Institute of Sound and Vibration Research

Feeling the Difference: Discrimination of Vibration Frequency and Acceleration Magnitude in the Tactile Channels

by

Sean R. Mills

ORCID ID: [0000-0001-7866-7225](https://orcid.org/0000-0001-7866-7225)

Thesis for the degree of Doctor of Philosophy

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"If you want to find the secrets of the universe, think in terms of energy, frequency, and vibration."

~ Nicola Tesla

This thesis is dedicated to:

My PhD supervisor and friend, Michael J. Griffin (1947–2019), for his patience, wisdom, and for persuading me to do this accursèd degree in the first place.

My grandparents, Peter G. Mills (1926–2017) and Sheila J. Mills (1930–2017), for their intelligence, love, and kindness.

My dog, Charlie (2006–2017), a very good boy.

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Abstract

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The sense of touch translates indentation of the skin into information about the physical properties of the world, including texture, shape, weight, hardness and motion. This complex system depends on subsystems of mechanoreceptive nerves that can be characterised as 'tactile channels'. Like any sensory system, the tactile system is vulnerable to damage and degradation from illness or environmental exposure. Characterising the relationship between physical vibrations that indent the skin and the subjective perception of those vibrations ("vibrotactile psychophysics") provides us with a powerful tool for understanding the tactile system, and therefore for diagnosing sensorineural disorders that affect it. However, our current methods are marked by profound limitations in sensitivity, validity, and capacity to characterise the full action of the tactile channels. The aims of the research presented in this thesis are to: 1) design a vibrotactile psychophysical paradigm that measures the sensitivity of the tactile channels beyond the capacity of current methods, 2) advance and extend the model of the tactile channels, and 3) make substantive links to applications of vibrotactile stimulation to the diagnosis and treatment of sensorineural disorders.

Four main experiments are reported. The first experiment instantiates and tests a two alternative forced choice paradigm for vibrotactile frequency discrimination and investigates whether contact area affects the sensitivity of two tactile channels. The second experiment builds on this work to evaluate the effect of recruiting additional channels on the sensitivity to frequency differences. The third experiment investigates whether these effects are paralleled in the discrimination of acceleration magnitude. The final experiment completes the series by investigating how sensitivity to vibrotactile frequency changes across the boundaries between channels. The results of these studies are combined to build a novel suprathreshold, diagnostic model of the tactile channels. This is then applied to improve the effectiveness of vibrotactile applications in translational medical science as haptic aids for CI users.

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Research Thesis: Declaration of Authorship

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I declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

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Signature:		Date:	

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I am enormously grateful to everyone who participated in my experiments, giving up their time to visit a small, cold, airless, basement laboratory to feel some tiny vibrations and click some buttons. You were all patient and generous beyond any normal measure, and I could not have done it without you.

Definitions and Abbreviations

a	Acceleration
f	Frequency
dB	Decibels, logarithmic units of displacement (vibration) or sound pressure
WF	Weber fraction, the minimum change in a stimulus dimension that can be reliably discriminated, in proportion to the baseline value of the stimulus dimension, (e.g. for frequency $WF = \frac{\Delta f}{f}$)
R.M.S.	Root-mean-square
P or PC	Pacinian Corpuscle mediated tactile channel
NP (1-3)	Non-Pacinian tactile channels: RA, SA1 and SA2
RA	Rapid-adapting tactile channel mediated by Meissner's corpuscles
SA1	Slow-adapting tactile channel mediated by Merkel-cell neurite complexes
SA2	Slow-adapting tactile channel probably mediated by Ruffini endings
CI	Cochlear Implant
NHCI	Normal-hearing participants using a CI simulation
SNR	Signal-to-noise ratio
SRT	Speech reception threshold
HA	Hearing Aid
F0	Fundamental Frequency
EHS	Electro-haptic stimulation

Chapter 1 Introduction

Perceptual systems translate information present in the external world interacting with our bodies – light hitting the retina, air pressure changes on the eardrum, the chemical composition of the air we breathe – into information we can use. In the case of tactile perception, vibrations transmitted through the skin contain detailed information about the physical interaction between the skin and a surface which can be systematically extracted, perceived as object properties like texture, friction, shape and hardness, and used to guide behaviour. Like any sensory system, the tactile system is vulnerable to damage and degradation, impairing sensation. For those that lose their sense of touch, the world becomes a numb and difficult place.

We can understand a sensory system by looking at the relationship between the physical properties of stimuli with observer's reports of their perception – a field known generally as psychophysics (Gescheider, 1976a). As we manipulate the information contained in the stimulus (e.g. by changing the frequency of the vibration), we can track the sensitivity of the tactile system to that information. Neurophysiology then helps to describe the structures that mediate this system (Bolanowski, Gescheider *et al*., 1988; Johnson, 2001; Saal & Bensmaia, 2014a). To understand how the tactile system works we reconcile the psychophysical results with our understanding of the underlying neurophysiology into a model of information processing in the tactile system. Vibrotactile psychophysics is also a crucial diagnostic tool for the disorders that affect sensory systems – just as we can use it to understand a sensory system in general, can use it to understand when it isn't operating as it should.

Psychophysics and physiology support the presence of four 'information processing channels' in the glabrous skin of the human hand (Gescheider, Wright, & Verrillo, 2010). Each channel is subserved by a specific neural system of mechanoreceptors and afferent nerve fibres. The unique characteristics of these systems modulate the neural and psychophysical responses to tactile stimuli (e.g. Johnson, 2001). It is the later integration of these independent signals that drives perception, resulting in a rich and informative sensory percept of tactile stimuli (Gescheider *et al.*, 2004; Gescheider *et al.*, 2010).

Accurately describing the information processing system depends on a fundamental understanding of the selectivity of the particular channels and building a model of how these signals are integrated as perception.

Our current diagnostic model of tactile perception is limited, however, by an emphasis on vibrotactile detection thresholds. Vibrotactile thresholds refer to the lowest amplitude vibration which can be reliably detected by an observer, and describes a range of procedures concerned with identifying this value as a function of the parameters of the vibration. Increasingly, the four-channel model built on vibrotactile thresholds fails to reflect what we know about the behavioural aspects of touch, and struggles to incorporate increasingly detailed descriptions of the underlying neurophysiology. Diagnostic procedures exhibit huge inter- and intra-subject variability, which raises questions about their reliability. They are used as a supplement to self-reported assessment of 'numbness' or 'tingling', and mostly in the context of simple vascular signs and symptoms (e.g. blanching of the fingers), rather than being diagnostic in themselves. Additionally, these techniques are used categorically – in which sensorineural problems are simply present or absent – rather than in a more informative, gradated way.

It is therefore crucial that we evaluate the limitations of vibrotactile detection thresholds, expand our working psychophysical model of the tactile system to suprathreshold, and make recommendations of how to improve and advance diagnostic procedures for the diagnosis of impaired touch perception. A better understanding of the information processing characteristics of the tactile system will also allow us to investigate scenarios in which additional information can be encoded and presented to the skin. This 'haptic' presentation of information could be a useful aid to people with cochlear implants, who receive relatively limited information through their implant.

This PhD project aims to:

1) Evaluate the ability of current psychophysical diagnostic tools, especially vibrotactile detection thresholds, to describe the operation of the human tactile system and detect impairments to the sense of touch.
2) Develop and expand the 'Tactile Channels' model of information processing in the tactile system to encompass both threshold and suprathreshold stimuli.
3) Conduct a robust psychophysical investigation of discrimination in the tactile system to supplement the body of work focussed on vibrotactile thresholds and advance a diagnosis model.

4) Make links to applications, particularly the development of informative diagnostic procedures for impaired of tactile perception and the use of vibrotactile stimuli to enhance perception in users of CIs.

1.1 Structure of this Thesis

Chapter 1 introduces the topic and outlines a set of research objectives that will be addressed in the thesis.

Chapter 2 reviews the available literature. I first provide a detailed review of how psychophysics has been used to generate and test an information processing model by isolating individual channel using their vibrotactile thresholds and an overview of the underlying neurophysiology of the afferent systems. The limitations of this model and methodology is then discussed. Existing psychophysical research of suprathreshold vibrotactile frequency and amplitude are systematically reviewed and evaluated.

Chapter 3 describes the research methodology, statistical techniques, and equipment used in the experiments described in this thesis.

Chapter 4 is the first experimental chapter. It describes the instantiation and testing of a novel two-alternative forced-choice procedure and investigates whether contactor size effects the ability to discriminate changes in vibrotactile frequency.

Chapter 5 is the second experimental chapter. It builds on the methodology of experiment one to investigate whether an acceleration magnitude thought to activate both the RA and PC channels results in better frequency discrimination than 1-channel alone.

Chapter 6 is the third experimental chapter. It investigates whether a parallel effect of multi-channel recruitment can be observed in the discrimination of vibrotactile acceleration magnitude, rather than frequency.

Chapter 7 is the fourth experimental chapter. It investigates whether the magnitude dependency of vibrotactile frequency discrimination are attributable to changes in the mediating tactile channels.

Chapter 8 discusses the results obtained in the experimental work reported in this thesis and advances a diagnosis model of the tactile channels suprathreshold, consistent with the findings of experiments 1-4. A candidate vibrotactile psychophysical paradigm is described and pilot data presented. Important limitations of the experiments are also discussed, and recommendations for future research are advanced.

Chapter 9 presents a large body of work conducted by the author concurrently with the PhD project, the 'electro-haptics project'. Insights gained from the basic science presented in experiments 1-4 are applied to the design of tactile stimuli that enhance listening for cochlear implant (CI) users by augmenting the limited signal from the CI with crucial sound information.

Chapter 10 presents the main conclusions of this thesis, summarises the knowledge added by this research, and proposes future work and clear routes for application of the findings of the PhD.

Chapter 2 Literature Review

2.1 The sense of touch

As we interact with objects in the world, we generate perceptual representations of those objects - rough or smooth, grippy or slippy, soft or hard, large or small, heavy or light – to guide our behaviour. Like any biological system, the sense of touch can become impaired. This may be due to degradation with age, disease, traumatic damage to the central or peripheral nervous system, or exposures to environmental hazards. A significant cause of impairment to the tactile system is Hand-Arm Vibration Syndrome (HAVS) – a pattern of peripheral vascular, muscular-skeletal, and sensorineural signs and symptoms associated with repeated exposures to hand-transmitted vibration. The sensorineural component is characterised numbness and tingling in the skin of the fingers and hand, and is strongly associated with measurably reduced sensitivity to tactile stimulation (Griffin, 1990). It is essential that we design, develop and test effective diagnostic tools that improve the sensitivity and specificity of diagnosis and inform research and treatment going forward.

2.1.1 Diagnosis

We can diagnose impaired perception by measuring the limits of information processing in the sensory system. Perhaps the simplest version of this idea is to focus on a detection threshold – the smallest physical stimulus that someone can detect. In disorders of hearing, for example, an audiologist will often measure a patient's auditory thresholds, the quietest tones they report being able to hear at different frequencies. To diagnose a disorder of the tactile system, one of our primary tools is an analogous procedure whereby we measure the lowest amplitude vibration at which observers stop reporting 'not feeling' and start reporting 'feeling'. Typically, a circular contactor attached to a vibrator protrudes through a rigid surface. The observer rests her hand on the contactor at a constant downwards force. Vibrations are delivered to the skin of the hand. They may vary in amplitude continuously (the 'von Bekesy algorithm') or be delivered in controlled intervals (the 'staircase algorithm'; ISO 13091-1:2001). By varying the frequency of the stimuli, the aim is to selectively test the sensitivity of the tactile channels.

2.2 A model of touch perception

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 & 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., the sensation of '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 literature review 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. A model of information processing based on this foundation is incomplete because it builds in a set of limitations (e.g. in sensitivity and specificity, ecological validity, and relation to the known neurophysiological properties of the channels). These limitations mean that thresholds provide an incomplete framework for the diagnosis of impaired touch perception.

2.2.1 Vibrotactile detection 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 precision.

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.

2.2.2 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, these channels are referred to throughout this thesis by labels referring to the neurophysiological structures mediating responses: Pacinian corpuscles (PC channel), rapid adapting (RA channel), slow adapting type two (SA2 channel) and slow adapting type 1 (SA1 channel), respectively.

We can consider these channels to have two key properties:

> **Selectivity**: they respond to a greater extent to stimuli with their preferred parameters (e.g. a vibration within a particular frequency range).
>
> **Independence**: they respond to stimuli without being influenced by how other channels are responding.

These properties mean that we can measure the sensitivity of the individual channels by using stimuli that selectively activate the target channel or attenuate the competing channels. For instance, the PC channel has a much lower threshold for detection of high frequency stimuli than for low frequency stimuli, and the non-Pacinian channels - SA1, SA2, and RA - display the opposite pattern. This robust psychophysical observation (e.g. Verrillo & Gescheider, 1975) has been supported by a body of neurophysiological work that has helped to specify channel selectivity for not only frequency but a wide range of other parameters, leading to an idea that each channel has a distinct function (see 2.2.5). Thresholds of the different channels can be manipulated independently through adaptation (e.g. Gescheider *et al.*, 1978; Hahn, 1968; Hollins *et al.*, 1990) and masking paradigms (e.g. Gescheider *et al.*, 1982). By using these techniques to raise the thresholds of specific channels, we can identify a curve that represents the threshold for each single-channel mediated detection. A typical design might involve an adapting stimulus of 20 Hz raising the threshold amplitude for detection of a low frequency stimulus, but not for the detection of a high frequency stimulus, which means that a larger portion of the frequency range will be mediated by the responses of a high-frequency selective channel (PC) rather than the desensitised low-frequency selective non-Pacinian channels. (Gescheider, Frisina, & Verrillo, 1979).

Psychophysical procedures that reveal the thresholds of particular channels (see Figure 1) 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. By varying the other parameters of vibratory stimuli, we can identify and derive tuning curves to further 'information processing channels' in a similar way - the channel that is most selective for those parameters will have the lowest threshold, and therefore mediate detection independently of the response from the other channels. This process is referred to in this thesis to as the 'isolation' of the tactile channel.

Based on the information-processing model, a psychophysical experiment allows inferences about which mechanoreceptors are responding to a particular stimulus. This rests on a key assumption:

detection of the lowest amplitude of a particular vibrator stimulus is determined by a single channel with the highest sensitivity (Gescheider *et al.*, 2004). This means that 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.

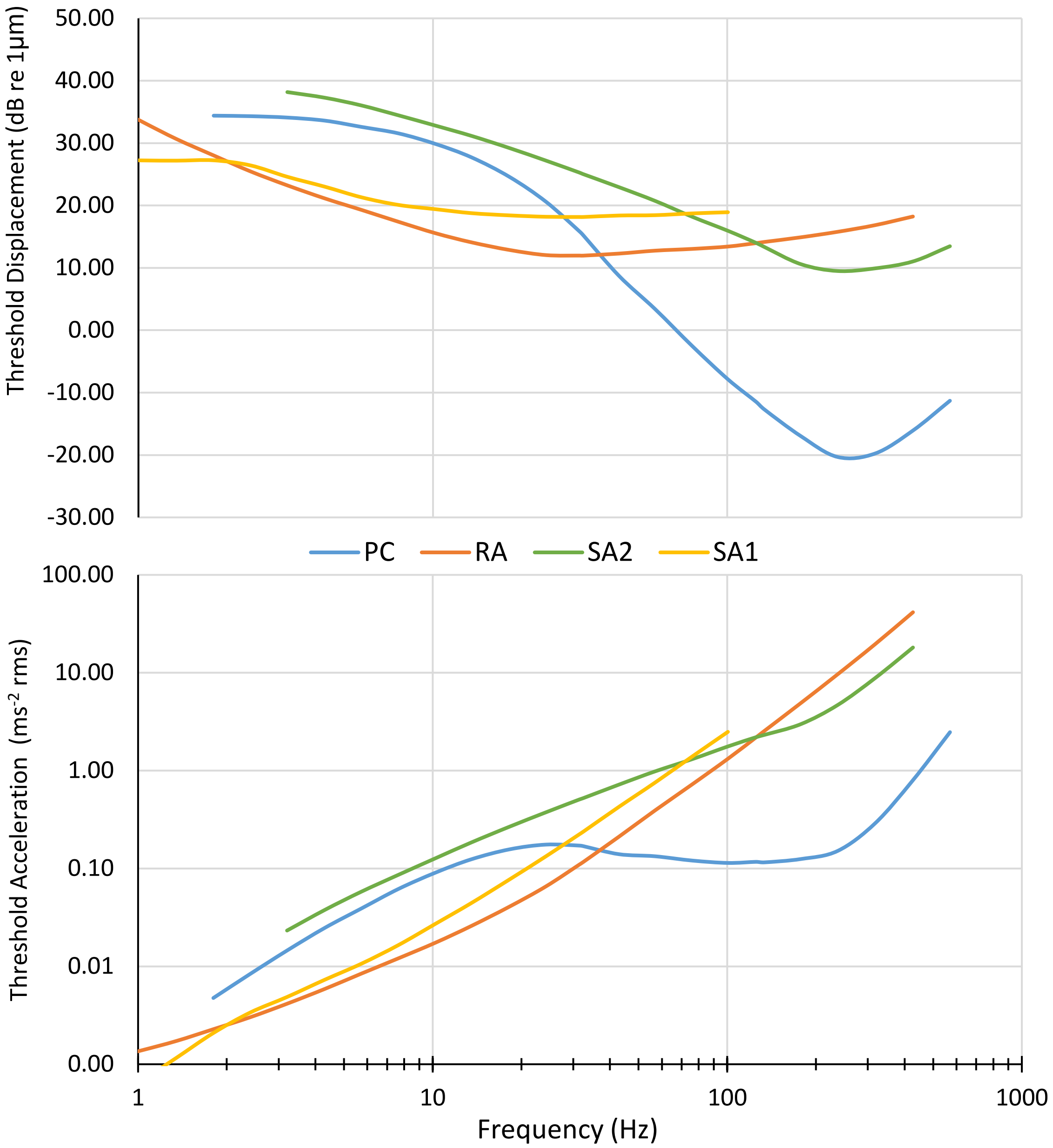

Figure 1. Vibrotactile detection thresholds expressed in terms of displacement (top) and acceleration (bottom) in four tactile channels as a function of frequency. Based on data from (Bolanowski, Gescheider, Verrillo, & Checkosky, 1988; Bolanowski & Verrillo, 1982; Gescheider, Sklar, Van Doren, & Verrillo, 1985; Verrillo & Bolanowski, 1986).

In parallel with the psychophysical approach, our understanding of the underlying neurophysiology has grown and developed. Each information processing channel corresponds with a different motion signalling neuron (mechanoreceptor) in the skin. 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 & 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.

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).

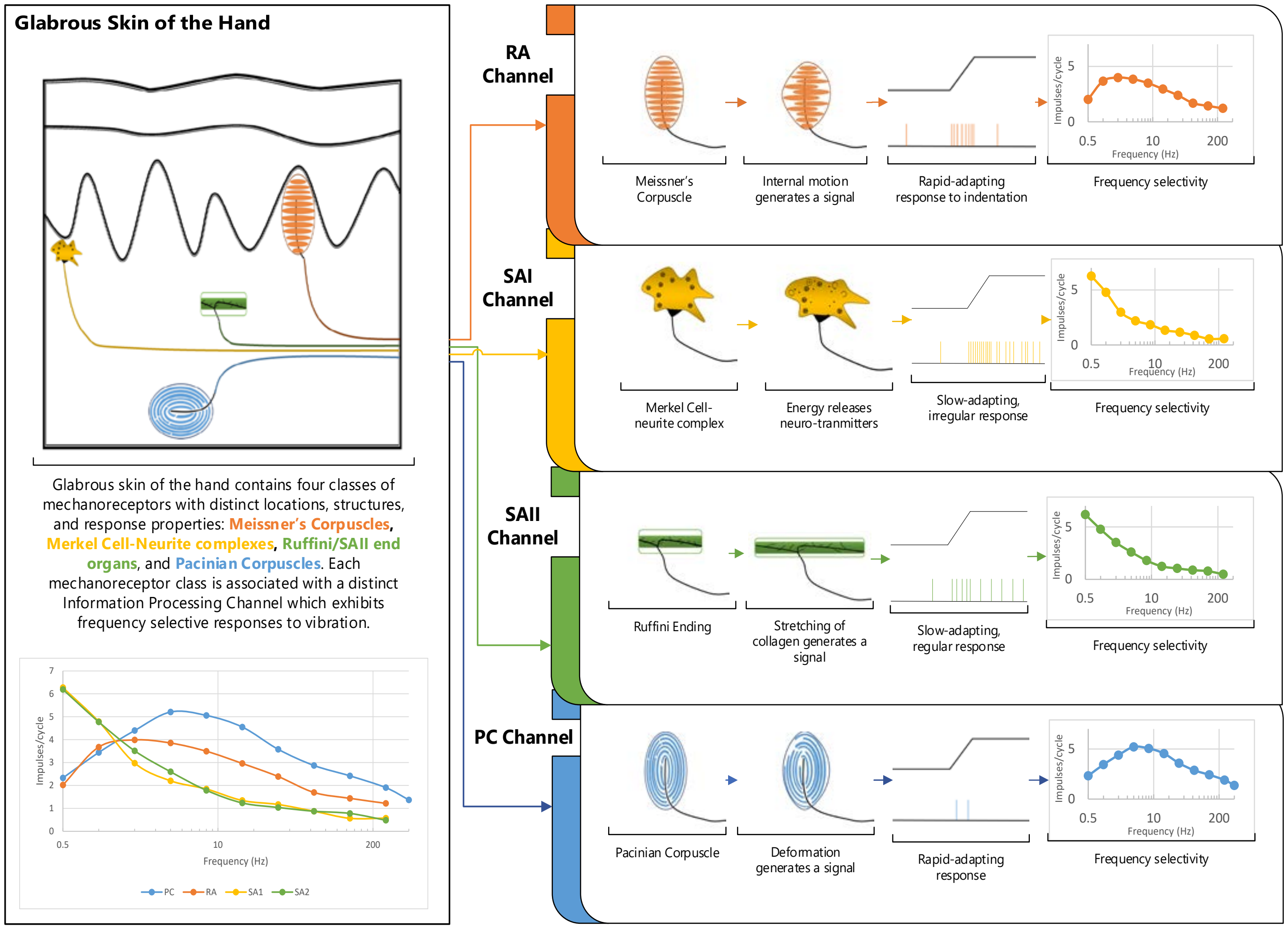

Figure 2. Summary of the physiological responses to vibration in mechanoreceptors and afferent neurons in the glabrous skin of the hand. Variation in the structure, location, and neural response cause the channels to respond selectively to particular frequencies. Frequency selectivity data was adapted from Johansson *et al.*, 1982.

2.2.3 PC channel

As we change the frequency of the stimulus, vibrotactile thresholds follow a stereotyped pattern of a shallow increase in sensitivity at low frequencies, followed by a steep U-shaped increase in sensitivity at higher frequencies (e.g. Bolanowski , Gescheider, Verrillo, & Checkosky, 1988). The initial evidence that this tuning curve reflected at least two overlapping systems came when Verrillo (1963) demonstrated that the U-shaped portion of the curve flattened when a smaller contactor surface was used – the high-frequency 'channel' was sensitive to contactor size. This is the basis of the two-channel, 'Duplex', system of complementary low- and high-frequency selective psychophysical channels (Verrillo, 1968). Figure 3 shows measured vibrotactile thresholds in the small and large contactor conditions, and see Figure 5 for more detail on the effects of contactor size.

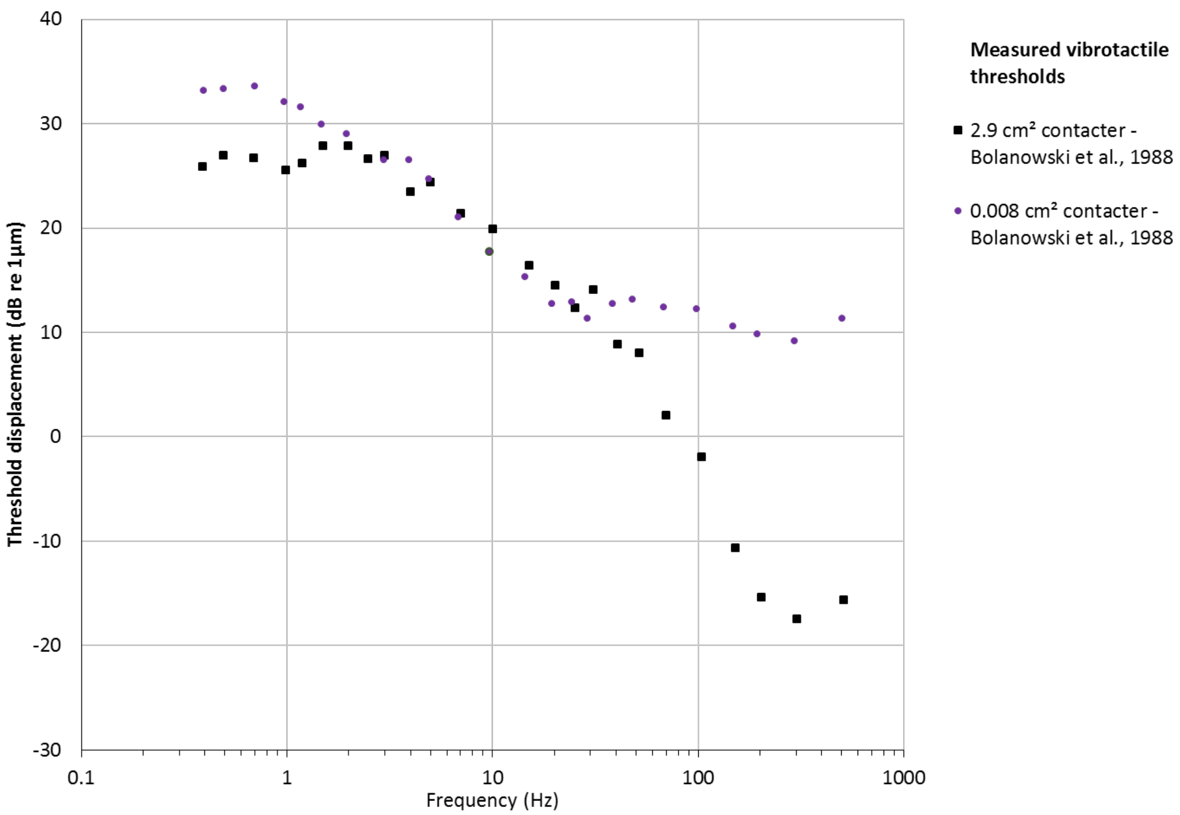

Figure 3. Vibrotactile thresholds at the thenar eminence as a function of contactor size. The PC channel's characteristic U-shaped frequency selectivity is absent in the small contactor condition. Based on data from Bolanowski *et al.* (1988).

Pacinian corpuscles are lamellar nerve endings found in many places in the body (Bolanowski, 1984; Bolanowski & Zwislocki, 1984a, 1984b; Hunt, 1974). Compared to other mechanoreceptors in the skin of the hand, they are large, sparsely distributed, and deep. In response to deformation of the skin the layers surrounding the receptor deform and move relative to one another, opening ion channels and generating action potentials. The response characteristics of the associated afferent nerve are well documented: they have large receptive fields, have a fast refractory rate, and are fast-adapting, in that they signal changes in indentation and then stop signalling.

These properties explain the sensitivity of the PC channel to high frequency vibrations across a wide area. This sensitivity is enhanced through spatial and temporal summation of Pacinian corpuscle signals in the skin - the combination of signals from across the skin, and over time, to support perception. At very low amplitudes, this selectivity is observed as a lower threshold for high frequency vibrations with large contactors and long durations. This has allowed researchers to 'isolate' the tuning curve of the PC channel by using these stimulus parameters to measure thresholds associated with the PC channel, without the influence of less sensitive channels.

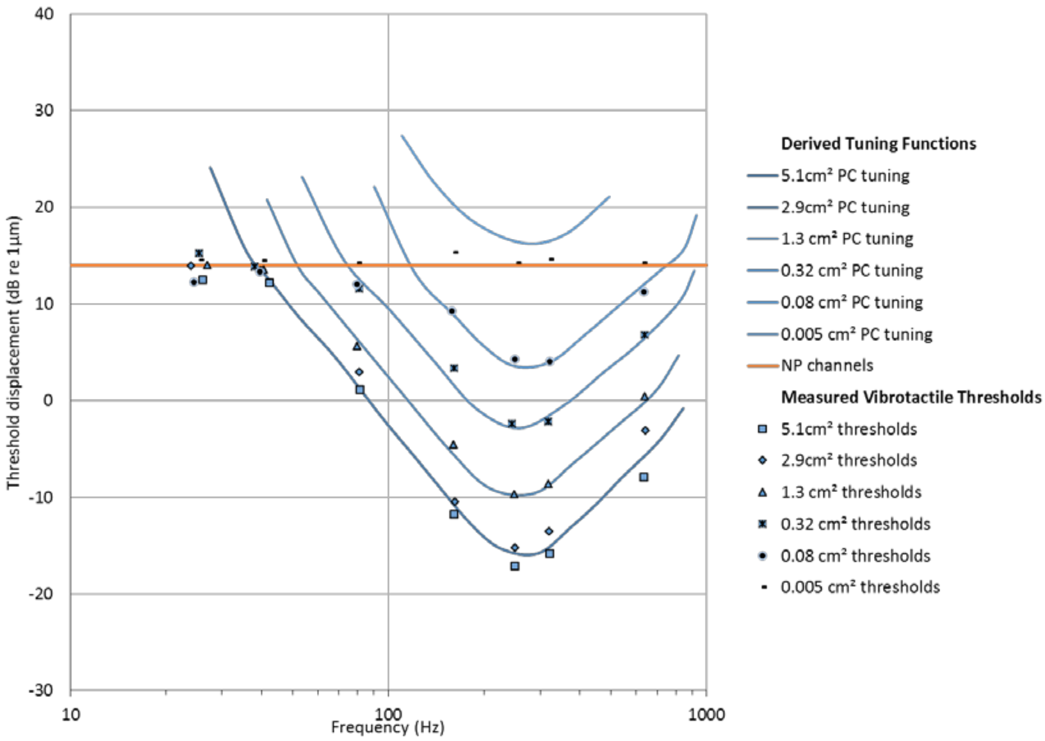

Figure 4. Illustration of attenuation of PC sensitivity with smaller contactor sizes. Blue lines and markers indicate tuning curves for the PC channel when vibrotactile detection thresholds were measured with contactors of different sizes. Based on data from: Verrillo (1963), Bolanowski *et al.* (1988), Bolanowski & Verrillo (1982) Gescheider *et al.* (1985), and Verrillo & Bolanowski (1986).

Because of its clear differences in selectivity, the PC channel has proved relatively easy to identify. Isolation of the tuning curve for the PC channel has arguably been made on the basis of: contact area (Verrillo, 1963a), selective adaptation of low frequency selective NP channels (Verrillo & Gescheider, 1977; Gescheider *et al.*, 1979), duration (Gescheider, 1976; Gescheider, Bolanowski, Hall, Hoffman, & Verrillo, 1994; Gescheider, Berryhill, Verrillo, & Bolanowski, 1999; Gescheider & Joelson, 1983; Verrillo, 1965), and temperature (Bolanowski & Verrillo, 1982). Manipulating these variables and observing changes in PC response has also been strong evidence for the independence of at least two information processing channels. The isolation of the PC channel using variable contact area is demonstrated in Figure 4 and put into the context of the four channel model in Figure 5.

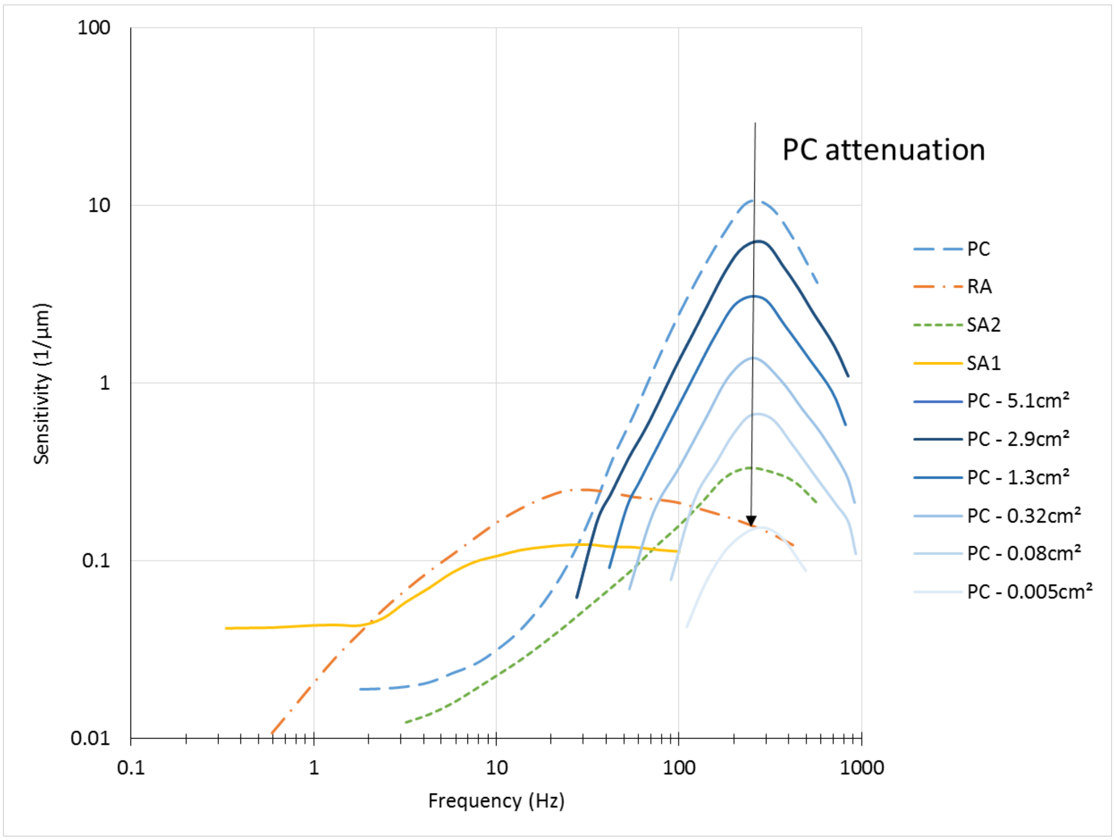

Figure 5. Vibrotactile thresholds as a function of contactor area. As contactor size decreases the PC channel becomes less sensitive and the portion of the vibrotactile thresholds that follow its characteristic U-shaped high frequency selective sensitivity decreases. At 0.005cm2, the PC channel is less sensitive than the NP channels at all frequencies. Based on data from Verrillo (1963).

The methodology of this isolation is clearest in the case of contact area, but generalises well to other parameters. If a channel is more sensitive than other channels to a particular stimulus, it will mediate a greater proportion of the psychophysical response. For example, the PC channel is more sensitivity to larger contact areas, meaning that its threshold is lower than that of other channels across a wider frequency range. This results in the PC channel mediating detection of vibrotactile stimuli for a wide portion of the frequency range when the contact area is large, but a smaller frequency range when the contact area is small. This is illustrated in Figure 4, where we can see that with a 5.1 cm^2 contactor the PC channel is the most sensitive from around 20 Hz, but with a 0.08 cm^2 contactor it remains less sensitive than other channels until around 105 Hz. Figure 6 shows the application of different contactor sizes to the thenar eminence of the left hand to scale.

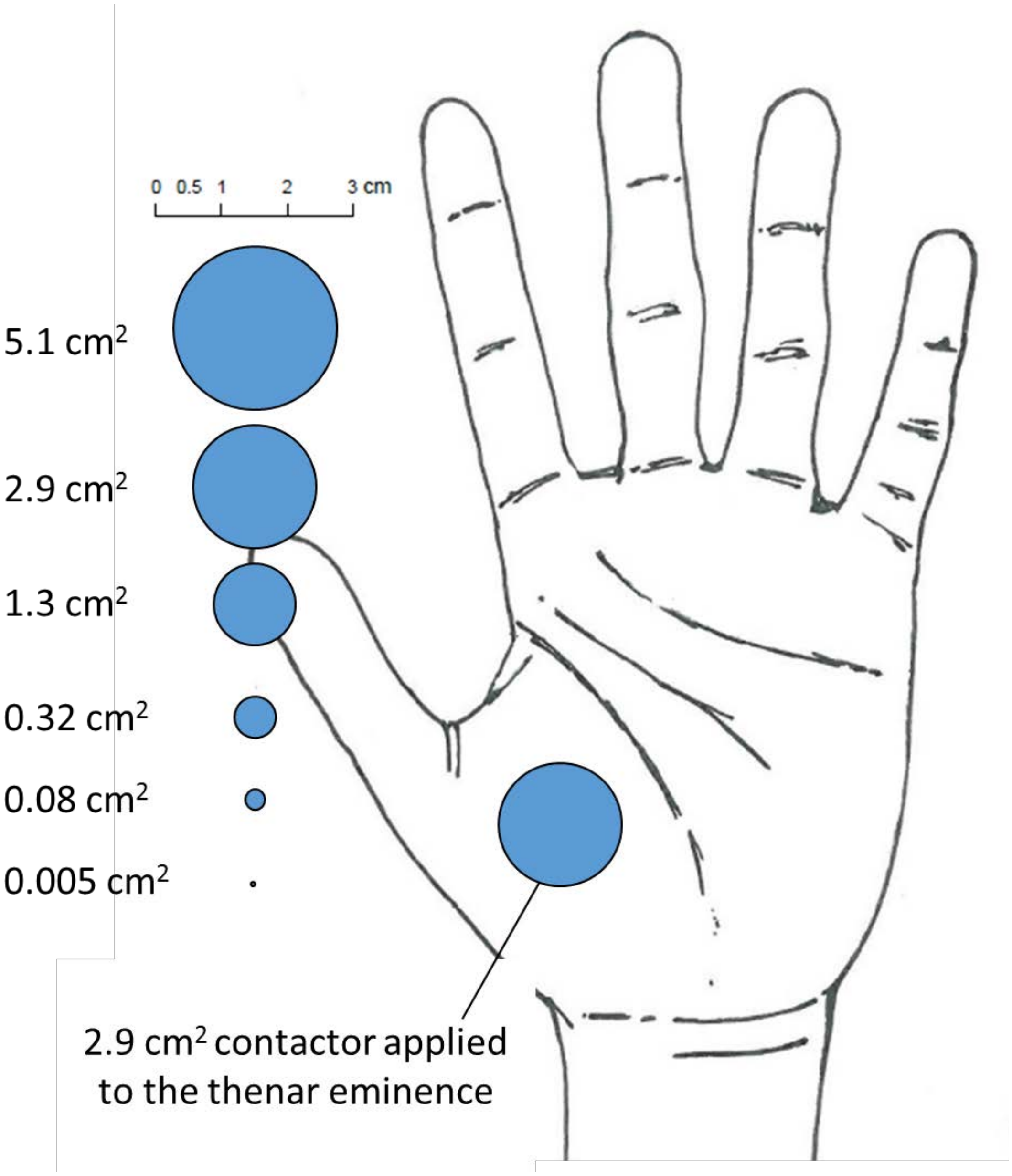

Figure 6. Diagram of the author's left hand with different contactor sizes to scale. In the literature, contactors are typically applied to the thenar eminence of the hand (pictured) or the distal phalanx of a finger. A surround (not shown) is sometimes employed 1-2 mm from the edge of the contactor to limit the spread of surface waves across the skin.

At higher amplitudes, these properties of the PC system are thought to support fine texture discrimination by encoding the temporal pattern of vibrations generated in the skin by contact with a surface (Bensmaia, 2016; Connor & Johnson, 1992). It remains unclear whether, in everyday touch, the PC channel encodes this temporal information alone, or in combination with other channels, whether spatial summation supports this suprathreshold perception, and, in controlled conditions, what the resolution of this system might be.

2.2.3.1 Pacinian Corpuscles

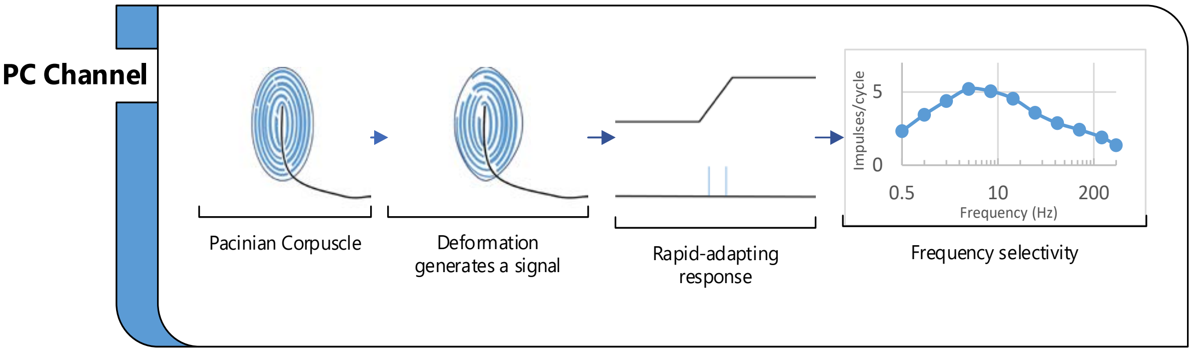

Figure 7. Summary of PC neurophysiological responses. Frequency selectivity data adapted from Johansson *et al.* (1982).

Pacinian corpuscles (Figure 7) are lamellar nerve endings about 1mm long. They are relatively large, sparse and deep compared to the other mechanoreceptor classes. In response to deformation of the skin the layers surrounding the receptor deform and move relative to one another. Changes in the shape of the corpuscle open sodium channels, allowing charged ions to flow into the cell and depolarise the membrane. The voltage generates action potentials, sending a signal to the brain.

The responses of the PC nerve fibres are notably fast adapting in response to static indentation – they signal changes in indentation and then stop signalling (see Figure 7). Because of the fast refractory rate of this process, they are able to respond strongly to high frequency vibrations. The receptive fields of individual Pacinian receptors are very large, and they are able to generate a response to a stimulus several centimetres away on the skin surface (Johansson, 1978).

2.2.4 RA channel

The first 'non-Pacinian' channel is supported by 'Rapid-Adapting' nerve fibres that carry the signal from Meissner's corpuscles (Bolanowski *et al.*, 1994). Meissner's corpuscles are located more shallowly in the skin and consist of layers of flattened cells. When the skin is deformed, the layers shift against one another, generating an action potential in the RA fibre. As the name suggests, the RA channel adapts quickly to static deformation; this allows it to encode the temporal characteristics of vibrating stimuli. Unlike the PC channel, the RA channel is most sensitive to medium frequencies, has a smaller receptive field, and is relatively insensitive to changes in contactor size and duration (Cohen & Kirman, 1986; Verrillo, 1963a). This selectivity to frequency is much less sharply tuned than the PC channel, supporting detection across a wide range of frequencies if the PC channel is sufficiently insensitive (Bolanowski *et al.*, 1988; Gescheider *et al.*, 2001). Figure 8 illustrates this 'duplex' model, where the channels can be seen be differentially sensitive with contactor sizes of different diameters (Verrillo & Bolanowski, 1982).

Suprathreshold, the RA channel has been somewhat implicated in encoding of vibration frequency, but, thanks to its smaller receptive field, is also thought to encode motion across the skin (Johnson, 2001), helping with detecting the slip of a gripped object, for example. This perspective may underestimate the contribution of information across channels (Saal & Bensmaia, 2014b).

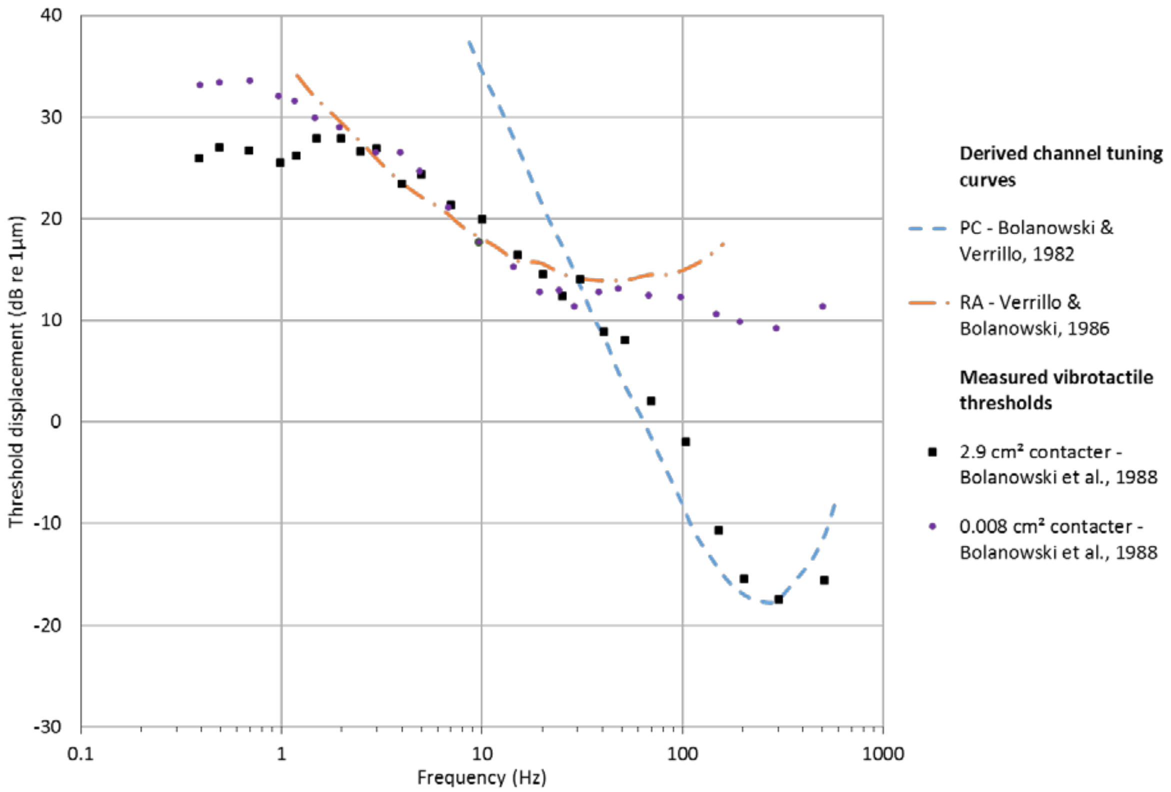

Figure 8. Derived tuning function for the RA channel. With a large contactor vibrotactile thresholds above 30 Hz are determined by the PC channel. With the small contactor, PC sensitivity is attenuated, and vibrotactile thresholds are mediated by the RA channel over a larger range. Based on data from Bolanowski *et al.* (1988) and Verrillo & Bolanowski (1986).

The discrimination of 'P' from 'NP' systems was relatively clear because the PC system exhibits a characteristically U-shaped frequency-dependent response while the NP system had a 'flat' response. Verrillo and Bolanowski (1986) were able to isolate a response of the RA system from other channels by exploiting a reported insensitivity to skin temperature, while both SA2 and PC channels are more sensitive at higher temperatures (Bolanowski & Verrillo, 1982; Green, 1977).

Verrillo and Bolanowski (1986) used a very small contactor to limit PC involvement, and determined thresholds over a wide range of skin temperatures at the thenar eminence and at the volar forearm (which does not contain Meissner's corpuscles, the structure that mediates the RA channel). By looking at the difference in shape between these two regions they identified the RA channel tuning curve insensitive to temperature, and attributed temperature sensitive response common to both regions to the SA2 channel.

Evidence that the PC and RA channels can be manipulated independently also comes from studies using adaptation, whereby a high intensity stimulus at a frequency to which a given channel is far more sensitive causes that channel's threshold to temporarily increase (see Gescheider *et al.* 1979). Figure 9 shows how PC and RA channels can be separately adapted, and new estimated tuning curves accounting for the pattern of responses.

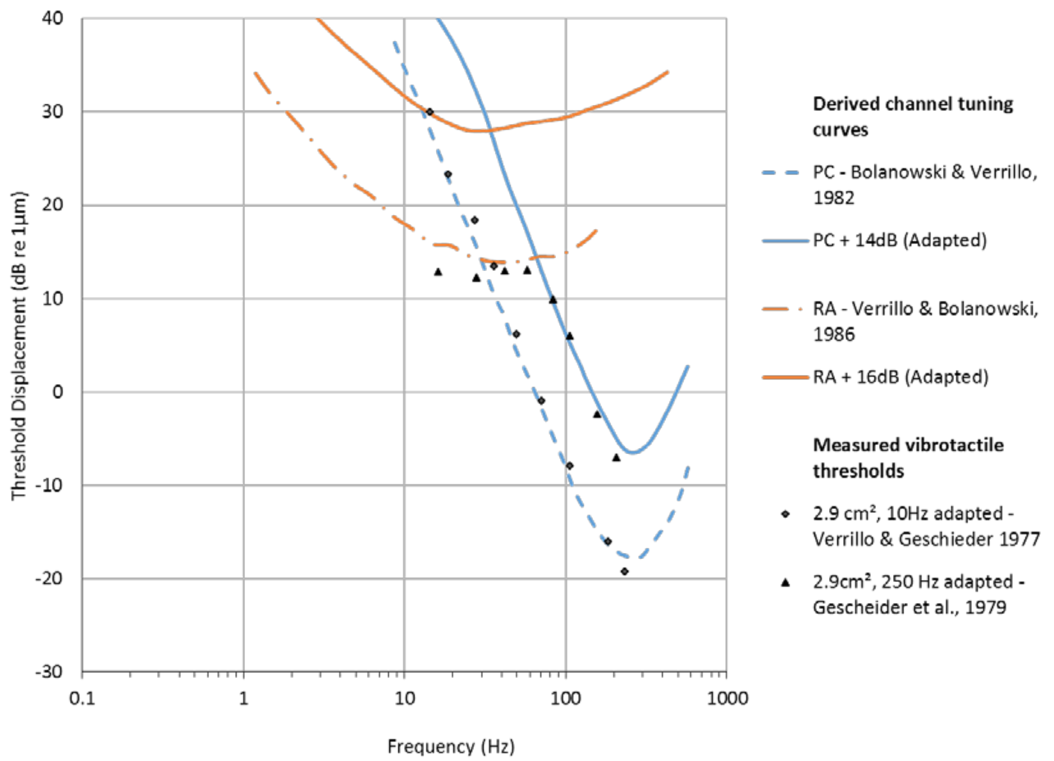

Figure 9. PC and RA tuning in response to adaptation. 250-Hz adaptation attenuates PC sensitivity by approximately 14dB, causing thresholds in the 30 – 60 Hz range to be mediated by the RA channel. 10-Hz adaptation attenuates RA sensitivity by approximately

16dB, causing thresholds above 20-Hz to be mediated by the PC channel. Based on data from Bolanowski & Verrillo (1982), Gescheider *et al.* (1979), Verrillo & Bolanowski (1986) and Verrillo & Gescheider (1977).

2.2.4.1 Meissner's Corpuscles

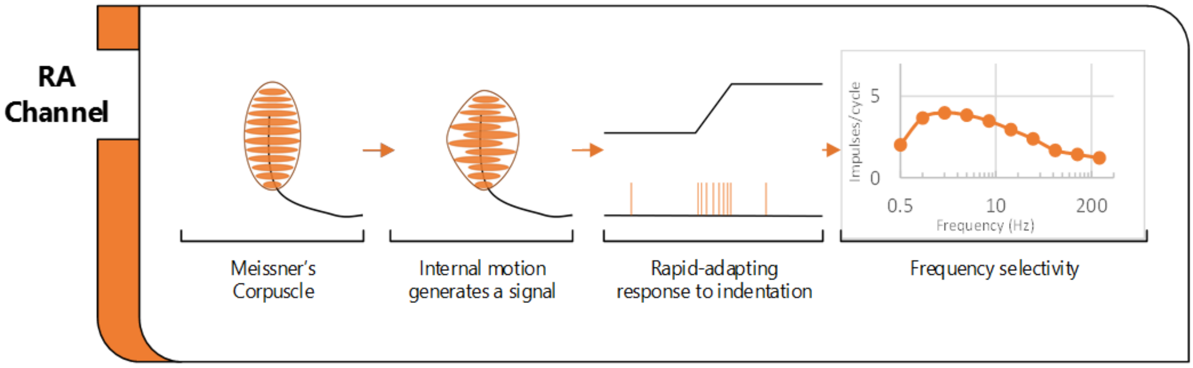

Figure 10. Summary of RA neurophysiological responses. Frequency selectivity data adapted from Johansson *et al.* (1982).

Meissner's corpuscles (Figure 10) are located more shallowly in the skin, just below the epidermis. Each corpuscle consists of layers of flattened cells. The neuron is coiled around these stacked cells, and is highly sensitive to small changes in relative position. When the skin is deformed, the layers shift against one another, generating a potential in the neuron and signalling deformation of the skin. Meissner's corpuscles are also rapidly adapting (hence RA channel), signalling changes in pressure at medium frequencies. Figure 10 gives a summary of Meissner/RA response properties.

2.2.5 SA2 channel

The second slow adapting channel, the SA2 channel, is probably supported by the activation of Ruffini endings (Birznieks *et al.*, 2009; Paré *et al.*, 2003). Like SA1, the properties of the mechanoreceptor have made it difficult to isolate a frequency dependent tuning curve. Because the SA2 channel operates in a similar frequency range to the PC channel, it was necessary to heavily desensitise the PC channel using a small contact area and a short stimulus duration. Because the SA2 threshold is relatively high, it was also necessary to desensitise the RA channel using a masking paradigm to raise its threshold (Gescheider *et al.*, 1979; Gescheider, Verrillo, & Van Doren, 1982; Gescheider *et al.*, 1983).

In a typical masking paradigm of this sort (e.g. Verillo 1983), the target stimulus would be presented simultaneously with a masking stimulus. The target stimulus was of a frequency to stimulate the SA2 channel while the masking stimulus was of a frequency to stimulate the RA channel. This simultaneous presentation of the masking stimulus has the effect of desensitizing the RA channel's sensitivity to the target stimulus, and the degree of desensitization can be manipulated by altering the magnitude and duration of the masking stimulus. By systematically manipulating the degree of desensitization of the RA channel, it is possible to identify a tuning curve for the SA2 channel.

Suprathreshold, the SA2 channel may be involved in detecting and responding to small slips across the skin, and possibly the encoding of hand position as a function of the pattern of stretched skin (Johnson, 2001; Saal & Bensmaia, 2014). Its high frequency selectivity and role in vibrotaction are not well understood.

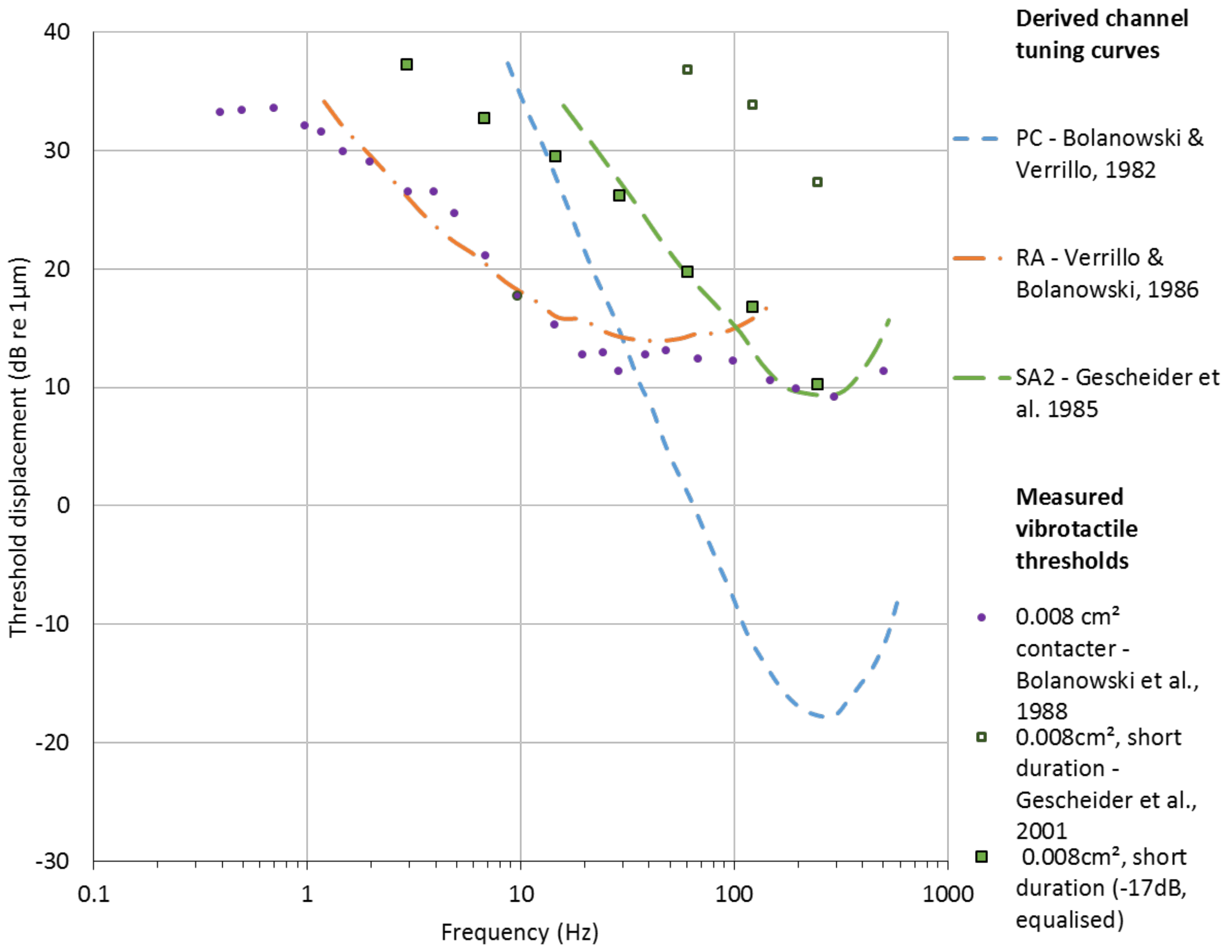

Figure 11. Derived tuning function for the SA2 channel (A. Gescheider *et al.*, 2001). Threshold displacemnet of the SA2 channel is adjusted here to reflect it's likely sensitivity when it is not attenuated by experimental conditions.

The existence of the SA2 channel was confirmed when Gescheider and colleagues (1985) isolated its tuning function. Because the SA2 channel operates in a similar frequency range to the PC channel, it was necessary to heavily desensitise the PC channel using a small contact area and a short stimulus duration. Because the SA2 threshold is relatively high, it was also necessary to desensitise the RA channel using a masking paradigm to raise its threshold (Gescheider *et al.*, 1979, 1982; Gescheider *et al.*, 1983). Gescheider and colleagues (2001) used a similar procedure to further identify its properties. On a single graph these thresholds look very high, but it is likely that this is due to the difficulty of identifying very short duration stimuli, purely in terms of task demands (Figure 11). To illustrate how the tuning curve has been arrived at, adjusted thresholds (17 dB lower) are also shown. Figure 12 illustrates the degree of PC and RA attenuation necessary for SA2 channel to be the most sensitive, and so mediate detection.

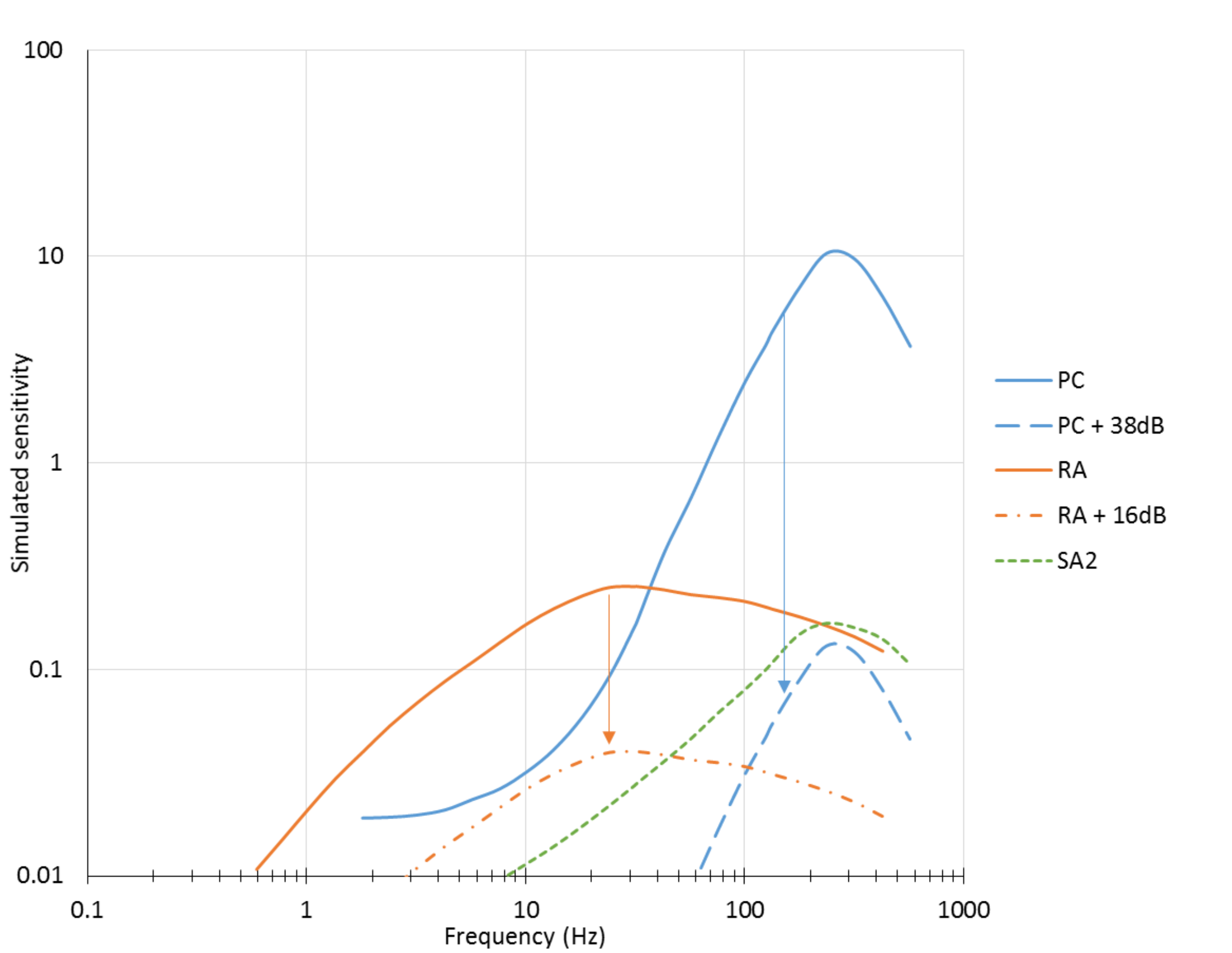

Figure 12. Approximate PC and RA attenuation necessary for SA2 channel to be the most sensitive.

2.2.5.1 Ruffini Endings

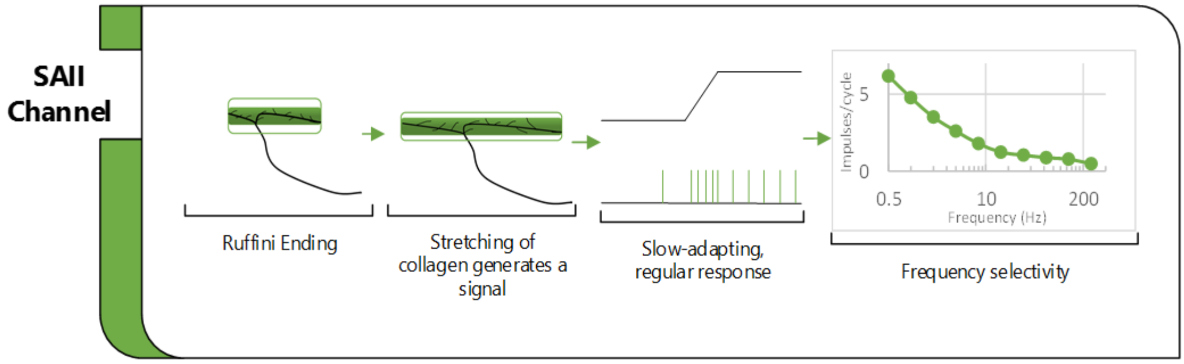

Figure 13. Summary of SA2 neurophysiological responses. Frequency selectivity data adapted from Johansson et al (1982).

Ruffini endings (Figure 13) are corpuscles in the dermis composed of a branching nerve fibre coated in collagen, a structural material ubiquitous within the skin. Stretching of the skin shifts the collagen, perturbing the nerve fibre and generating action potentials. Ruffini endings are strongly responsive to lateral motion of the skin, are slow-adapting, and respond regularly in response to static indentation and low frequency vibrations (see Figure 13).

There is some controversy over whether Ruffini endings, specifically, are the end organs of the SA2 channel. They are reported in some microneurographic studies of the human hand but are conspicuously absent from others (Paré *et al.*, 2003; Paré, *et al.*, 2002). However, given the neurophysiological evidence of the stereotyped response properties of SA2 afferent nerves it's clear that some analogous structure with similar properties – such as some kind of paciniform receptor (Gescheider *et al.*, 2010), a simpler structure than the Pacinian corpuscle – compose the end organ of the SA2 channel.

2.2.6 SA1 channel

In contrast to the PC and RA nerve fibres, the Slow-Adapting type-1 channel (SA1) is characterized by prolonged responses to static indentation. This channel is supported by Merkel cell complexes, specialised versions of normal epithelial cells, located very shallowly in the skin (Lacour *et al.*, 1991). They contain vesicles holding a neurotransmitter that, when released, opens ion channels in the nerve ending. Perturbation of the skin releases the neurotransmitter and generates action potentials, in a characteristic sustained, irregular pattern (Bisley *et al.*, 2000; Duclaux & Kenshalo, 1972). These cells are clustered around the fingertips, with very small receptive fields.

Bolanowski and colleagues (1988) derived a tuning function for the SA1 channel using an extensive set of masking procedures in which masking stimuli were paired with 0.7 Hz test stimuli. The masks elevated the thresholds for RA, PC and SA2 channels until SA1 responses were mediating detection. The tuning curves were then derived from the amplitude of the masks necessary for this to be the case. Gescheider and colleagues (1994) extended this tuning curve to frequencies below 2 Hz.

The response dynamics of the underlying neurophysiology suggest that, rather than encode the temporal characteristics of a vibration, SA1 channel is instead responsible for information about coarse surface textures and other spatial information including detection and localization of very small indentations (Johnson, 2001; Skedung *et al.*, 2013; Weber *et al.*, 2013).

2.2.6.1 Merkel Cell-Neurite Complexes

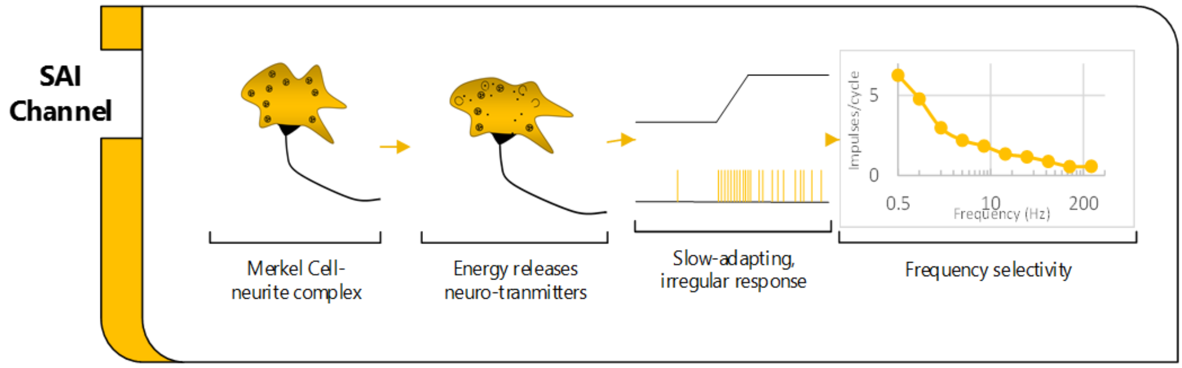

Figure 14. Summary of SA1 neurophysiological responses. Frequency selectivity data adapted from Johansson et al (1982).

Merkel cell complexes are specialised versions of normal epithelial cells, located in the epidermis. They are full of vesicles containing full of neuro-peptide, a neurotransmitter that opens ion channels in the nerve ending that terminates at the cell. Perturbation of the skin releases the peptides and generates action potentials in the neuron. Unlike Meissner and Pacinian responses to vibration, this neurochemical response persists in response to static indentation. Because it is slow adapting it responds most effectively to very low frequency vibrations. It also displays a characteristic irregular response over time because of the dynamics of this process (see Figure 14). Merkel receptors are densely packed in glabrous skin, and have very small receptive fields, making them highly responsive to differences in spatial indentation.

2.2.7 Matching psychophysics to neurophysiology

The idea of a sensory threshold cannot be easily transplanted into neurology. All neurons display some level of baseline activity independent of stimulation, and respond to stimulation in a probabilistic and idiosyncratic way (Doya, 2007). Some researchers have attempted to match psychophysical thresholds generated from detection designs with some level of corresponding activity in the associated nerve fibres (e.g. Bolanowski *et al.*, 1988). Clearly this kind of research creates a model highly dependent on the particular neural thresholds chosen: if response criterion is expressed in spikes per second then the shape of the tuning curve changes as the specified firing rate changes, whereas if the criterion is expressed in terms of spikes generated by the stimulus exposure, then the tuning curve changes as a function of stimulus duration.

Bolanowski and colleagues (1988) brought together many different considerations to estimate values which could be used as vibrotactile thresholds on a neurological, rather than a psychophysical, level. These characterizations rest on relatively sparse evidence, and different assumptions are made for each channel based on the degree of characterization of the neurophysiological response and psychophysical properties:

> **PC** – 4 spikes per stimulus burst to account for the predominant role of temporal summation – characterised by lower thresholds for longer stimuli – in the PC channel. The 'minimal neural response' must therefore be more than a single pike per stimulus burst but less than a spike per stimulus cycle (Van Doren, 1985).
>
> **RA** – one spike per stimulus cycle based on evidence that observers are able to reliably detect a single action potential elicited in RA fibres (Vallbo *et al.* 1984).
>
> **SA1** – 0.8 spikes per second based on the observation that only at this arbitrary threshold would match the shape of the neural response criterion curve match that of the psychophysically derived curve (Bolanowski *et al.*, 1988).
>
> **SA2** – 5 spikes per second because of the high baseline activity of this fibre. Any detectible signal must be distinguishably higher than this noise. This activation seems to depend on a broader population; only when several fibres are activated will detection be elicited (Ochoa & Torebjörk, 1983).

Characterising information processing in the tactile system in terms of both psychophysics and neurophysiology is complicated by the complexity of the selectivity of the channels. They are usually characterised by their frequency selectivity, but they also display marked selectivity to a broad range of other parameters. These factors include: contact area (Lamoré & Keemink, 1988; Maeda & Griffin, 1994; Verrillo, 1985), stimulus duration (Gescheider & Joelson, 1983; Verrillo, 1965), the static force of the contactor (Brisben *et al.*, 1999; Craig & Sherrick, 1969; Harada & Griffin, 1991; Lamoré & Keemink, 1988; Maeda & Griffin, 1994), skin temperature (Bolanowski *et al.*, 1988), active or passive movement (Yıldız *et al.*, 2015), pressure distribution (Srinivasan & LaMotte, 1991), body location (Forta *et al.*, 2012), skin indentation (Whitehouse & Griffin, 2002), and surface topography (Skedung *et al.*, 2013). Even the fundamental selectivity for frequency is a complex interaction with amplitude (Bensmaia, 2008; Freeman & Johnson, 1982, 1982; Muniak *et al.*, 2007).

Some of these factors have been instrumental in isolating the channels. However, it remains difficult to understand what information is being captured by each of the channels. In part, this can be attributed to the central role of the detection design, which ultimately asks 'is there any information' in the tactile system, rather than 'what is the information'.

The neural coding strategies employed by the different classes of mechanoreceptor may help identify the sort of information to which we might expect them to be sensitive. However, this exercise of assigning neural thresholds to match psychophysical vibrotactile thresholds typically assumes that the tactile channels employ a variant of a 'rate code' (Bolanowski et al, 1988). This refers to a code in which the number of action potentials (or change in number) provides information about the strength of the stimulus. The idea behind vibrotactile thresholds is that at some point this value crosses a threshold and results in perception of vibration.

However, more recent work has suggested 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 use a 'temporal code' in which the precise timing of spikes contain information about the stimulus. This coding scheme allows mechanoreceptors to encode the frequency of a stimulus – as we might expect from channels that respond to changes in indentation and then rapidly adapt. There is also the possible influence of coding across broader populations to consider when designing tests of tactile perception. Güçlü and Bolanowski (2004), for example, found that 5-10 RA fibres needed to be activated to mediate detection – not the single spike suggested by Bolanowski and colleagues (1988).

Fundamentally, this approach is limited by the weaknesses of the psychophysical design. Instead of attempting to match neurological recordings to psychophysical thresholds, we should be trying to design psychophysical tasks that better reflect the properties of the underlying neurophysiology. In particular, future research should advance a model of tactile perception as mediated by four-independent information processing channels, that operate as part of a system of 'active touch' that operates in an ecological setting to discriminate suprathreshold stimuli.

2.3 Limitations of vibrotactile detection thresholds

The results of measuring vibrotactile detection thresholds has been central to building our model of the human tactile system and forms the framework for the diagnosis of impaired touch perception. However, the method is marked by a number of important limitations.

2.3.1 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 & Swets, 1966; Macmillan & 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 & Swets, 1966).

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 & Swets, 1966; Macmillan & Creelman, 1991; Morioka & 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 & 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.

2.3.2 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 & 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 & 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 & 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.

2.3.3 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.

2.3.4 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 & Sherrick, 1969; Harada & Griffin, 1991; Lamoré & Keemink, 1988; Maeda & Griffin, 1994), contact area (Lamoré & Keemink, 1988; Maeda and Griffin, 1994; Verrillo, 1985), stimulus duration (Gescheider & Joelson, 1983; Verrillo, 1965), skin temperature (Bolanowski *et al.*, 1988), skin indentation (Whitehouse & Griffin, 2002), active or passive movement (Yıldız *et al.*, 2015), pressure distribution (Srinivasan & 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 & Bensmaia, 2014).

2.3.5 Neural thresholds versus psychophysical thresholds

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).

2.3.6 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 & Vierk, 1993; Harvey *et al.*, 2013; Hollins & 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.

2.3.7 Choice of vibrotactile stimuli

In order to study the human tactile system, we need a way to estimate the likely response of each vibrotactile channel to a vibration stimulus having specific characteristics (e.g., frequency, force, area, surround). From here, we can identify those stimulus conditions likely to selectively activate the target channel. Only with these estimates of channel sensitivity can we design stimuli in order to measure any impairment of touch perception.

Channel sensitivity with different contact conditions can be estimated from tuning curves derived by Bolanowski and colleagues (1988), Bolanowski and Verrillo, (1982), Gescheider and colleagues (1985), and Verrillo and Bolanowski (1986). The effects of contactor size have been reported by Verrillo (1963 and 1968) and may be implemented into a model by applying a multiplier to absolute thresholds such that the pattern of responses is consistent with studies of vibrotactile thresholds over wide frequency range (Bolanowski *et al.*, 1988). The effects of stimulus duration can be based on data from (Gescheider *et al.*, 1999; Gescheider and Joelson, 1983; Verrillo, 1965). Effects of adaptation (e.g. Gescheider *et al.*, 1979) may also be modelled by raising the thresholds of individual channels.

International Standard 13091-1:2001 specifies stimuli and psychophysical procedures for diagnosing dysfunction in vibrotactile perception. The standard specifies three sets of conditions intended to individually activate the SA1, PC, and RA tactile channels. An elevated threshold (i.e., reduced sensitivity) is an indicator that some aspect of the selectively activated neural population is impaired.

The International Standard specifies a skin temperature in the range 27 to 35°C and a room temperature in the range 20 to 30°C. The conditions employ a smooth, circular, rigid contactor with a diameter in the range 2 to 7 mm that either indents into the skin by 1.5 mm ± 0.8 mm or is applied with a static force in the range 0.7 to 2.3 N (estimated to be equivalent to the indentation). The contactor is positioned on the glabrous skin of the fingertip distal to the centre of the whorl and more than 2 mm from the fingernail. The presence of a surround will have a substantial impact on the sensitivity of the channels, so it is significant that the standard allows two methods: one without a surround and one with a rigid surround separated from the probe by an annulus of width 1.5 mm ± 0.6 mm. The stimulus targeting the SA1 channel is a 4-Hz oscillatory vibration of the probe. The stimulus targeting the RA channel is a 31.5-Hz vibration. The stimulus targeting the PC channel is a 125-Hz vibration. The psychophysical procedure can be either a variant of an up-down method of limits with the duration of each vibration less than 10 seconds, or a von Békésy algorithm with stimuli continuously presented with an amplitude that increases and decreases at a specified rate according to whether the subject is able to feel the vibration.

The expected sensitivity of each tactile channel to the conditions specified in ISO 13091-1:2001 was simulated by adjusting the sensitivities so that they correspond to experimentally determined thresholds. The PC thresholds corresponding to the sensitivities shown in Figure 15 were raised by 8 dB to account for higher thresholds with a smaller 6-mm diameter contactor at the fingertip (Morioka *et al.*, 2008; Figure 15) compared to a 19.2-mm diameter contactor at the thenar eminence (Bolanowski *et al.*, 1988). The thresholds of the non-Pacinian channels were raised by 6 dB to account for the effects of other systematic differences including the influence of the surround and differences in experimental methods so that the new sensitivity curves for the lower frequencies in Figure 2 are also consistent with thresholds obtained with a 6-mm contactor by Morioka *et al.* (2008).

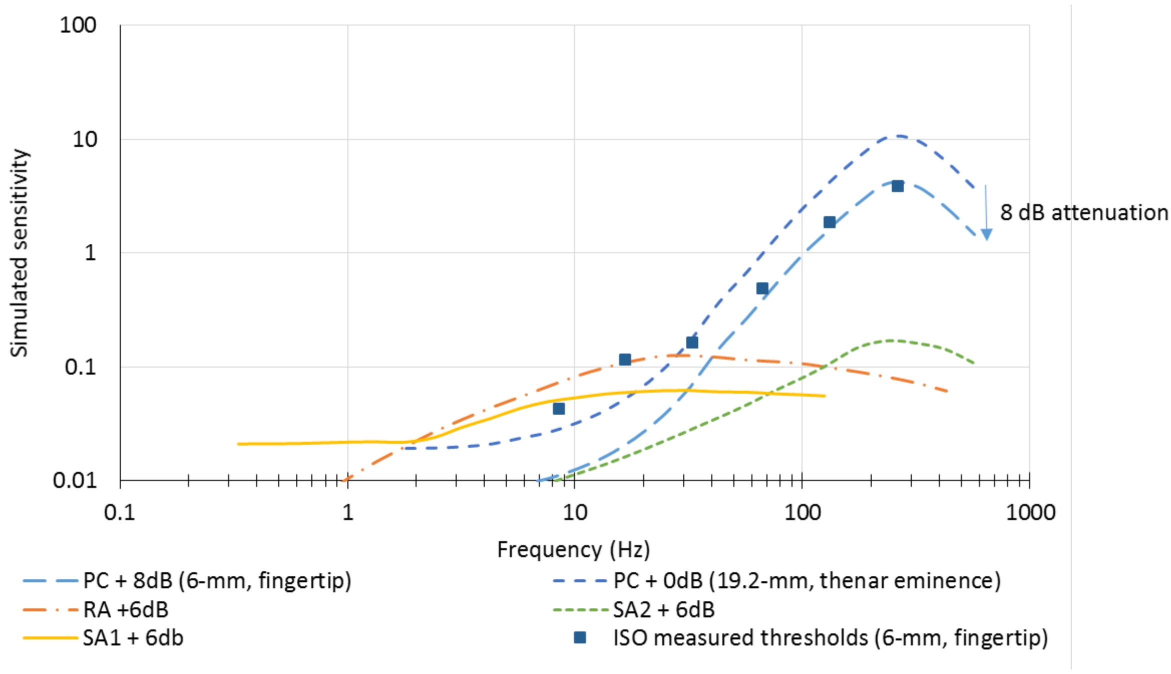

Figure 15. Channel sensitivity (1/(threshold peak displacement in μm)) with a 6-mm contactor. The PC channel is attenuated by 8 dB and the non-Pacinian channels are

attenuated by 6 dB in order to fit measured vibrotactile thresholds with a 6-mm contactor (Morioka *et al.*, 2008).

The model in Figure 15 was used to investigate whether the stimulus parameters recommended in ISO 13091-1:2001 are likely to selectively activate their target tactile channel Figure 16. In order to estimate normal thresholds, the following conditions were assumed: a 6-mm diameter contactor with a surround and sinusoidal (i.e., pure tone) vibration stimuli at 4, 31.5, and 125 Hz. There was no adjustment for sensitivity to duration due to the widespread use of the von Békésy algorithm. It was assumed there were no substantial effects of skin temperature or static force within the range of conditions specified in the standard. It was assumed that the multi-channel model of tactile perception, which is mostly based on thresholds at the thenar eminence, is applicable to the fingertips. Although mechanoreceptor densities may differ, the cell types are thought to be similar in these two locations.

Figure 16 illustrates that sensitivity to other (non-target) tactile channels may mean that thresholds are not always mediated by the targeted channel:

- The conditions with 4-Hz vibration specified for selectively activating the SA1 channel are likely to activate the RA channel (Figure 16 A)
- The conditions with 31.5-Hz vibration specified for selectively activating the RA channel are likely to primarily activate the RA channel but the contributions from other channels may be significant, especially if the patient has abnormally high thresholds in the RA channel (Figure 16 B)
- The conditions specified for selectively activating the PC channel are very likely to primarily activate the PC channel, although the conditions do not maximise the difference between the response of the PC channel and the responses of other channels (Figure 16 C).

The findings of psychophysical studies are sufficient to estimate how the sensitivity of the tactile channels to vibration depend on the frequency of vibration, contactor size, stimulus duration, skin temperature, adaptation, and masking. This information can be used to predict the tactile channels that will be activated by different vibration conditions.

It seems that although the conditions suggested for determining vibrotactile thresholds in ISO 13091-1:2001 may identify the response of the PC channel, they will be less reliable in identifying the response of the RA channel and probably fail to identify the response of the SA1 channel.

An important consequence of this lack of channel specificity for the RA targeting conditions is the failure to identify a raised threshold in the RA channel if the PC channel is sufficiently sensitive. This can be illustrated by the following scenario: a patient with an impairment in the RA channel characterised by a detection threshold in that channel of greater than .4 (ISO 13091-1:2001). In this patient, the PC channel is unimpaired, and is able to mediate detection for the 31.5 Hz stimulus at an acceleration magnitude of less than 0.4. According to the diagnostic criteria, this patient would have no sensorimotor impairment, despite having a severely impaired, or even absent, detection threshold for the RA channel. The problem, as discussed previously, is that detection always *looks like* detection, and we lack the capability to distinguish between perception between one channel and another. This reduces the sensitivity and specificity of vibrotactile detection thresholds both as a diagnostic and as a research tool.

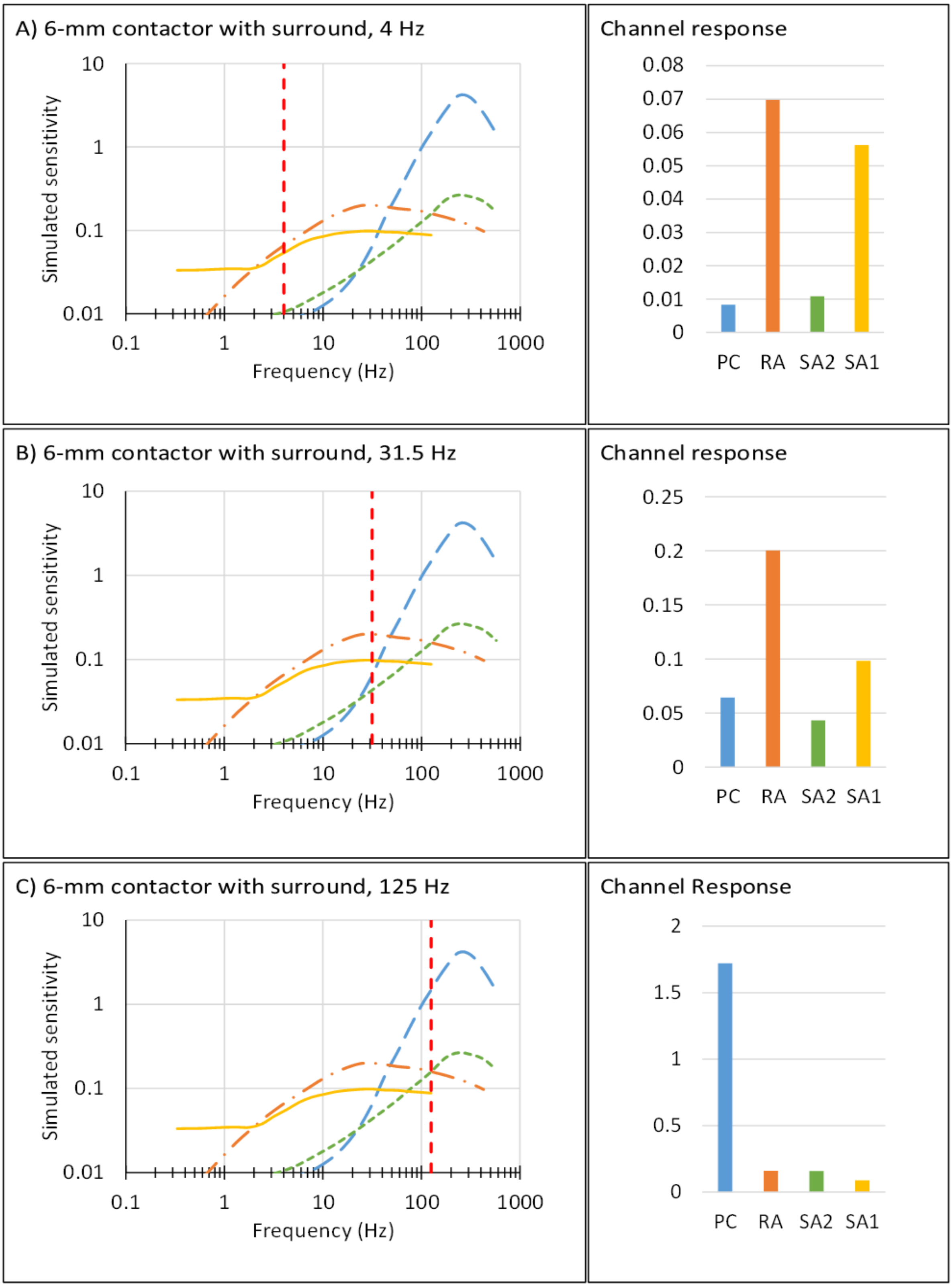

Figure 16. Predicted channel sensitivity (1/(threshold peak displacement in μm)) to vibration parameters specified in ISO 13091-1:2001. (A) illustrates the channel response to a 4-Hz stimulus designed to activate the SA1 channel. (B) shows channel sensitivity to a 31.5-Hz stimulus designed to activate the RA channel. (C) shows channel sensitivity to a 125-Hz stimulus designed to activate the PC channel.

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. The model is therefore fundamentally limited to low energy stimuli unrepresentative of the normal neurophysiological response of the channels. Diagnostic methods should therefore 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.

2.4 Suprathreshold touch

There is a sharp divide in the literature between earlier researchers who have focussed on vibrotactile detection thresholds (notably the pioneering work of George Gescheider and Ronald Verrillo, among others) and more recent authors who have focussed on suprathreshold touch (including Kenneth Johnson and Sliman Bensmaia). The original threshold work has primarily informed diagnostic tools, but very few substantial links have been made between the 'tactile channels' at threshold and the suprathreshold perception of texture, for example.

Most authors agree that perception arises from the integration of these separate tactile channels. In everyday touch, tactile information is of an amplitude and range that all four channels are stimulated well above threshold, providing detailed and useful representations of objects and textures (Hollins & Bensmaïa, 2007).

Clearly, this body of psychophysical and physiological research concerning thresholds of perception for tactile stimuli needs to be complemented by research looking at suprathreshold information processing. From this point of view, we can ask two fundamental questions about how suprathreshold information processing diverges from information-sparse threshold-based model of the tactile channels:

2.4.1 What information is contained in each tactile channel?

Threshold approaches allow us to talk about the sensitivities of the individual channels, but they don't access the normal function of the channels in extracting information from the external world. There is evidence of dissociation between discrimination at threshold and suprathreshold (Kuroki, Watanabe, & Nishida, 2012). This provides a basis for the series of frequency discrimination studies proposed in Chapter 5.

It is clear that channels are differently selective for different parameters within a tactile stimulus. This selectivity enables them to function as feature encoders, which respond to particular properties of a tactile stimulus (e.g. particular frequencies of vibration) and signal that information to the brain. The role of the individual tactile channels in this process is less clear. One approach has been to look at the neurophysiological response properties of the associated mechanoreceptors and nerve fibres, and conjecture what features they are well suited to encode (e.g. Johnson, 2001; Johnson, Yoshioka, & Vega–Bermudez, 2000). Looking at how the responses might be combined and integrated suggests that this perspective is simplistic and ignores the possibility of 'team effort' (Saal & Bensmaia, 2014b) between channels with overlapping selectivity.

2.4.2 How is this information combined and integrated as perception?

Because the threshold approach looks only at the channel with the lowest threshold it is unable to inform us about the second key point of the information processing structure: that it is the later integration of these independent signals that drives perception, generating a rich and informative percept of tactile stimuli. Without integration, perception is in a sense one-dimensional, coding only for the presence of a particular feature, rather than giving rise to complex percepts.

There are essentially two perspectives on the nature of this integration. The first view identifies 'functions' which individual channels perform (Johnson *et al.*, 2000). These aspects of stimuli are then combined to give a global perception of the world. From this viewpoint, the RA channel responds strongly to motion across the skin and can therefore be considered to 'do' or 'code' motion. If, equally, the PC channel codes for vibration, then observers are able to get a full impression of some moving vibrating surface by adding these signals together as distinct aspects of the stimulus.

An alternative perspective of integration of information across the channels considers the relative selectivity of different channels to particular stimulus properties as part of a 'team effort' (Saal & Bensmaia, 2014b). They act as feature encoders in a continuous way, each responding to a greater extent to stimuli rich in their preferred feature than to stimuli with less capacity to excite the channel. This is far more consistent with the viewpoint that has come from the psychophysical model of tactile perception.

2.4.2.1 Perception of surface texture

The PC channel has been strongly implicated in texture perception. The PC channel can be characterised by the extreme sensitivity and deep location of Pacinian corpuscles, heavy filtering of low frequency stimuli, and characteristic phase locked response (Johnson *et al.*, 2000). These properties mean that despite their sparse distribution, a large number of PC afferents will respond strongly to high frequency vibrations and accurately encode its frequency (Freeman & Johnson, 1982; Johnson *et al.*, 2000). This property has implicated the PC channel in key roles requiring frequency discrimination: notably fine texture perception, as well as the perception of transmitted vibration, such as during tool use.

Humans are exquisitely sensitive to microgeometry. The smallest detectible features are in the order of tens of nanometres, while the smallest spatial gaps are in the order of hundreds of nanometres (Johansson & Flanagan, 2009). Tangible features span 4 orders of magnitude. Coarse features in the order of millimetres contribute to texture and to macro-shape perception.

A vibrating surface is perceived as rougher than a surface which is not vibrating and vibrotactile adaptation reduces the perceived roughness of fine surfaces (Hollins, 2001), providing direct evidence for the role of vibration in perception of texture.

Bensmaia and Hollins (2003) characterised the relationship between the perceived texture of the surface and the vibrations elicited in the skin. They found that peak frequency of vibration was inversely proportional to the spatial period of the texture. This is because the rate at which elements pass a given point on the skin is inversely proportional to the spacing between elements. Looking at the psychophysical correlates of these stimuli they found that perceived roughness increased with spatial period, and was therefore a negative function of peak frequency.

Importantly, other channels also make important contributions to texture perception. Coarse features are encoded in the spatial pattern of SA1 responses rather that the vibrations elicited and coded by the PC channel. This is the basis for the duplex theory of texture perception in the tactile system (Hollins & Risner, 2000). Fine features are filtered by the mechanical properties of the skin, but are captured during exploration by the vibrations they elicit during lateral motion across the surface. Because tactile channels respond selectively to different stimuli this information is still captured by the system, and the integration of these signals results in a rich unified percept. Sensory signals about tactile stimuli may even be integrated across modalities – e.g. touch and audition (Kayser, Petkov, Augath, & Logothetis, 2005).

2.4.2.2 Perception of motion across the skin

Meissner's afferents innervate the skin very densely, adapt quickly to static indentation, and are very sensitive to dynamic stimuli (Johnson *et al.*, 2000). They respond equally across their 3-5mm receptive fields, making them less well suited to resolve spatial details. Instead, RA afferents are strongly implicated in detecting and discriminating motion across the skin (Johnson, 2001; Johnson *et al.*, 2000).

Again, this explanation may ignore the contribution of tactile channels that are less obviously sensitive to the parameter. Theoretically, motion direction is available to SA1 neurons as a function of spatial pattern over time, is likely to generate vibrations in the skin, and cause skin stretch. We can draw a general principle that other channels may still extract useful information, even if they are less precisely tuned to that parameter.

2.4.2.3 Grip control

Insufficient grasp force or friction causes objects to slip across the skin. These slips generate fast corrective increases in gasp force. The normal viewpoint is that these grip responses are mediated by the detection of motion across the skin by the RA channel (Westling & Johansson, 1987).

However, changes in grip force are also generated in the absence of slip (Westling & Johansson, 1987). Other stimulus properties also have clear impacts on fine grip control: object curvature (Jenmalm, Birznieks, Goodwin, & Johansson, 2003), force direction (Birznieks, Jenmalm, Goodwin, & Johansson, 2001), and tangential torque (Birznieks *et al.*, 2010), which are all thought to be mediated primarily by both SA1 and RA afferents.

The forces associated with grip control are also likely to activate the relatively little studied SA2 afferent. SA2 end organs innervate the skin less densely than other receptors, and are 2-4 times more sensitive to skin stretch than SA1 afferents (Johnson *et al.*, 2000). A sensitivity to skin stretch suggests a role in detecting slips between surfaces and the skin, as well as possibly providing information about the shape of the hand – which could be interpreted as a signal dictating grip strength on objects (Collins, Refshauge, & Gandevia, 2000; Collins & Prochazka, 1996; Edin & Johansson, 1995; Olausson, Wessberg, & Kakuda, 2000).

Equally, PC afferents are activated by making and breaking contact with objects (Westling & Johansson, 1987), so by the same logic are also suitable for a contributing to slip detection (Srinivasan, Whitehouse, & LaMotte, 1990).

2.4.2.4 Perception of object shape

Merkel receptors densely innervate the skin at around 100 per cm^2 (Johnson *et al.*, 2000). They have small receptive fields and therefore a high spatial resolution (0.5mm). Because they respond with sustained, slow adapting responses linearly related to indentation depth (Blake, Hsiao, & Johnson, 1997; Johnson *et al.*, 2000; Vega-Bermudez & Johnson, 1999), they have been argued to provide a hyper-acute spatial image of tactile stimuli, coding for spatial differences in indentation, local shape, and coarse texture perception (Johnson & Phillips, 1981).

The ability to sense the shape of an object grasped in the hand is dependent on both cutaneous and proprioceptive signals. The cutaneous component of tactile perception of shape has been investigated with dot patterns (Johnson & Lamb, 1981), embossed bars (Johnson & Phillips, 1981), spheres (Goodwin, John, & Marceglia, 1991; Goodwin, Macefield, & Bisley, 1997), and letters (Phillips, Johnson, & Hsiao, 1988). Skin deformation across the hand is combined with detailed information on the position of the fingers to provide information on macro features of a stimulus, either statically or as a function of active exploration. In active touch, proprioceptive information has to be combined with motor plans (Salimi, Brochier, & Smith, 1999) and with cutaneous responses. This high-level integration of information remains largely unspecified.

SA1 alone cannot, however, account for evidence that participants are able to discriminate shape on the basis of vibrating pins in an OPTACON ('OPtical to TActile CONverter', an array of vibrating pins used to convert printed material into a tactile signal for visually impaired people; Craig, 1980), provided the letter covers a relatively large surface. OPTACON pins are argued to elicit responses in RA and PC afferents but not SA1 – their spatial component is of vibrating or not vibrating skin, rather than indented or not indented skin. The letters must be discriminable on the basis of the spatial pattern of activation elicited in RA neurons, but less precisely. Again, less sensitive tactile channels provide information which contributes to tactile perception from outside of their apparent 'function'.

2.4.2.5 Perception of vibrotactile intensity

Gescheider and colleagues (2010) argue that constructing a test of the idea that tactile channels are integrated as perception requires a full understanding the characteristics of the individual channels, and the rules by which they interact. One approach that begins to meet these criteria is to relate activation of two or more specific tactile channels to an intuitive percept that comes out of their joint activation: stimulus intensity. An important point is that the representation generated by touching a stimulus will have properties of its own, related but not identical to the physical properties of the stimulus (in much the same way that the perceptual quality of colour is related but not identical to the wavelengths of light reflected by an object). Stimulus intensity is one such quality. In many ways, we can think of these perceptual qualities as a product of the information extracted by the channels.

Initial support for the idea that channel interactions in response to suprathreshold stimuli mediate representation of vibrotactile intensity came from the finding that the intensity of two vibrations summed together is calculated differently within channels than across channels. Verrillo and Gescheider (1975) presented two brief (20 ms, 25 Hz and/or 300 Hz) stimuli in quick succession and asked participants to adjust the intensity of a matching stimulus. They found that the perceived intensity of the pair was equal to the sum of the perceived intensities of each stimulus presented alone, but only if the two vibrations were in different channels, and the time interval between the two was short. When this was the case, the participants set the amplitude of the matching stimulus 6 dB higher when matching to the pair than when matching to the second vibration alone. The 6 dB difference corresponded to a doubling of subjective intensity when assessed through magnitude estimation (Verrillo, Fraioli, & Smith, 1969). A pair of identical vibrations, on the other hand, produced a difference of only 3 dB in the matching stimulus, which better corresponds to a doubling of the physical energy.

It has often been noted that this pattern of results closely mirrors the concept of auditory critical bands. Critical Band Theory (Zwicker & Scharf, 1965) describes perception of loudness with a system of overlapping bandpass filters; the overall loudness of a sound is equivalent to the sum of loudness within each activated band. If two frequencies are similar, they may fall within the same band and their loudness is computed in the domain of stimulus energy. If two frequencies fall in different bands, their loudness is determined by the linear summation in the perceived loudness domain.

Marks (1979) built on this idea by presenting two vibrotactile frequencies simultaneously. He generated a set of complex waveforms containing 20 Hz and 250 Hz frequency components, which combined these frequency components at seven different amplitudes - 49 waveforms in total - and asked participants to estimate their subjective magnitude. The key finding was that estimates of the intensity of the complex stimulus containing both high frequency and low frequency components was equal to the sum of the intensities of the components presented separately. When both vibrations recruited the same channel the ratings of intensity were better modelled as responding to 'total stimulus energy', as opposed to subjective intensity or to amplitude of displacement.

Cohen and Vierk (1993) provided behavioural evidence that subjective ratings of intensity cannot be explained by the activation of a single population of afferents. They presented participants with trapezoidal indentations and found that ratings of intensity differed for different portions of the stimulus: the sustained period generated a sensation of intensity, but onset and offset were perceived as more intense than the sustained period of indentation. It's argued that SA1 afferents were the only channel activated by the sustained period, suggesting that this channel contributes to perception of the intensity of a vibrotactile stimulus, but activation of RA or PC fibres by the onset and offset of the stimulus resulted in higher ratings points to a code where a number of channels combine to generate perception of intensity.

Asking participants to estimate the intensity or pitch of different suprathreshold vibrotactile stimuli has a clear advantage: it provides a measure of a perceptual quantity that arises from the interaction of tactile channels. Unfortunately, it fails to provide a full account of the structure of the information processing structure for two reasons. Firstly, it's inherently dependent on the assumption that the instruction to match the 'intensity' or 'loudness' or 'pitch' is interpreted as the same perceptual quantity across participants, and reported free of bias. Given the substantial inter-subject variability endemic to the field, we have good reason to doubt both of these assumptions.

Secondly, one of the key features of information processing channels in whatever modality - including audition and vision - is that they enhance the system's ability to discriminate (Gescheider *et al.*, 2010). By reducing the dimensionality of the response to a single magnitude estimation, we lose access to many of the features extracted by the information processing channels in the tactile system, and to the perceptual qualities they generate, simply as a product of the experimental design.

2.4.3 Suprathreshold diagnosis of impaired touch perception

One way to begin to address the limitations of vibrotactile detection thresholds as a research and diagnostic tool is to investigate the use of a different paradigm. The predictions that thresholds make about information processing in the tactile system can be tested by directly measuring discrimination suprathreshold.

The weight of previous research in neurophysiology supports the idea that the RA and PC channel are not just encoding the presence of absence of a vibrating stimulus, but also the temporal properties of the vibration. A psychophysical method that investigates this coding may be able to mitigate some of the endemic limitations of detection thresholds:

> **The 'high threshold' assumption and vulnerability to response bias:** the design and analysis of a novel psychophysical method can aim to control for response bias.
>
> **The role of active perception in normal touch:** although the frequency discrimination designs do not incorporate the motor component of touch, the stimuli more closely resemble those elicited by active exploration of a surface.
>
> **The ecological validity of vibrotactile detection thresholds:** touch with the hand is more likely to be used to discriminate between vibrations elicited by textures, rather than to detect them. One of the key characteristics of these vibrations is their frequency.
>
> **Mechanoreceptors display complex selectivity:** suprathreshold discrimination designs can take a different view on the sensitivity of the channels. Instead of trying to *exclusively* activate a channel with very complex selectivity, we choose stimuli to *primarily* activate one channel over others.
>
> **Neural thresholds versus psychophysical thresholds:** a neural threshold for detection must identify a rate or population code that is sufficiently different from noise, which may not be fully characterised. A frequency discrimination allows us to identify when two signals are sufficiently different from one another, allowing us to characterise both components.
>
> **The implications of neural coding strategies:** RA and PC channels appear to be coding frequency. This makes it more difficult to understand the significance of an absolute threshold, but not a threshold difference in frequency.
>
> **Choice of vibrotactile stimuli:** The conditions suggested for determining vibrotactile thresholds in ISO 13091-1:2001 may identify the response of the PC channel, it will fail to specifically measure the response of the SA1, SA2 channels, and, under a number of plausible circumstances, the RA channel. Suprathreshold diagnostics may be able to overcome this limitation by providing a measure not just on whether a tactile stimulus evokes *any sensation* but on the information content of the activated tactile system, increasing the specificity of the diagnostic tool.

Specifically, the capacity of the RA and PC channels to mediate differences in vibration magnitude and frequency provides a potential measure of the sensitivity of these two channels. The RA and PC channels have been chosen for closer examination in this project because the neurophysiological data suggests an accurate encoding of vibratory stimuli with varying temporal properties, whereas the slow-adapting channels have responses that vary less systematically with vibration frequency and amplitude.

It is argued in this thesis that suprathreshold discrimination has the potential to complement existing diagnostic methods. It can be considered advantageous to explore this potential for 3 key reasons: 1) the limited sensitivity, specificity and reliability of vibrotactile detection thresholds as a diagnostic tool means that a new method could measure changes not measured through this standard, and more importantly that the combination of the two measures is going to be more informative than a single, flawed, methodology; 2) the greater ecological validity of suprathreshold discrimination against the normal action of the tactile system means that it is more likely to be a reliable measure of touch sensitivity In a behaviourally relevant way; and 3) that suprathreshold discrimination has a closer resemblance and connection to the observed neurophysiological sensitivity of the underlying physiology of touch. Suprathreshold discrimination paradigms, of course, have their own limitations. Not least, it has not benefitted from the systematic research of vibrotactile detection thresholds.

2.5 Vibrotactile magnitude perception in the tactile channels

PC and RA responses to vibration are primarily temporally coded – that is, they respond in a way proportional to the frequency of a vibrating stimulus. This means that an individual PC or RA afferent is unable to code changes in amplitude over a large part of its dynamic range. Representative PC and RA responses are illustrated in Figure 17.

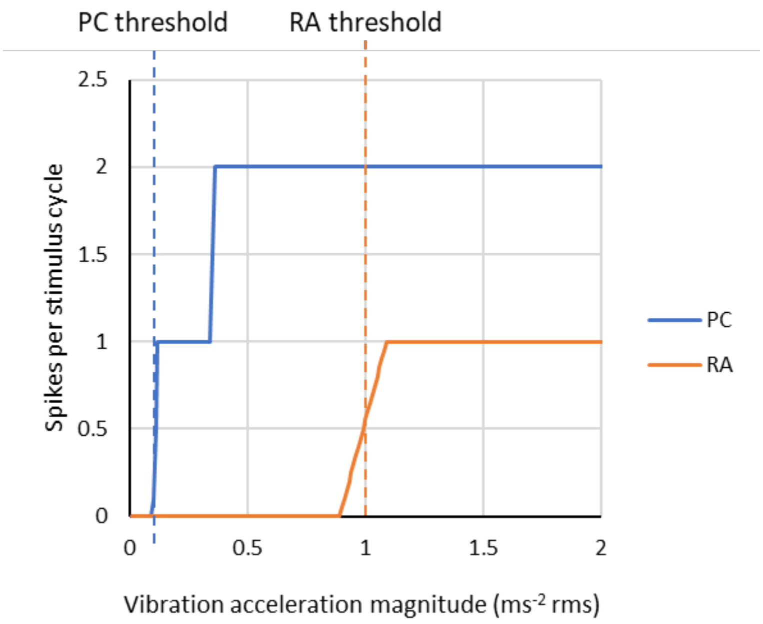

Figure 17. Representative PC and RA responses to a 100 Hz vibration stimulus. Because responses are phase locked to the temporal properties of the stimulus, there is very little change in response with vibration amplitude, only the surpassing of PC thresholds, the elevation of PC responses to 2 spikes/cycle, and the surpassing of RA threshold. This suggests that the perception of the intensity of a 100 Hz stimulus would only ever have 4 values – below threshold, PC 1-spike/cycle, PC 2 spikes/cycle, and PC+RA. Summary of data from Johansson et al (1982), Bolanowski et al (1988) and Gescheider et al (2010).

Because vibration intensity is crudely coded within a single PC or RA mechanoreceptor, and shows little to no change in response unless a new threshold level is reached, vibration amplitude must be conveyed by a population code. A population code is one where stimulus information is conveyed by a group of neurons responding differently, rather than by the responses of a single neuron. A huge number of population codes have been suggested to account for perception of vibration intensity, but they can be summarised in two categories:

Within channel: where intensity is coded within the population of a single kind of mechanoreceptive afferent (always either RA responses or PC responses; e.g. Hollins, 1974). An example of this would be that intensity is coded as the summed responses of all activated RA afferents (e.g. Hollins, 1974; Guclu, 2007, Gracyzk *et al.* 2016)

Across channel: where intensity is coded across populations of more than one kind of mechanoreceptive afferent. An example of this kind of population code would be that intensity is a weighted sum of RA, PC and SA1 afferent activity (Hollins and Roy, 1996).

The two forms of population code make different suggestions about whether there should be differences in the coding of magnitude as a function of frequency and magnitude, and therefore whether we would expect weber fractions to change as a function of these two parameters.

For example, a within channel code should be frequency dependent because channel sensitivity changes with frequency. E.g. RA sensitivity is relatively flat across low-medium frequency (in terms of displacement thresholds), and then becomes less sensitive gradually, which suggests that an RA mediated response may have a larger weber fraction at higher frequencies. A purely PC code might show the opposite pattern.

A within channel code should provide consistent weber fractions for intensity if every increase in amplitude creates a corresponding increase in the number of mechanoreceptors responding, and the resulting summed rate. There may be parts of the amplitude range where this does not occur. We might also expect a difference with contactor size and location, as more fibres of the chosen type are activated.

On the other hand, and across channel code (e.g. weighted sum of all activated nerve fibres (Hollins and Roy, 1996; Bensmaia *et al.*, 2007) *can* provide consistent weber fractions for amplitude because one or the other channel is more sensitive at both low and high frequencies – so the code can operate accurately across a broader frequency range. An across channel code for amplitude differences should, however, vary with vibration amplitude because low amplitudes are likely to excite only one mechanoreceptor type: RA at low frequencies and PC at high frequencies. Note that the population code need not be exclusively across channel – amplitude could be coded both within and across channels. However, we would expect across channel to result in lower weber fractions because of the increased degrees of freedom in resolving amplitude differences.

We can then look at the balance of psychophysical data to see whether weber fractions for amplitude change with frequency and amplitude, whether this supports the idea of amplitude as coded within or across channel, and what we would expect the response of the system to be with novel vibration stimuli. We want to determine what pattern of weber fractions the population code predicts. To do this, the small number of studies that have measured weber fractions for vibration magnitude at different frequencies and amplitudes must first be reviewed. These studies are briefly summarised in Table 1.

Table 1. Summary of existing studies that experimentally measured weber fractions for vibrotactile magnitude presented in reverse chronological order.

Study	Summary of findings
Forta *et al.* (2007)	Measured difference thresholds for vibration magnitude at 2 frequencies (16 and 125 Hz) and 5 magnitudes (6 – 36 dB SL). Vibration was delivered through a 30-mm diameter rigid metal handle, gripped with the whole hand. They found that median weber fractions were in the range for 16 Hz and in the range 14.6% to 23.0% for 125 Hz. 16-Hz weber fractions were between 16.0% and 20.5%, and were not significantly affected by vibration magnitude. 125-Hz weber fractions were dependent on vibration magnitude, with low amplitude discriminations having a lower weber fraction.
Gescheider *et al.* (1996)	Studied perception of amplitude differences at thenar eminence with a 250 Hz stimulus. Amplitude weber fractions decreased slightly with increasing vibration magnitude (at 0.015 dB per dB increase in sensation level) over vibration magnitudes from 14 dB SL to 40 dB SL. The reported values of the Weber fractions are somewhat variable ranging from 0.05, a value corresponding to a 0.4-dB change in amplitude. Two aspects of this study limit its interpretability: 1) The relatively high amplitudes studied may be obscuring higher weber fractions at near threshold amplitudes. 2) The high frequency used limits the potential influence of other tactile channels if a cross-channel code improves discrimination.
Gescheider *et al.* (1994b)	Broadband masking had no effect on weber fractions for vibration amplitude
Gescheider *et al.* (1994a)	Longer durations had smaller difference limens for intensity, up to a limit of 1000 ms, after which longer durations had no effect
Gescheider *et al.* (1992)	At higher 'pedestal levels' (equivalent to baseline amplitude), smaller amplitude increments were needed to discriminate a change in amplitude. Large weber fractions were found for near threshold amplitudes, then a flat weber fraction for the rest of the amplitude range.
Gescheider *et al.* (1990)	Used 25 and 250 Hz stimuli (sinusoids, narrow band-, or wide band noise). They found a 'near miss' to Weber's law for all stimuli – i.e. a slight decline with increasing stimulus amplitude. They found no effect of frequency condition.
Fucci *et al.* (1982)	Reported a small frequency effect for the magnitude discrimination on the tongue.
Craig (1972, 1974)	Found an effect of sensation level on weber fractions for 160-Hz vibration intensity delivered to the finger during a masking design. Controlling for the effects of masking, Weber fractions were only constant for high amplitude stimuli. The weber fraction for all stimuli was found to be around .25 once stimuli were raised to a 20dB sensation level regardless of the amplitude of the masking stimuli.
Sherrick (1950)	Reportedly found a 30% weber fraction for vibration intensity. It is not known how this changed with frequency or what range of amplitudes were tested.

Broadly, these studies show a ‘slight’ decline in weber fraction with amplitude, amounting to a so-called ‘near miss’ to the weber fraction. However, many of these studies are limited in what amplitudes they used. Very few studies have addressed the effect of frequency on a discrimination design (a large number have on a magnitude estimation design, and built the corresponding differences into the cross-channel model, but this does not allow us to analyse weber fractions). Those that have found no effect of frequency.

The balance of evidence from the psychophysical and neurophysiological data does also seem to support a cross-channel model of intensity coding.

2.6 Vibrotactile frequency perception in the tactile channels

2.6.1 Systematic literature review

In order to advance our understanding of vibrotactile frequency discrimination in the tactile channels in the context of augmenting our current diagnostic tools, we must first understand what the existing literature suggests. The literature on this subject is somewhat sparse and highly variable, with many authors using vibrotactile stimuli of different frequencies, contactor parameters, waveform and duration. A systematic review was therefore conducted to exhaustively identify relevant papers. Data were extracted from these papers for direct comparison between studies, in order to identify any patterns or trends in the data. Finally, the papers were critically reviewed to determine what we can learn from this existing literature and what research questions (and pitfalls) should be considered for the experimental component of this thesis.

A set of relevant studies was identified by searching PubMed for *(((vibrotactile OR vibro-tactile)) AND (frequency OR pitch)) AND (discrimination OR difference limen).* Of the search results (118 studies), those that experimentally identified difference limens for vibrotactile frequency in humans at more than one test frequency are summarised here (10 studies). The inclusion criteria were chosen as follows:

> **Experimental.** Only experimental estimations of vibrotactile frequency difference limens were analysed.

Identify difference limens for vibrotactile frequency. Studies that used a vibrotactile difference test but reported a % correct score for a set of stimuli (a common paradigm for neuroimaging) were not considered.

More than one test frequency. At least 2 test frequencies were required so that their relative values could be considered. If there is systematic variance in the absolute values of the weber fractions between studies, it is hoped that the relative difference limens as a function of frequency, measured in otherwise similar conditions, will provide a sense of the shape of the tuning curve, or the pattern of results as a function of frequency.

Where available, the number of subjects, vibration site, contactor size, waveform type, duration and amplitude (or sensation level) of the test stimuli are reported. Some experimenters adjust the amplitude of the test stimuli to control for changes in perceived intensity – whether this is understood to be the case is included on Table 2.

Table 2. Summary of systematically selected research in vibrotactile frequency discrimination, listed in chronological order.

Authors	Year	Weber Fraction (% approximate)	Subjects	Location	Pitch/ intensity	Amplitude	Contactor		Waveform	Stimulus Duration	Feedback	Psychophysical method
							Area (cm2)	Diameter (cm)				
Mowbray & Gebhard	1957	2 to 7.5	5	Two fingertips	no	17-26 dB SL	>5.00	2.52	Pulses	unknown	No	method of adjustment
Goff	1967	20 to 50	~	Fingertip	yes	20 - 35dB SL	unkn own	unknown	Sinusoids	unknown	No	method of limits
Franzen & Nordmark	1975	~3	6	Fingertip	yes	30dB SL	0.03	0.20	Pulses	0.015-0.5s pulses	No	method of adjustment
Rothenberg *et al.*	1977	10 to 30	5	Forearm	yes	14-16dB above threshold	0.28	0.60	Sinusoids / Pulses	1s	No	method of limits target “higher/lower”
Horch	1991	~9	4	Fingertip	no	Varied	0.10	0.35	Sinusoids and di-harmonic tones	0.5s	No	method of adjustment “higher” & “lower”
Sinclair & Burton	1996	10 to 30	8	Fingertip	yes	30-35dB SL	3.00	1.95	Sinusoids	1s	Yes	method of limits target “higher/lower”
Tommerdahl *et al.*	2005	9 to 50	3	Fingertip	yes	20dB SL	0.50	0.80	Sinusoids	1s	Yes	method of limits interval “higher”
Mahns *et al.*	2006	14 to 38	5	Fingertip/F orearm	yes	4x SL	0.13	0.40	Sinusoids	1s	No	method of limits target “higher/same”
Deco *et al.*	2007	30 to 40	8	Fingertip	yes	15% gain in the soundcard	3.80	2.20	Sinusoids	0.5s	No	method of limits interval “higher”
Kuroki *et al.*	2013	17 to 120	6	Fingertip	yes	6db/16dB suprathreshold	1.13	1.20	Sinusoids	0.2s	Yes	method of limits target “higher/lower”

2.6.2 Limitations of existing vibrotactile frequency discrimination research

The following limitations were identified from a close reading of the studies identified through this search:

Paucity: this promising methodology is hampered by the small number of studies systematically measuring suprathreshold difference thresholds for frequency of vibrations. As a crude comparison, the search criteria for this systematic literature review of vibrotactile frequency discrimination generated 118 results for 10 pertinent studies, while a search of PubMed for *((vibrotactile OR vibro-tactile)) AND (sensitivity OR detection threshold OR threshold)* yields 458 results, with a higher proportion containing relevant psychophysical data.

Contactor location: the 10 studies identified here are divided between stimulating the glabrous skin of the fingertip and hairy skin of the forearm. It is not clear whether the same understanding of information processing in the tactile system can be applied to both locations, given their differences in mechanoreceptor type and innervation density, skin structure, and stereotyped behaviours.

Contactor size: no two studies reviewed here have used the same size of contactor, and it is mostly unclear whether the experimental setups included a rigid surround to limit the area of skin being stimulated. If spatial summation in the PC channel supports suprathreshold discrimination, this should be evident from changes in contactor area with the same experimental paradigm. It is also important to note that changing the gap between a probe and a solid surround, when present, also has a significant impact on detection thresholds by effectively increasing the area of skin excitation where this gap is larger (see Gescheider *et al.* 2010). These diameter of the gap is, again, frequently unreported.

Training: some studies reference extensive training periods for participants, or include experimenters as subjects before subjects provide stable difference limens for vibrotactile frequency. It is unclear how much training this might involve. It is also unclear how performance changes with training, or whether this is a limitation of studies which do not involve training.

Inter-subject variability: a probable reason for the extensive training is the high inter-subject variability observed in many of these studies. This may obscure changes in difference limen not visible in the comparison of means.

Small sample sizes: psychophysics typically involves small numbers of participants because of the time spent running experiments. These small numbers, however, limit our ability to interpret potentially informative inter-subject variability through correlation or multi-variate methods.

Response Bias: the precise task design varies substantially across studies, some of which maybe be vulnerable to response bias. Notably, some studies report designs that ask participants to identify whether a second stimulus was 'higher' frequency or 'same' frequency, and mistakenly identify this task as '2AFC'. SDT analysis could identify response bias in these designs.

Directional decisions: this 'higher' frequency designation requires participants to make a highly unintuitive decision. Unlike audio pitch, vibration frequency is not an intuitive lay concept, and tasks need to be designed towards this.

Intensity and Pitch, Amplitude and Frequency: all but two of the selected studies equalise stimuli of different frequencies to the same perceived 'intensity' in order that the decision be made on the basis of perceived 'pitch' only. These perceptual dimensions are not necessarily equivalent to the physical dimensions of amplitude and frequency of the vibration, and are known to interact with one another (Morley & Rowe, 1990). To understand information processing in the tactile system, it is necessary to study perceptual responses to physical variations in the stimuli. For example, if a higher frequency stimulus can be discriminated as 'more intense', although the physical amplitude of the stimulus is equal, then that change in frequency has been encoded by the tactile system.

Choice of amplitude: even with unequalised stimuli, the choice of amplitude at which stimuli are presented will have a strong impact on the recruitment of different mechanoreceptors. Most studies chose a sensation level (amplitude above threshold) in the 16dB-35dB range. It is unclear how this level affects performance, although Kuroki and colleagues (2016) show evidence that frequency difference limens may be dramatically larger at low amplitudes. Given the variability in identifying vibrotactile thresholds, there may also be substantial differences between the effective amplitude of stimuli delivered to two subjects in the same study.

Observed difference limens for the 10 pertinent studies are shown in Figure 18. Where studies had more than one condition that matched the inclusion criteria of the literature search, these tuning curves were also plotted (Figure 18).

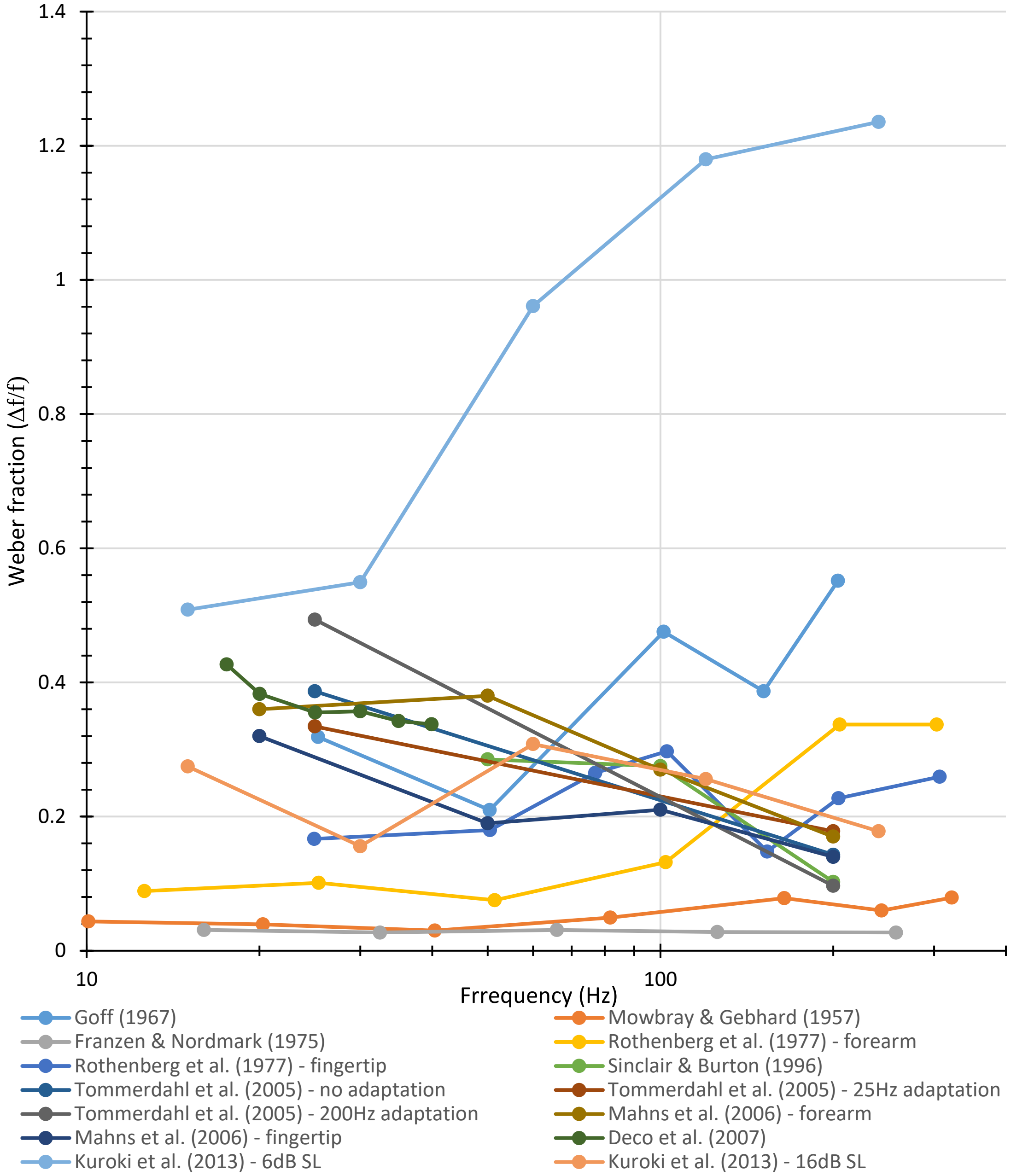

Figure 18. Observed difference limens for frequency for 9 pertinent studies expressed as weber fractions. Where multiple experimental conditions with more than one test frequency are reported, these are also plotted. Data from: Deco, Scarano, & Soto-Faraco, 2007; Franzén & Nordmark, 1975; Goff, 1967; Kuroki, Watanabe, & Nishida, 2013; Mahns, Perkins, Sahai, Robinson, & Rowe, 2006; Mowbray & Gebhard, 1957; Rothenberg, Verrillo, Zahorian, Brachman, & Bolanowski, 1977; Sinclair & Burton, 1996; Tommerdahl *et al.*, 2005.

One of the studies (Horch, 1991), although informative, was not plotted because difference limens were not calculated independently of amplitude changes. As illustrated here, the absolute values of weber fractions across studies vary between 0.03 and 0.5 at low frequencies, and 0.03 and 1.2 at high frequencies (Franzén & Nordmark, 1975; Kuroki, Watanabe, & Nishida, 2013). The patterns of results within studies are also extremely variable. Some studies found consistent weber fractions across the whole frequency range (Franzén & Nordmark, 1975; Horch, 1991; Mowbray & Gebhard, 1957), some found increasing weber fractions with frequency (Goff, 1967; Kuroki *et al.*, 2013; Rothenberg, Verrillo, Zahorian, Brachman, & Bolanowski, 1977), some found declining weber fractions with frequency (Deco, Scarano, & Soto-Faraco, 2007; Mahns, Perkins, Sahai, Robinson, & Rowe, 2006; Tommerdahl *et al.*, 2005), and others found inconsistent weber fractions as a function of frequency (Kuroki *et al.*, 2013; Rothenberg *et al.*, 1977). The scale of these differences, both within- and between-studies, is remarkable. Some studies seem to indicate, for example, a temporal resolution of <0.5 Hz at 16 Hz (Franzén & Nordmark, 1975), while others report that the frequency that can be reliable discriminated from 16 Hz is more than 15 times that value (Kuroki *et al.*, 2013).

Evidently, no clear conclusions can be drawn from extant data on vibrotactile frequency discrimination. This leads us to a set of research questions:

1. What is the effect of contactor size on the discrimination of vibration frequency differences?
2. What is the effect of vibration magnitude on the discrimination of frequency differences?
3. How do the patterns of weber fractions for frequency compare to those for acceleration magnitude differences?
4. Are weber fractions for the discrimination of frequency different when different tactile channels are mediating perception, and if so, do we observe a change in weber fraction as we change tactile channel?

Effect of contactor size on discrimination of vibration frequency: There is no clear pattern of results to indicate a systematic difference between weber fractions measured across these studies as a function of contactor size. The PC channel combines signals from Pacinian corpuscles from across the skin surface exposed to vibration to support detection at lower amplitudes (Capraro *et al.*, 1979). This spatial summation in the PC channel may also be able to support frequency discrimination suprathreshold. A psychophysical experiment testing this hypothesis experimentally is reported in Chapter 4.

Effect of vibration magnitude on discrimination of vibration frequency: Most studies chose a sensation level (amplitude above threshold) in the 16dB-35dB range. It is not yet known whether this particular range results in differences in the ability to discriminate vibration frequency,

The multi-channel model suggests that one of the main effects of increasing vibration magnitude on the response of the tactile system would bet the recruitment of additional tactile channels as we surpass their threshold. For example, at 20 Hz, where the RA channel is more sensitive, we might expect a sufficient increase in magnitude to recruit the PC channel as well.

It can be hypothesized that increasing the number of tactile channels supporting discrimination by recruiting a second channel will result in better discrimination of frequency differences. A psychophysical experiment testing this hypothesis experimentally is reported in Chapter 5.

Discrimination of magnitude within and across channel: Discrimination of vibrotactile magnitude likely relies on a related, but not identical population code across the RA and PC channels. We would expect weber fractions to be larger for vibrotactile magnitude than for frequency, and follow a different pattern as the second tactile channel is recruited. A psychophysical experiment testing this hypothesis experimentally is reported in Chapter 6.

Effect of tactile channel: To understand frequency discrimination within and across the PC and RA channels, we are interested, firstly, in whether differences in weber fraction can be observed as we move stimulus conditions from one channel to another, and secondly in whether weber fractions are consistent within a channel.

Two sources of evidence provide fragmentary clues of a consistent weber fraction within channels, and the prospect of different weber fractions between channels. Neurophysiological studies of the properties of RA and PC systems are likely to provide the best evidence of the properties within a particular mechanoreceptive channel, and psychophysics provides the best evidence of changes to weber fraction across channels.

Neurophysiological research has provided strong reasons to believe that both the PC and RA channels are both able to encode the temporal properties of vibration stimuli. This will vary with frequency and amplitude, however, in several ways. The mechanoreceptive systems may have preferred frequency ranges in which they are able to accurately encode the vibration frequency, which might be expressed as a minimum and maximum frequency to which they can become entrained. The mechanoreceptive systems may have preferred magnitude ranges in which they are able to accurately encode the vibration frequency. This could take the form of a minimum amplitude they can detect against noise, or as an amplitude dependent response, in that changes in amplitude will cause changes in the coding of frequency unrelated to a change in frequency.

PC afferents have been extremely well characterised. Bolanowski and Zwislocki (1984) characterised PC afferents as having a steep initial response to increasing vibration amplitude then quickly plateaued at a multiple of the stimulus frequency. An analysis of the timing of the firing showed that this was due to a temporal code. This means that the characteristic PC response is to fire in response to very small vibration, then fire in time with the vibration stimulus. You can imagine this as the corpuscle firing 0 times per stimulus cycle if the vibration is below its threshold, once the amplitude is sufficient the corpuscle will fire at once per stimulus cycle, increasing the amplitude sufficiently will result in 2 per cycle, and so on. This means that an individual receptor is well adapted to encode small changes in the frequency of a stimulus but poor at encoding its amplitude, which can only be coded in wider population. This data suggests that the PC channel should be able to encode frequency extremely accurate for as low as 40 Hz and as much as 200 Hz at a wide range of amplitudes – that discrepancies in amplitude between two stimuli has little effect on the ability to discriminate their frequencies has been supported psychophysically (Horch, 1991).

We must assume that if this information is accurately captured by the peripheral neurology then it will be used to discriminate between stimuli on a behavioural level, although there will be effects of noise at both a biological and decision level, this should not vary as a function of frequency.

It can therefore be hypothesized that increasing the number of tactile channels supporting discrimination by recruiting a second channel will result in better discrimination of frequency differences as we move experimental stimuli from one channel to multi-channel conditions. A psychophysical experiment testing this hypothesis experimentally is reported in Chapter 7.

2.7 Conclusions

The limitations of past research into vibrotactile frequency discrimination and discrimination of vibrotactile magnitude point to clear research questions which can be addressed through a series of psychophysical experiments. These experiments are described in detail in chapters 4 through 7. The results of these studies allow us to build a model of suprathreshold information processing in the RA and PC channels, which will directly inform recommendations for the design of diagnostic procedures for impaired touch perception.

Chapter 3 Methods and Materials

3.1 Summary

This chapter contains detailed information on apparatus, stimuli and procedures used for the experiments reported in the following chapters. Sufficient detail is contained in each chapter to replicate the reported experiment. Commonalities and differences between the experimental set ups and procedures are summarised here (see Table 3).

Table 3. Summary of experimental setups and procedures for experiments 1-4.

Experiment #	Psychophysical method	Stimulus duration	Contact location	Contactor size(s)	Response Device
1	Von Bekesy method of limits (detection thresholds); 2AFC Method of constant stimuli (frequency differences)	0.5s	Left index finger	1 mm; 10 mm	Keyboard
2	2AFC method of limits (frequency, detection)	1s	Left middle finger	1 mm; 10 mm	Mouse
3	2AFC method of limits (magnitude, detection)	1s	Left middle finger	1 mm; 10 mm	Mouse
4	Von Bekesy method of limits (detection thresholds) 2AFC method of limits (frequency)	1s	Left middle finger	1 mm	Mouse

3.2 Psychophysical Methods

The series of psychophysical experiments reported in this thesis (chapters 4 to 7) used two key psychophysical methods: the method of constant stimuli (experiment 1), and the method of limits (experiments 2-4). Both describe approaches for determining a threshold change in a stimulus parameter that can be reliably detected, and each has its own advantages and disadvantages.

3.2.1 Method of constant stimuli

The method of constant stimuli consists of the presentation of stimuli with levels of a certain property of the stimulus presented randomly from trial to trial (Gescheider, 1976a). This should prevent the participant from being able to predict the level of the next stimulus, reducing errors of habituation and expectation. Because participants respond to a pre-determined set of stimuli from across the full range of possible comparisons, this method allows for full sampling of the psychometric function. Unfortunately, this can result in a large number of trials, including many that with a difference that participants find very easy or very difficult.

3.2.2 Method of limits

The method of limits involves presentation of stimuli that starts at a highly detectable difference and reduces until the participant can no longer detect the difference (descending method), or undetectable differences that increase until the participant begins to be able to detect the difference (ascending method) (Gescheider, 1976a). Experimentally, these methods are alternated in order to 'zero-in' on a threshold where performance is at a pre-determined level.

This is formalised in the experiments reported in this thesis as a 'staircase procedure' (von Békésy, 1960; Levitt, 1970). When the participant is making correct discriminations, the stimulus parameter difference reduced until an error is made, at which point the staircase 'reverses' and the parameter difference is increased until the participant responds correctly, triggering another reversal. The values for a fixed number of reversals averaged to determine a threshold.

A 1-up-3-down procedure is used throughout the thesis, in which a single error causes the difference to become larger, and three sequential correct responses cause the difference to become smaller. Theoretically, this converges on the 79.6% level of performance at threshold.

3.3 Participants

For each study reported in this thesis (chapters 4 through 7) participants were recruited from the staff and students of the University of Southampton. Participants were asked to complete a screening questionnaire (Appendix A), which aimed to identify any conditions or medications that may affect their sense of touch.

3.3.1 Power analyses

Prior to each study, power analyses were conducted to determine the number of participants required to have sufficient power to investigate the hypotheses using the planned statistical tests. This was conducted using GLIMMPSE software (GLIMMPSE version 2.2.8, 2016-18; (Kreidler *et al.*, 2013) and estimates of the mean and standard deviation derived from pilot or historical data to achieve an estimated power of at least .80.

3.4 Apparatus

Vibration stimuli were delivered using *HVLab* Tactile Vibrometers (VTT). An electrodynamic vibrator is used to drive a vibrating probe housed within the vibrometer unit. The probe protrudes upwards through a rigid 'surround' annulus built into the case. A Ling accelerometer is attached to the probe, which allows for simultaneous measurement of the signal delivered by the vibrometer, which in turn allows concurrent calibration of the experimental stimuli. The VTT is placed on a table. The participant sits at the table and positions the height of the chair so that they can comfortably rest their forearm on the case. During the task, the participant presses down on the surround and an integral strain gauge provides feedback, allowing us to control the static force of the probe into the skin. The probe has a counterbalance providing a constant upward force, calibrated prior to each testing session to be 2N of force.

Vibration stimuli were delivered with two VTT shakers, one with a 1-mm diameter contactor and surround (labelled 'A') and one with a 10-mm diameter contactor and surround (labelled 'B'). Vibration was always applied to the distal phalanx of the left forefinger or middle finger (see experimental chapters) with a static force of 2N. The gap between the probe and contactor was 1-mm in all set ups described in the thesis. Figure 19 shows the experimental setup.

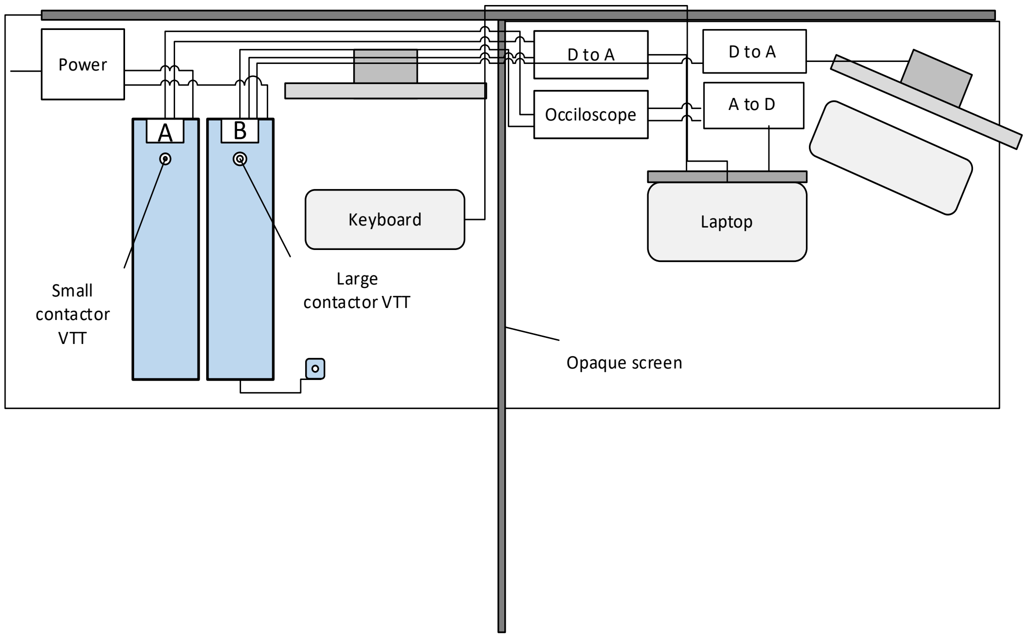

Figure 19. Schematic of experimental setup for experiment 1. Participants sat on the left behind an opaque screen. They rested their arm on VTT being used for that block, used cues from the PC monitor, and made responses on the keyboard. The experimenter sat on the right.

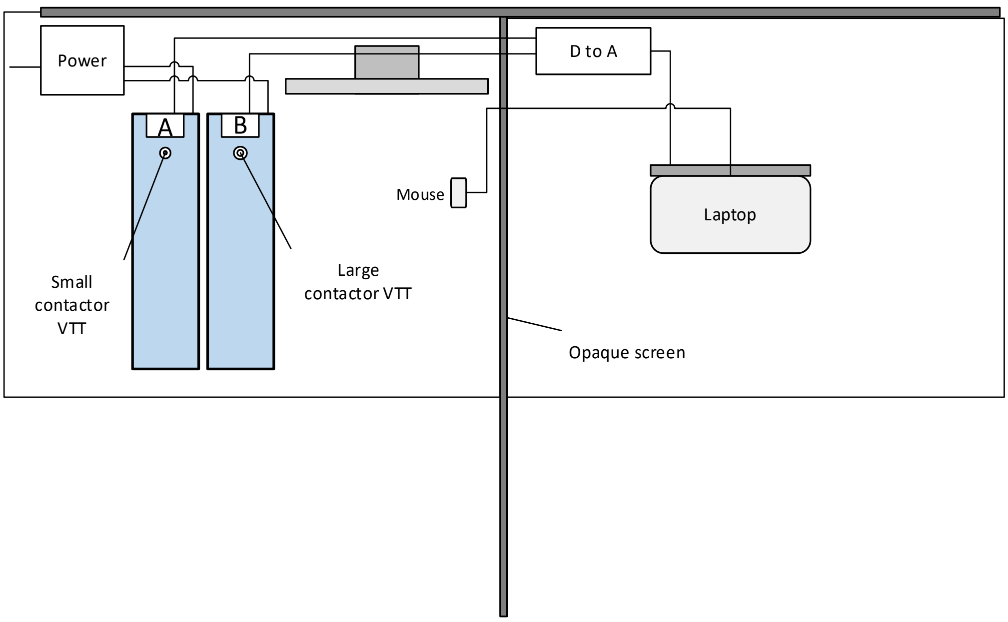

Figure 20 Schematic of experimental setup for experiment 2-4. Participants sat on the left behind an opaque screen. They rested their arm on VTT being used for that block, used cues from the PC monitor, and made responses on the mouse. The setup for Experiment 4 was identical, except that vibrometer B was removed.

Visual instructions and stimuli were delivered with a computer monitor. Pink noise was delivered with a noise machine and headphones at 75dB. In the threshold task responses were made with a button, and in the discrimination task responses were made on a pc keyboard. Testing took place in a temperature-controlled room (21°C).

The experimental procedure was controlled with 2 computers. The threshold task was controlled by *HVLab* diagnostic software. The discrimination task was controlled by MatLab using the *HVLab* signal processing toolbox to generate and present vibration stimuli, and Psychtoolbox to generate and present visual stimuli.

3.4.1 Calibration

Calibration of the VTTs occurred just prior to the start of each study, when the experimental set up had been positioned and finalized. The output of the VTTs was calibrated using a B&K calibration exciter (type 4294) that produces a vibration of known frequency (143 Hz) and acceleration magnitude ($10ms^{-2}$). Within each study, the target stimulus magnitude was calibrated against the observed magnitude of the stimulus delivered to the participants finger.

In Experiment 1, the stimuli were calibrated for the individual participant's finger prior to the frequency discrimination task. Participants were instructed that they did not need to make any responses. The participant kept a constant force of 2N on the surround while 3 iterations of each of the stimuli to be used in the experiment were presented at increasing accurate amplitudes. The order in which the contactors were calibrated was randomised.

In the following studies, this procedure was improved by calibrating in this fashion on each trial, and ensuring that trials were discarded and immediately repeated if the magnitude differed from the target stimulus by a more than 5% margin. This occurred on less than 1% of all trials, and was consistent across studies 2-4. A mechanism was built into the procedure to cancel a staircase if more than 10 errors of this kind occurred, but this did not happen except in piloting.

3.5 Stimuli

All tactile stimuli were sinusoidal vertical vibrations delivered to the distal phalanx of the index or middle finger of the left hand. Duration, frequency and acceleration magnitude conditions are listed within each experimental chapter, with explanations for those choices in the context of the experimental design.

3.5.1 Estimations of channel sensitivity

Experiments 2-4 employ an estimate of the sensitivity of the RA and PC channels in order to estimate target amplitudes likely to activate one or both channels. Channel sensitivity with different contact conditions was estimated from tuning curves derived by Bolanowski and colleagues (1988), Bolanowski and Verrillo, (1982), Gescheider and colleagues (1985), and Verrillo and Bolanowski (1986). The effects of contactor size and frequency were implemented into a model by applying a multiplier to absolute thresholds such that the pattern of responses is consistent with studies of vibrotactile thresholds over wide frequency range (Bolanowski *et al.*, 1988). The multiplier was generated using a least squares method to determine the value at which the curves bets fit the target data.

3.5.2 Safe sound and vibration exposures

3.5.2.1 Vibration exposure

The 8-hour equivalent magnitude A(8) of a vibration exposure of T seconds is given by:

$$A(8) = \left(\frac{1}{T_0}\int_{t=0}^{t=T} a_{hw}^2(t)dt\right)^{1/2} = a_{hw}\sqrt{\frac{T}{T_0}}$$

Where a_{hw}(t) is the frequency weighted acceleration, T is the daily exposure duration, and T_0 is the reference exposure duration of 8 hours (28800 seconds).

This value was calculated prior to each experiment, ensuring that vibrations were presented at a safe level. For example, a discrimination task consisting of sessions containing a maximum of 320 1-second vibrations (5 staircases x maximum 60 trials, + 20 practice trials), as in Experiment 4 (chapter), we simplify calculations by determining an 8-hour equivalent energy value representing the 'worst case scenario'. In this case we assume that every exposure is at the maximum possible amplitude in the experiment (5.0 ms^{-2} RMS), and at a frequency with the highest weighting factor (<16Hz, *a* weighting = 1.0).

To calculate $A(8)$ for multiple exposures:

$$A(8) = a_{hw}\sqrt{\frac{T}{T_0}}$$

$$A(8) = 5\sqrt{\frac{320}{28800}} = 0.53$$

Pursuant to the ISVR technical memorandum no. 808, this exposure is categorized as "USUAL" because the vibration exposure will not exceed:

- An 8hr energy equivalent magnitude of 2.8 ms^{-2} r.m.s in any one day.
- A frequency weighted acceleration of 50 ms^{-2} r.m.s over any duration.

3.5.2.2 Sound exposure

Participants will be presented 75 dB white noise during testing to obscure any auditory cues. Noise is generated by a calibrated HFRU noise device and presented through headphones. Duration of exposure will not exceed 1 hr. Headphones could be removed during breaks. This exposure is classified as USUAL because it does not exceed:

- The daily exposure level LEP,d of 76 dB(A)
- The sound pressure level of 120 dB(A) regardless of duration

3.5.3 Harmonic resonance

The response of the two VTT devices was measured across the frequency and magnitude range used in the experimental work of this thesis. The signal necessary to accurately generate 1-second sinusoids was determined at frequency increments of 1 Hz from 4 to 350 Hz, and at acceleration magnitude increments of 0.1 ms^{-2} RMS. The degree of harmonic distortion was calculated at each stimulus increment terms of Total Harmonic Distortion (THD), defined as the ratio of the sum of the powers of all harmonic components to the power of the fundamental frequency. All experimental stimuli were generated in a range where THD was less than 1%, and harmonic distortion was monitored by eye on an oscilloscope during all experimental sessions.

3.6 Statistical tests

Parametric statistics were used throughout the studies reported in this thesis. The data collected met assumptions to be normally distributed/symmetric and having homogeneity of variance. These assumptions were tested using Chi-square and Levene's test respectively. Means and standard deviations (SDs) or standard errors (SEs) are reported throughout, and error bars always show the standard error of the mean.

The primary analysis for each of the studies reported here consisted of repeated measures analyses of variance (ANOVAs). Mauchly’s test of sphericity was conducted in all cases, and, where this was significant, a Greenhouse-Geisser correction was applied. Effect sizes are reported for all effects and presented as partial eta squared values.

Secondary analysis with the aim of identifying differences in the mean between sessions consisted of repeated measures t-tests. Bonferroni corrections for repeated comparisons were applied in all cases. Effect sizes are reported for all effects and presented as Cohen's *d* values.

Any post-hoc analysis of correlations consisted of Pearson's R correlation coefficients.

IBM SPSS 25 (2018) was used to conduct all statistical tests reported in this thesis.

3.7 Procedures

Experiments 1 and 4 consisted of 3 1-hour sessions on different days, while experiments 2 and 3 consisted of a single 1-hour session. At the first session of an experiment, the participant completed a health questionnaire designed to identify factors that may influence their touch perception (Appendix A), including vibration exposure, drug use, and medical conditions. In each session the participants skin temperature was measured using a digital thermal meter pinched between their left thumb and forefinger to ensure that skin temperature was not below 25°c or above 31°c. The participant then completed two of the following tasks.

3.7.1 Von Bekesy vibrotactile detection procedure (Experiments 1 & 4)

This version of the threshold task closely matches current diagnostic methods. It consisted 31.5 Hz or 125 Hz sinusoidal vibration that steadily increased in amplitude (5 dB/second) until the participant responds by pressing and holding a button with their right thumb, at which point they gradually decrease at 3 dB/second until the participant released the button because they could no longer perceive the vibration, at which point the amplitude began to increase again. After 6 reversals, the mean of the peaks is taken as an estimate of threshold amplitude. The task was repeated on the left index finger at 2 frequencies on 2 contactors, with each run taking no more than 45 seconds. This is an example of the von Bekesy variant of the Method of Limits.

3.7.2 2AFC frequency discrimination procedure (Experiments 1, 2, & 4)

Figure 21 summarises the discrimination task trial structure. Each trial consisted of 3 sequential vibrations delivered to the skin of the finger. The first vibration was always a reference 'standard' vibration of 20 or 100 Hz. The second and third vibrations were another standard and a target vibration, with half of trials having the target in the second position and half in the third, presented in a random order. Following the 3rd vibration the participant responded with the left hand button if the second vibration was the *odd one out*, or the right hand button if the third vibration was the odd one out.

The discrimination task session consisted of blocks of 20 trials with breaks in between, during which participants were encouraged to rest their fingers. Where more than 1 contactor was used, blocks were presented through the two contactors in a random order. The contactor to be used for the block ('A' or 'B') was given by a visual instruction during the break and throughout the block.

This test has the advantage of being an 'unspecified difference' test, so participants do not have to be trained on what a frequency, pitch or intensity difference feels like. Difference limens in unspecified difference tests are generally higher than in specified difference tests (typical 2AFC or 3AFC tests), but this may be attributable to the different levels of training participants receive.

Visual cues were synchronised to the vibration presentation. These consisted of white squares that appeared on the grey screen from left to right labelled 'Ref', 'z', and 'x' (when using a keyboard as response device, e.g. experiment 1) or 'Ref', 'L' and 'R' when using the left and right mouse buttons to respond (later experiments). Participants responded by pressing a button to indicate the 'odd one out' of the last two stimulus intervals. In experiments 3 and 4, these two squares were coloured orange, to indicate that the stimulus presentation was complete, and participants were now able to respond- which was done to reduce the incidence of participants responding too early. Feedback was given by colouring the participant's chosen square for 1 second; green for a correct answer and red for an incorrect answer. The screen was blank for 1 second between trials. Instructions were presented to the participant before the discrimination task. They completed a practice block of randomly sampled trials (Experiment 1) or a random set of staircases (Experiments 2-4), on a randomly designated contactor and were given the opportunity to repeat the practice and ask questions about the procedure.

In experiment 1, this followed a method of constant stimuli psychophysical design, with a full set of discrimination stimuli presented in a randomised order. Stimuli were presented in blocks of 20 trials, with breaks of no less than 30 seconds between trials. This was done to avoid long-term adaptation of vibrotactile sensitivity. In the remaining experiments, this followed a method of limits adaptive track 'staircase' procedure based on Levitt (1971). The stimuli were presented in blocks of 20 trials, with breaks of at least 60 seconds between blocks, as this was found to better encourage participants to rest between blocks.

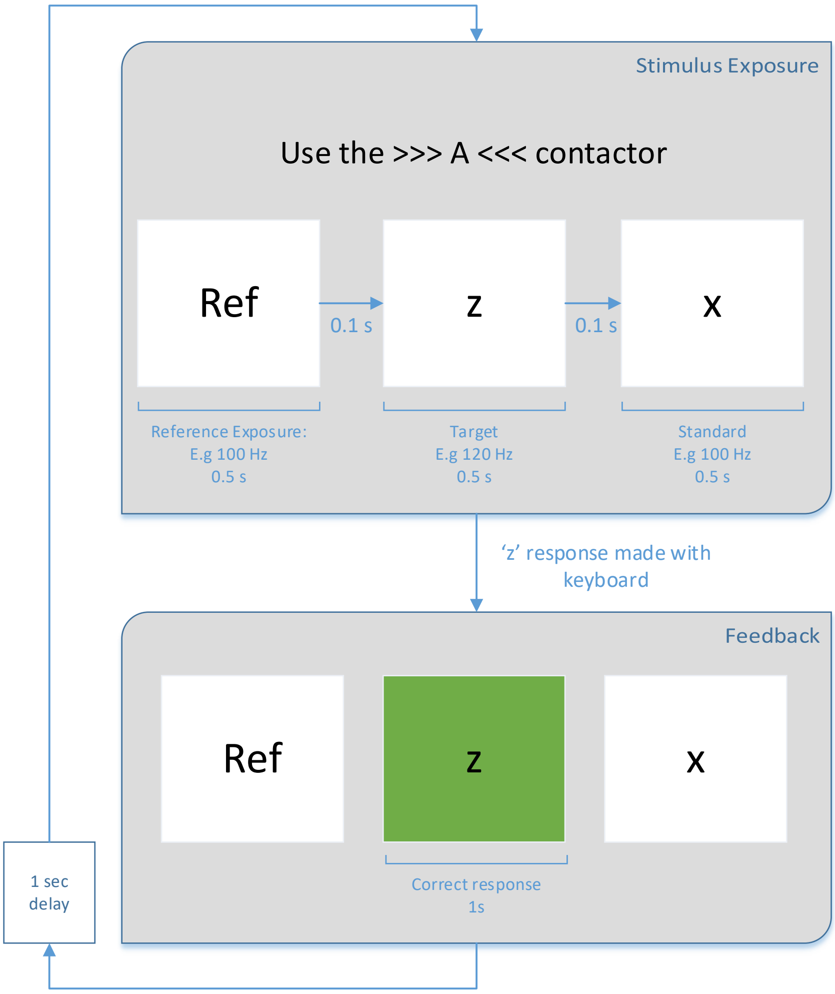

Figure 21. Schematic of an example trial from the discrimination task at high frequency on the small contactor (Experiment 1). The chosen interval was coloured red in the case of an incorrect trail.

3.7.3 2AFC magnitude discrimination procedure (Experiment 3)

This followed an identical procedure to the 2AFC frequency discrimination, except that the change of stimulus parameter was of acceleration magnitude rather than vibration frequency. This followed a method of limits adaptive track 'staircase' procedure.

3.7.4 2AFC vibrotactile detection threshold procedure (Experiments 2 & 3)

In this 2AFC version of the detection task, participants were again asked to identify the 'odd one out' of 3 intervals, with the difference being that a vibration was presented in only one interval (and was therefore the odd one out). the 'target' stimuli consisted of a 1-second sinusoidal vibration with a 0.05 second taper at either end. The 'target' was presented in either the second or the third interval. No vibration was played in the remaining two intervals. The magnitude of the target was manipulated until the participant was able to identify the target stimulus from the blank reference intervals using a 3-down 1-up method of limits staircase as described above. This followed an identical 3-down 1-up method of limits staircase to frequency and amplitude discrimination tasks, and trials of this type were randomly interleaved throughout those suprathreshold tasks.

Chapter 4 The effect of contactor size on vibrotactile frequency discrimination

4.1 Introduction

Our understanding of touch perception in human glabrous skin as a system of four 'information processing channels' is built on the idea of a minimum amplitude of vibration that can be detected – a vibrotactile threshold. One of the fundamental findings of the multichannel model is that the PC channel is more sensitive to large contact areas and high frequencies (Verrillo, 1966; Verrillo, 1963a, 1968). This results in a stereotyped pattern of thresholds – lower thresholds at high frequencies when the contactor is large, but similar thresholds at high and low frequencies when the contactor is small. In the acceleration domain used here, this effect is observed as an increase in threshold at high frequencies with the small contactor (see 2.2.4).

This can be explained by the PC channel's capacity for population coding across the skin (Bensmaia, 2008; Goble, Collins, & Cholewiak, 1996; Weber *et al.*, 2013), which enhances detection and the discrimination of stimulus intensity suprathreshold. More recent neurophysiological work, however, has emphasized the precision of temporal coding in both the RA and PC channels (Cascio & Sathian, 2001; Harvey *et al.*, 2013; Saal & Bensmaia, 2014b; Salinas, Hernández, Zainos, & Romo, 2000; Weber *et al.*, 2013). It is thought to be this precise, phase-locked coding that allows for the accurate discrimination of textures over a wide range of scales (Bensmaia & Hollins, 2003; Skedung *et al.*, 2013; Weber *et al.*, 2013).

Research has thus far failed to integrate these two ideas. This initial experiment investigates the discrimination of vibration frequency at the fingertip from two base frequencies (20 Hz and 100 Hz) using two contactor sizes (1-mm and 10-mm diameter probes). This is based on the idea that stimuli explicitly designed to activate individual channels will test whether the channel structure can be extended to suprathreshold information processing of vibrations. Since we might expect the Pacinian channel to better code the frequency of a stimulus when it is most sensitive to it, at high frequencies with large contactors, it is hypothesized that smaller weber fractions for vibration frequency will be observed at high frequencies when the contactor is large, but similar weber fractions for vibration frequency at high and low frequencies when the contactor is small.

This study will also instantiate and test a novel 3-interval 2-alternative forced choice (2AFC) discrimination design as an adaptable structure for future experiments. This design addresses a number of key limitations of existing frequency discrimination research (see 2.3) by: using naïve participants rather than highly-trained participants; recording any training effects over the three sessions; asking participants to make non-directional, non-specified discriminations of 'difference' rather than frequency; and by not intensity-matching stimuli, avoiding confounds of frequency, amplitude, pitch and intensity.

4.2 Methods

4.2.1 Participants

Participants were recruited from staff and students at the University of Southampton.

A sample size of at least 8 was estimated using GLIMMPSE software (Kreidler *et al.*, 2013) to have sufficient statistical power for a 2x2 analysis of variance, based on estimates of the standard deviation from piloting. Because this study trialled a new psychophysical design, and some exploratory statistics were anticipated, a larger sample was recruited. 12 participants took part in the experiment, but 4 were excluded from the analysis because they had conditions that may affect their touch perception (4 participants; autism, dyspraxia) and/or were unable to perform the threshold task (1 participant). Data was therefore analysed from 8 participants (5 male, 3 female) with normal touch perception, 21 – 29 years old.

4.2.2 Apparatus

Vibration stimuli were delivered with two VTT shakers, one with a 1-mm diameter contactor and surround (labelled 'A') and one with a 10-mm diameter contactor and surround (labelled 'B'). Visual cues and instructions were presented with a computer monitor. 75dB noise was delivered with a noise machine and headphones. In the threshold task responses were made with a button, and in the discrimination task responses were made on a pc keyboard. Testing took place in a temperature-controlled room (21°C). The participant sat on one side of an opaque screen, so they could not see the experimenter or control equipment. This setup is detailed in Chapter 1

4.2.3 Procedure

Each participant attended 3 1-hour sessions on different days. At the start of each session, vibrotactile thresholds were determined for the left forefinger at 2 frequencies: 31.5 and 125 Hz using the von Bekesy method of limits (see section 3.7 for details). Stimuli for the frequency discrimination task were set at a magnitude equal to 3x the acceleration magnitude of this detection threshold at the same base frequency (equivalent to a sensation level of 9dB re 1μm of displacement).

The frequency discrimination task in this first experiment used a method of constant stimuli design. Although this psychophysical strategy requires a larger number of samples than the 'adaptive track' staircases used for later experiments, it allows us to measure a broader range of frequencies with a sufficient number of trials to plot psychophysical functions.

The experimental protocol was approved by the University of Southampton Ethics Committee (ID: 27435).

4.2.4 Stimuli

Stimuli for the discrimination task consisted of 'standards' of 20Hz and 100Hz and 'target' stimuli of 10 frequency increments of 10% to 100% increases in frequency from the standards. All stimuli were 0.5 seconds long with a taper of 0.05 s at each end. Stimuli were calibrated in each session for the participant's individual finger. Each trial consisted of three sequential 0.5 second vibrations delivered to the left forefinger, with pauses between stimuli of 0.1 s duration. The first vibration was always a reference 'standard' vibration of 20 or 100 Hz. The second and third vibrations were another standard and a target vibration, with half of trials having the target in the second position and half in the third, presented in a random order. Following the 3rd vibration the participant responded with the 'z' key if the second vibration was the *odd one out*, or the 'x' key if the third vibration was the odd one out. Visual cues were synchronised to the presentation of vibration and changed colour to provide immediate feedback.

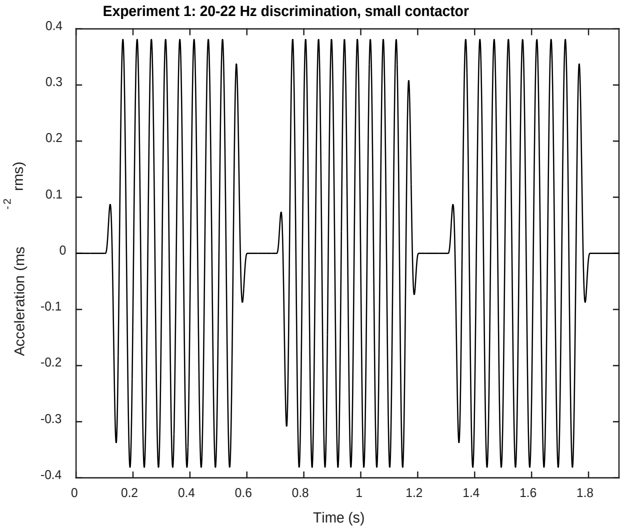

Figure 22. Example stimuli for the frequency discrimination task. The target stimulus (middle) is 2 Hz higher than the comparison stimuli (left and right), a weber fraction of .1.

4.3 Results

4.3.1 Vibrotactile detection thresholds

A 2x2 (contactor size x frequency) repeated measures analysis of variance (ANOVA) was used to analyse data from the threshold task, with an alpha level of 0.05. The analysis revealed that the hypothesized interaction effect of contactor size x frequency was significant, $F(1,7) = 38.9$, $p < .01$, $\eta_p^2 = .85$. Figure 23 shows that the increase in threshold acceleration at 100 Hz, but not at 20 Hz, was greater for the small contactor than for the large contactor.

The analysis also showed significant main effects of frequency, $F(1,7) = 22.5$, $p < .01$, $\eta_p^2 = .76$, and contactor size, $F(1,7) = 35.2$, $p < .01$, $\eta_p^2 = .83$, on vibrotactile thresholds.

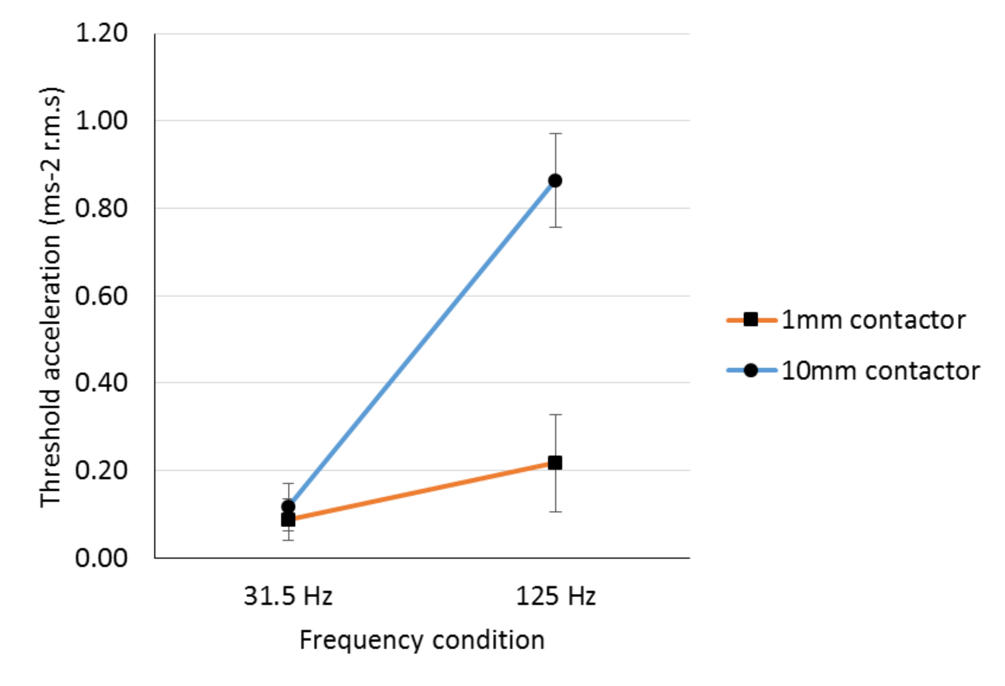

Figure 23. Vibrotactile detection thresholds as function of frequency and contactor size. Error bars are defined by the standard error.

4.3.2 Frequency Discrimination

4.3.2.1 Psychometric Functions

Psychometric functions were plotted from the frequency discrimination data. Weibull functions were fitted to the data with a maximum likelihood estimation. Just noticeable differences (Δf) were extracted at the 75% correct level and plotted as weber fractions ($\Delta f/f$). Figure 24 shows psychometric functions for P1, and individual psychometric functions from all participants (included those excluded from further analysis) can be found in Appendix B.

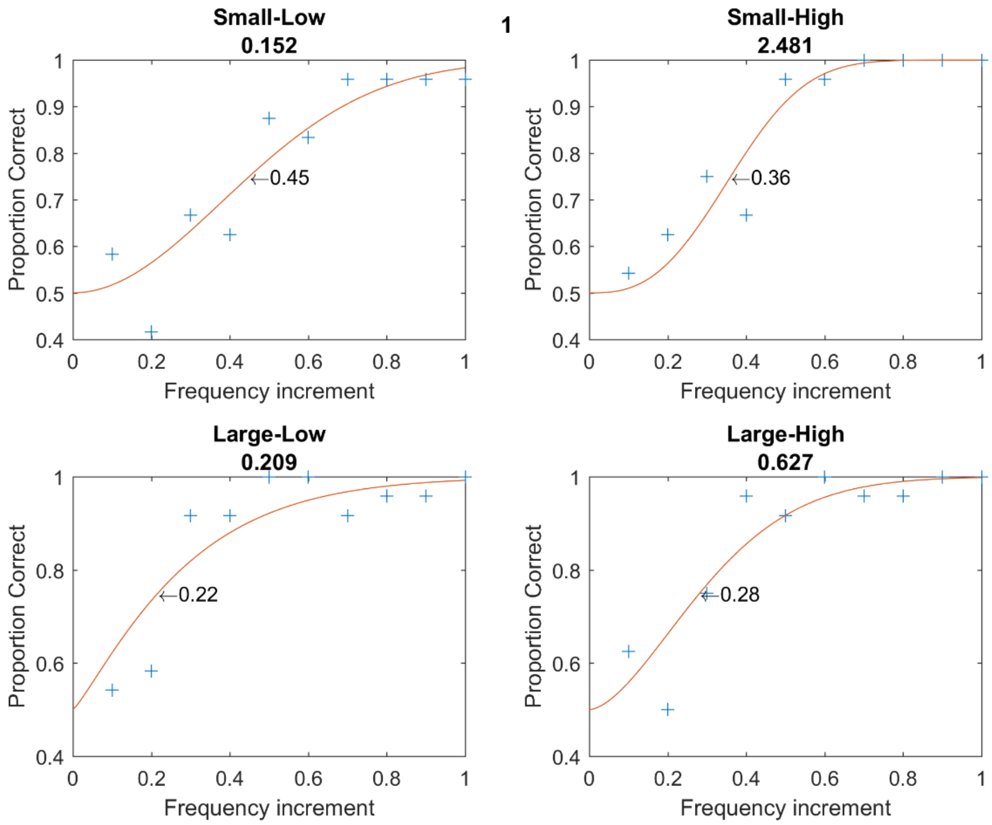

Figure 24. Psychometric functions in 4 conditions for P1. Points give measured performance in proportion correct, lines give maximum likelihood estimation psychometric functions. The labelled points are frequency increments corresponding to 75% correct (i.e. Weber fraction). Numbers below each graph title refer to the magnitude of the test stimuli in that condition (in ms^{-2} RMS).

4.3.2.2 Main and interaction effects

A second 2x2 (contactor size x frequency) repeated measures ANOVA was used to analyse data from the discrimination task, with an alpha level of .05. The hypothesized interaction effect was non-significant. The main effect of contact area was also non-significant. There was a significant main effect of frequency, $F(1,7) = 10.4$, $p = .01$, $\eta_p^2 = .60$, such that weber fractions were larger in the high frequency condition. Figure 25 shows the higher weber fractions at high frequencies. In non-normalised frequency, the mean JND in the low frequency condition was 5.58 Hz (*SE* = .68 Hz), while the mean JND in the high frequency condition was 57.5 Hz (*SE* = 10.6 Hz).

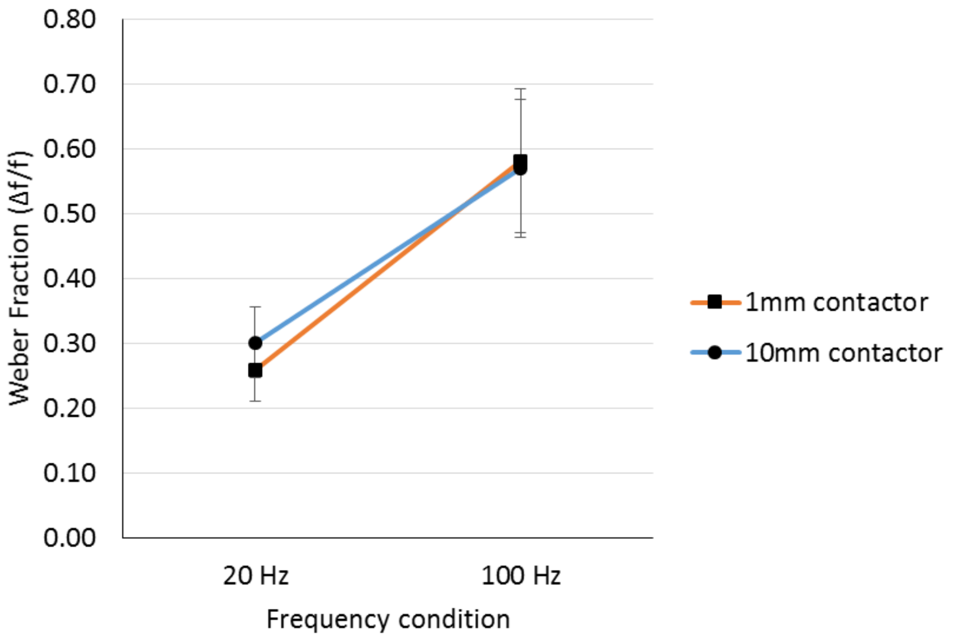

Figure 25. Weber fractions for frequency as function of frequency condition and contactor size. Error bars are defined by the standard error.

4.3.2.3 Training effects

Individual participant's weber fractions for vibration frequency in each of the three sessions were determined by fitting Weibull functions to the data collected in each session with a maximum likelihood estimation. Note that, although the sessions were balanced for the number of trials in each condition, the relatively small number of decisions at each frequency increment is likely to result in comparatively poorly fitted psychometric functions. A 3x2x2 (session x contactor size x frequency) repeated measures ANOVA was used to analyse data from the discrimination task in each session, to look for changes in performance over time. There was no significant effect of experimental session, $F(2,14) = .416$, $p > .05$. Figure 26 shows individual frequency discrimination weber fractions across sessions.

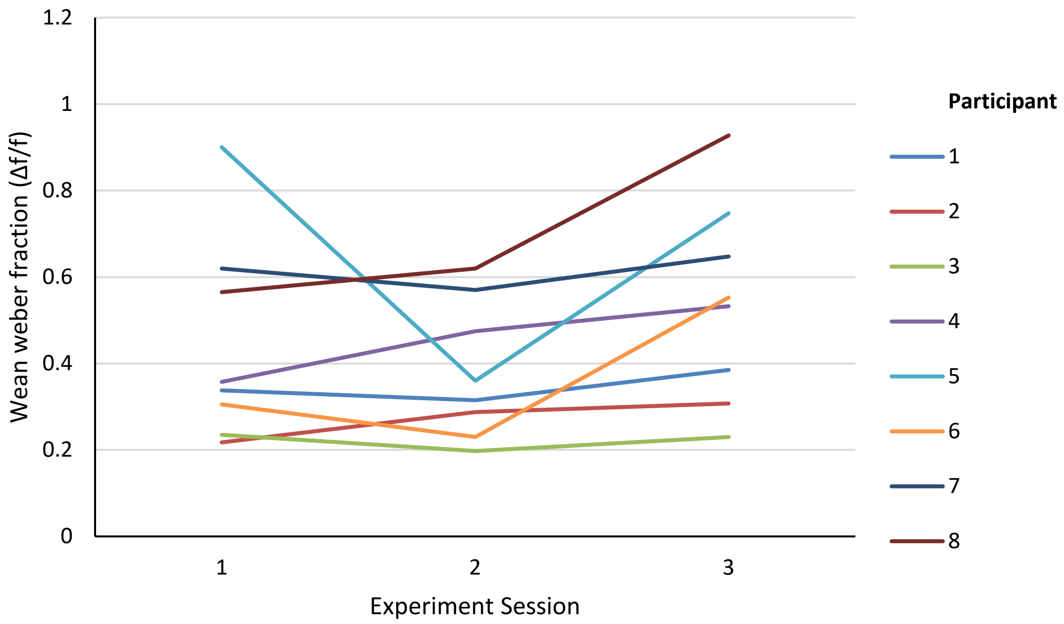

Figure 26. Individual frequency discrimination weber fractions across sessions. Note that participants completed a random subset of trials in each session, so this data is vulnerable to too sparse data at each frequency to reliably calculate a psychometric function.

4.3.2.4 Individual results

Results were marked by high inter-subject variability, especially at high frequencies (Small contactor *M* = .58, *SE* = .11; large contactor *M* = .68, *SE* = .10). As the cause for this variability is not known, it may be worthwhile to examine this to attempt to determine whether some other factor affects frequency discrimination across the four conditions differently in different participants.

In the threshold task, where an analysis of variance was significant, all participants showed the characteristic interaction: an increase in threshold at higher frequencies with the smaller contactor, but a much more similar detection threshold at the two frequencies with the larger contactor. The magnitude of this effect varies substantially between participants. Figure 27 shows individual results for the threshold task for the small contactor (A) and large contactor (B).

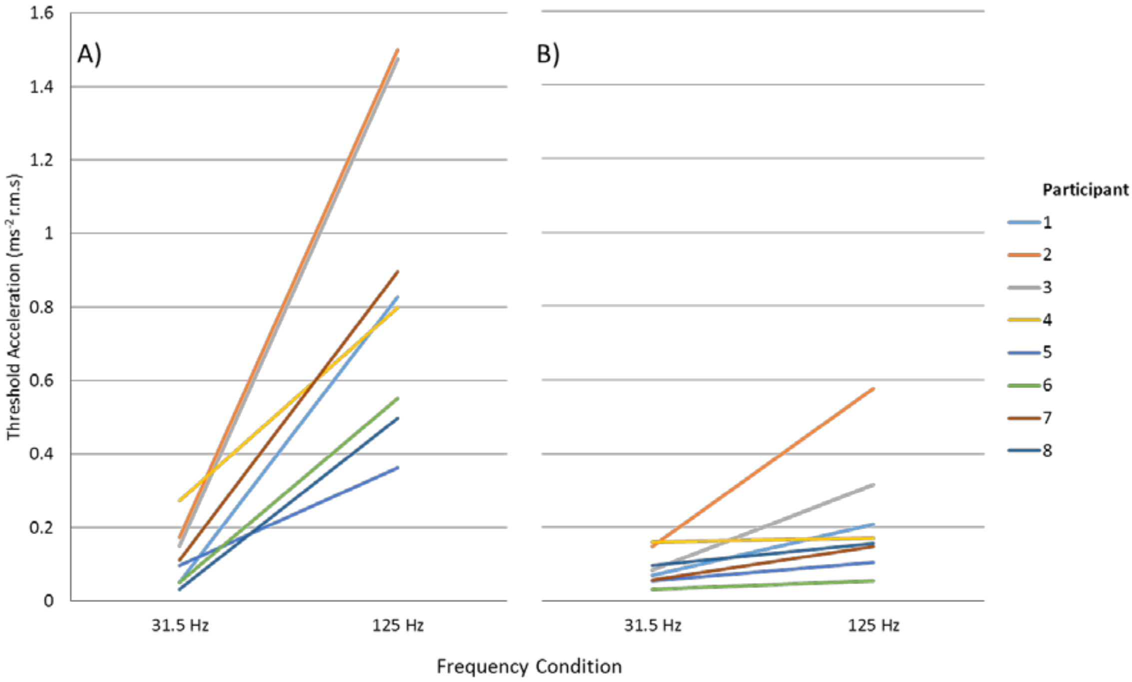

Figure 27. Individual results for vibrotactile thresholds. A) 1-mm contactor condition. B) 10-mm contactor condition.

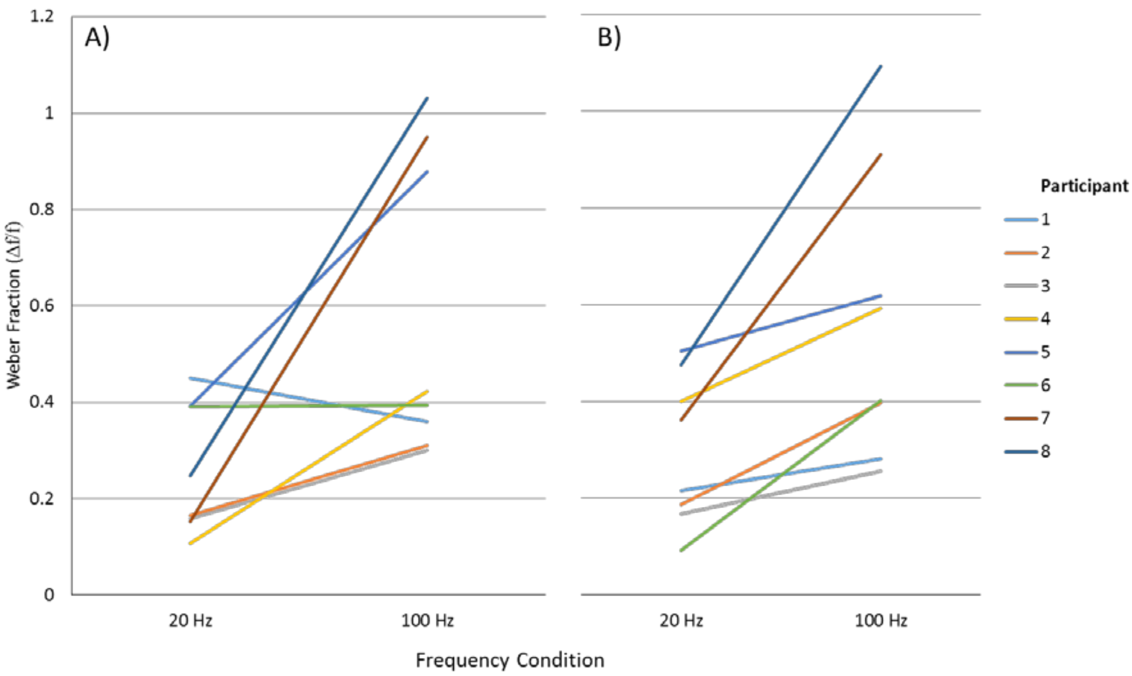

Figure 28. Individual results for frequency discrimination. A) 1-mm contactor condition. B) 10-mm contactor condition.

In the discrimination task however, there were different patterns of performance within the cohort. Figure 28 shows individual results for the frequency discrimination task for the small contactor (A) and large contactor (B). With the small contactor, some participants exhibited a large increase in weber fraction with frequency (e.g. P8, P7, P5), whereas others had more consistent weber fractions (e.g. P6), or even showed a smaller weber fraction for high frequencies than low ones (P1). The size of this difference between weber fractions at low and high frequencies varied between -.09 and .79 (M = .33, SE = .11). With the large contactor, weber fractions for vibration frequency were higher in the high frequency condition than in the low frequency condition for all participants. The size of this increase from weber fraction at low frequencies and at high varied between .06 and .61 (M = .26, SE = .07). That participants exhibited very different patterns of results suggests that some other between-subjects factor, not controlled by the experimental design, may have influenced performance.

Another possibility is that, although performance varied widely across participants, there may was a pattern of results across conditions. As an exploratory measure, Pearson product-moment correlation coefficients were calculated to assess the relationships between weber fractions in the four contactor-frequency conditions measured here: small-low, small -high large-low, and large-high. Performance was found to be highly correlated between small-high and large-low (R = .80, p = .02), small-high and large-high (R = .91, p < .01), and large-low and large-high (R = .75, p = .03). Performance in the small-low condition was uncorrelated with performance in the other conditions (R = .02, -.11, and -.24 with small-high, large-low and large-high respectfully). These relationships are illustrated Figure 29.

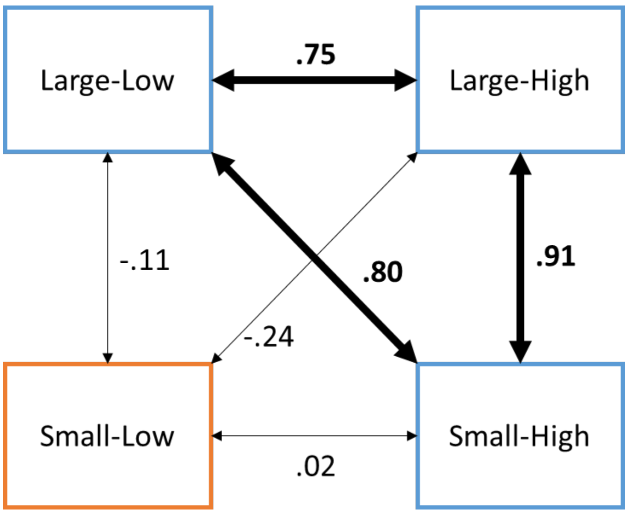

Figure 29. Correlations between frequency discrimination stimuli with the conditions *contactor size* (Large, 10mm; Small, 1mm) and *frequency condition* (Low, 20 Hz; High, 100 Hz). Performance in Large-Low, Large-High, and Small-High conditions were highly inter-correlated, and uncorrelated with performance in the Small-Low condition. Significant Pearson's correlations are printed in bold.

4.4 Discussion

This study investigated detection thresholds and vibrotactile frequency discrimination in two frequency conditions (20 Hz and 100 Hz standard frequencies) with two contactor sizes (1-mm and 10-mm diameter probes). The results from the threshold test successfully reproduced a longstanding observation in vibrotactile psychophysics: an increase in threshold at high frequency with a small contactor, but not with a large contactor. This is a key piece of evidence that at least two 'information processing channels' support the detection of vibration, and that they have different selectivity for frequency and contact conditions (Gescheider *et al.*, 2010; Verrillo, 1963, 1968). A parallel effect was found to be absent from the vibrotactile frequency discrimination task, with mean weber fractions being similar at on both small and large contactors being very similar. These results suggest that spatial summation in the PC channel may not support better discrimination of the frequency of vibration suprathreshold.

This study found support for the null hypothesis for the frequency discrimination task. There are two ways to interpret this statistical finding: 1) that we have accurately identified there is no effect present, or 2) that an effect is present, but we were unable to identify it because of a flaw in the experimental design (a type 2 error). For the sake of completeness – and to guide further experiments in this thesis – both possibilities are considered here.

The results of the threshold task provide support for the idea that, at threshold, the PC channel draws on activity from across the skin to support detection of vibration at a lower acceleration magnitude. Taking the null result of this study at face value, we find that, suprathreshold, a larger area of skin stimulation does not result in more effective discrimination of vibration frequency. One interpretation is that the mechanisms of population coding in the PC channel that support detection at lower amplitudes do not serve to improve discrimination between suprathreshold stimuli on the basis of stimulus frequency. This indicates that the mechanism of spatial summation operates as a specific, rather than a general, mechanism of information processing across the skin.

In this study, there was an effect of frequency condition on weber fractions, such that high frequency stimuli had a higher weber fraction than stimuli in the low-frequency condition. This is contrary to some reports of consistent weber fractions across a broad frequency range (Bensmaïa, Hollins, & Yau, 2005; Franzén & Nordmark, 1975; Mahns *et al.*, 2006; Skedung *et al.*, 2013), but may be consistent with reports of differential effects of adaptation on high and low frequencies (Goble & Hollins, 1994). This inconsistency of reported weber fractions within the domain of vibrotactile frequency discrimination warrants further investigation in future experiments. It may be that an experimental parameter has not been adequately controlled across studies of vibrotactile frequency discrimination.

One important possibility is that the RA channel, which is not thought to be affected by contact area, was the primary determinant of weber fraction for vibration frequency in across all conditions. Stimuli in this experiment were not explicitly designed to test the consequences of suprathreshold stimuli activating more than one tactile channel, and how this might alter the capacity to discriminate on the basis of vibration frequency. Later experiments reported in this thesis should be able to explicitly address this possibility.

It is likely that the magnitude of the vibration stimuli used will affect the number of tactile channels involved in perception of a stimulus, and the degree to which they are activated. Following from previous literature on vibrotactile frequency discrimination, this study used a 'sensation level' to determine the acceleration magnitude of the vibration stimuli for each participant. The idea is that, by setting stimuli at an amplitude a fixed amount above threshold – in this experiment 3x the acceleration magnitude (equivalent to 9dB) – we present stimuli of similar detectability or intensity, control for different sensitivities of the participants. A limitation of this approach is that the absolute acceleration magnitude of the stimulus depends on the measurement of detection threshold – which can be vulnerable to both random and systematic error, as well as substantial response biases. We saw in this study that measured thresholds can vary substantially between participants (see Figure 28), and these particpants will therefore have been presented with vibration stimuli of very different amplitudes. These differences in amplitude are likely to have recruited different sub-sets of tactile channels, which may have resulted in very different weber fractions for vibration frequency between conditions and participants. This might be controlled in future experiments through control of acceleration magnitude in order to target a specific combination of tactile channels rather than an equal 'sensation level'.

There was very high inter-subject variability, especially in high frequency conditions. High inter-subject variability is common to vibrotactile research. Although it is not clear precisely wwhat the casue of this variability may be, researchers have limited its impact by extensively training participants until they produce results that are 'consistent', although it is usually unclear what standard this refers to. Looking at the pattern of individual results in this study, in which a subgroup of participants presented a different set of responses, suggests that it may be beneficial to investigate these discrepancies in performance. Exploratory correlational analysis revealed that the Small-Low condition was uncorrelated with the other test conditions, which were all highly inter-correlated. A possible interpretation is that the small-low condition almost exclusively activated the RA channel, whereas the other conditions were supported primarily by the PC channel, and that performance in the two sub-systems is independent. It may be interesting to directly test whether measures of the sensitivity of a particular tactile channel are correlated across participants to measures of that channels capacity to discriminate on the basis of vibration frequency. The current study is limited in a few ways that make it difficult to draw these kinds of conclusions. One of these limitations was the number of subjects that took part in the study. A key limiting factor on the number of participants that can be practically recruited for the study is the longer duration of a Method of Constant stimuli design compared to adaptive psychophysical methods. Later studies reported in this thesis adapt the 3-inetrval 2-AFC task tested here to a track of interleaved adaptive staircases that allow more measurements to be made in a shorter period of time, allowing for a larger number of participants to be recruited and tested. This would allow for the use of other analytical tools, as well as a better resilience to inter-subject reliability.

Data from only eight participants was analysed statistically (although data from all 12 is presented in Appendix B). This decision was made because four participants volunteered that they had autism spectrum disorder and/or dyspraxia, which may have affected their sense of touch. One of these participants was unable to complete the threshold task in some conditions within the dynamic range of the VTT, others failed to display the characteristic sigmoid shape of a psychometric function. This may be due to the sensory component of autism spectrum disorder (Marco *et al.*, 2011). This is interesting in itself, and future research could investigate the effect of ASD and dyspraxia on tactile sensitivity and the ability to perform psychophysical tasks in the domain of touch perception. Although a sample of eight participants was estimated to have sufficient power for an analysis of variance, it severely limits our ability to draw conclusions from correlations.

4.5 Conclusions

This study looked for parallels between information processing in the tactile system in glabrous skin of the human hand at threshold, with vibrotactile detection thresholds, and suprathreshold, with vibrotactile frequency weber fractions. We saw that frequency affected weber fractions for discrimination of vibration frequency, but that this did not interact with the size of the contact area as hypothesized. This may suggest that spatial summation does not support frequency discrimination in the PC channel, or that some experimental parameter – such as vibration magnitude – was not sufficiently controlled across participants. Further research should streamline the experimental procedure, recruit a greater number of participants, and focus on the difficult interaction between frequency and amplitude in tactile processing in order to explain the dissociation between processing at threshold and suprathreshold vibration magnitudes.

Chapter 5 Effect of stimulus magnitude on discrimination of the frequency of vibration in the PC and RA channels

5.1 Introduction

When we brush our fingers across a surface, we perceive it as hard or soft, rough or smooth, grippy or slippy. These sensations depend on systems of mechanoreceptive neurons in the skin that encode the parameters of the complex physical interaction between the surface and the skin. These systems are known as the 'tactile channels' (Gescheider, 1976; Capraro *et al.*, 1979; Gescheider *et al.* 2010). At least four tactile channels exist, mediated by four different kinds of mechanoreceptive neurons in the skin (Johnson, 2001; Gescheider *et al.*, 2010).

The channels behave in different ways to capture information from the physical environment (Johnson and Hsiao, 1992; Johnson, 2001; Saal and Bensmaia, 2014). In the case of fine texture, perception depends on the ability to encode the frequency of the vibration induced in the skin by brushing it across the surface (Hollins *et al.*, 2002; Bensmaia and Hollins, 2003). We can investigate this capacity to encode frequency by asking people to make discriminations between a vibration and a target vibration of a different frequency, and then estimating their Weber fraction – the smallest change in the frequency of vibration they can reliably detect, proportional to the original frequency (i.e., $\Delta f/f$).

Vibration frequency is encoded by Pacinian corpuscles (the PC channel). This is suggested by electrophysiological evidence that the PC channel responds to small changes in skin indentation in a phase-locked way, encoding the frequency of the vibration (Freeman and Johnson, 1982; Bolanowski and Zwislocki, 1984; Horch, 1991). As the magnitude of the vibration increases, a second channel mediated by Meissner's corpuscles, known as the Rapid-Adapting (RA) channel, is activated. This channel has also been implicated in encoding frequency (Mountcastle and Steinmetz, 1990; Mountcastle *et al.*, 1990; Salinas *et al.*, 2000) and shares the capacity to respond to vibrations in a phase-locked way (Talbot *et al.*, 1968). The purpose of this study was to address whether there is a difference between Weber fractions for frequency in conditions thought to activate the PC channel alone and those that activate both the PC channel and the RA channel.

There have been few studies of the discrimination of vibrotactile frequency (e.g., Roberts, 1932; Mowbray and Gebhard, 1957; Goff, 1967; Franzén and Nordmark, 1975; Rothenberg *et al.*, 1977; Horch, 1991; Sinclair and Burton, 1996; Tommerdahl *et al.*, 2005; Mahns *et al.*, 2006; Deco, Scarano, and Soto-Faraco, 2007; Kuroki *et al.*, 2013). These studies do not address the question of how the recruitment of the RA channel affects Weber fractions. Most researchers have used stimuli with 'sensation levels' (SL; levels greater than the observer's absolute threshold) of between 16 and 35 dB. These levels are likely to activate all the tactile channels, and the findings may vary because of variability in individual absolute thresholds within each channel. In this study, the acceleration of the vibration, rather than the perceptual intensity, was controlled across target and comparison stimuli. This allows us to better control the activation of the target channels, without being dependent on a noisy or cumbersome detection threshold measurement.

It was hypothesized that Weber fractions for vibrotactile frequency would be smaller in the 2-channel magnitude condition than in the 1-channel magnitude condition. There are two ways in which the recruitment of a second channel may improve Weber fractions: 1) the recruitment of a more sensitive channel supersedes, or replaces, the less sensitive channel or, 2) the recruitment of a second channel is additive, and always improves discrimination, regardless of which of the two is more sensitive. The effect of magnitude condition is expected to interact with the effect of target channel, such that discrimination in the PC targeting condition improves with the recruitment of the more sensitive RA channel.

This study also builds on the results of experiment 1 by adapting it's 3-interval 2AFC task into an adaptive method of limits design, which allows us to measure weber fractions in a smaller number of trials and a shorter period of time, which in turn allows for a larger sample size. This design also provides us with the opportunity to incorporate the measurement of vibrotactile detection threshold into the 2-AFC task, to be completed in parallel with the frequency discrimination task. Participants completed detection threshold 'staircases' in PC- and RA-targeting conditions, which allows us to investigate whether measures in the individual channels correlate with frequency weber fractions associated with those thresholds suprathreshold.

5.2 Methods

5.2.1 Participants

Sixteen participants were recruited from the staff and students at the University of Southampton (11 male and 5 female, with an average age of 27 years [*SD* = 5.45]). On a screening questionnaire, the participants reported that they had no problems with their touch perception, and that they had not been exposed to vibration or taken medication that may have affected their sense of touch.

5.2.2 Apparatus

Vibration stimuli were delivered with two *HVLab* Tactile Vibrometers (VTT). One VTT had a 10-mm diameter contactor, and the other had a 1-mm diameter contactor. Rigid surrounds, with a 1-mm gap to the contactor, were used to limit the spread of surface waves. The output of the VTT was calibrated using a Brüel and Kjaer calibration exciter (type 4294). During testing, participants were instructed to maintain a constant 2N downward force on the contactor with the distal phalanx of their left middle finger using feedback from a force sensor. Pink noise was played to the participants over circumaural headphones at 75 dB to mask any auditory cues to the frequency of vibration. Visual cues to the timing of the presentation of the stimuli were shown on a computer monitor, and responses were made by clicking a mouse. All stimuli were controlled with custom MatLab software and monitored by the experimenter. Testing took place in a temperature-controlled room (21 ±1°C). The participants sat on one side of an opaque screen so that they could not see the experimenter or the control equipment.

5.2.3 Procedure

Participants completed a single two-alternative forced choice (2AFC) task that measured both weber fractions for discrimination of vibration frequency and detection thresholds. Vibrotactile frequency discrimination was measured in conditions designed to primarily activate two different tactile channels: a PC-targeting condition (10-mm contactor and 100 Hz reference stimuli) and an RA-targeting condition (1-mm contactor and 20 Hz reference stimuli). Performance in each condition was measured in two acceleration magnitude conditions (a 1-channel condition designed to activate only the target channel, and a 2-channel condition designed to activate both the target channel and the less sensitive channel). Vibrotactile detection thresholds were measured in two conditions, randomly interleaved into the frequency discrimination task.

Each trial type followed 3-down 1-up method of limits staircases, with the three staircases evolving in parallel. The two frequency difference staircases had the initial frequency of the 'target' (e.g. 100 Hz) plus 10%, and step sizes starting at 30% and decreasing in size by 5% with each reversal. The detection threshold staircase had the initial magnitude of the 'target' as 0.5 ms^{-2} r.m.s. with step sizes starting at 0.3 ms^{-2} r.m.s. and decreasing in steps of 0.05 ms^{-2} r.m.s with each reversal, to a minimum step size of 0.05 ms^{-2} r.m.s. Each staircase was considered complete after 10 reversals or 50 trials. The difference limen was taken as the average of the 4^{th} through to the 10^{th} reversals. Theoretically, this method converges on the 79.4% correct level of performance (Levitt, 1971).

A single trial of the task consisted of three intervals. The first interval was always the presentation of a 'reference' stimulus. The second and third intervals contained a 'target' stimulus, and a repeat of the reference stimulus in a randomised order. Visual cues were presented on the computer monitor for each stimulus interval. One, two, and then three white boxes appeared across the screen in front of the subject as each interval occurred. When all the stimuli had been presented, the two boxes representing the intervals in which a 'target' may have been presented turned orange. Participants then indicated which interval was most likely to contain the 'target' with a left or right mouse click. Feedback was provided by the box turning green (correct) or red (incorrect). Experimental trials were completed in blocks of 20, each lasting around 2 minutes. Between each block, a break of at least 1 minute was enforced, during which participants rested their finger and removed their headphones. This was to limit any effect of temporary threshold shift (TTS) from exposure to vibration, and to reduce any fatigue. Participants completed a supervised training block at the start of the experiment to ensure that they had understood the instructions and maintained the correct contact with the vibrator.

Visual cues were presented with each stimulus interval. Three white boxes appeared across the screen in front of the subject as each interval occurred. When all the stimuli had been presented, the two boxes representing the intervals in which a 'target' may have been presented turned orange. Participants then indicated which interval was most likely to contain the ‘target’ with a mouse click. Feedback was provided by the box turning green (correct) or red (incorrect).

The experimental protocol was approved by the University of Southampton Ethics Committee (ID: 40132).

5.2.4 Stimuli

All vibration stimuli consisted of consisted of 1-second sinusoidal vibrations with a 0.05-second taper at either end. For the frequency discrimination task, participants were required to identify the ‘odd one out’ of three sinusoidal vibrations. On the 10-mm contactor, the ‘reference’ stimuli always had a frequency of 100 Hz and on the 1-mmm contactor the ‘reference’ stimuli always had a frequency of 20 Hz. The ‘target’ stimuli were identical to the ‘reference’ stimuli except for their frequency, which was higher than the reference (never exceeding 250 Hz). For the detection threshold task, the ‘target’ stimulus consisted of a sinusoidal vibration of either 31.5 Hz (small contactor) or 125 Hz (large contactor). The ‘reference’ ‘stimuli’ were 1 second intervals during which visual cues were provided but no target was presented. Amplitude was manipulated until the participant was able to reliably identify the target from the blank reference intervals.

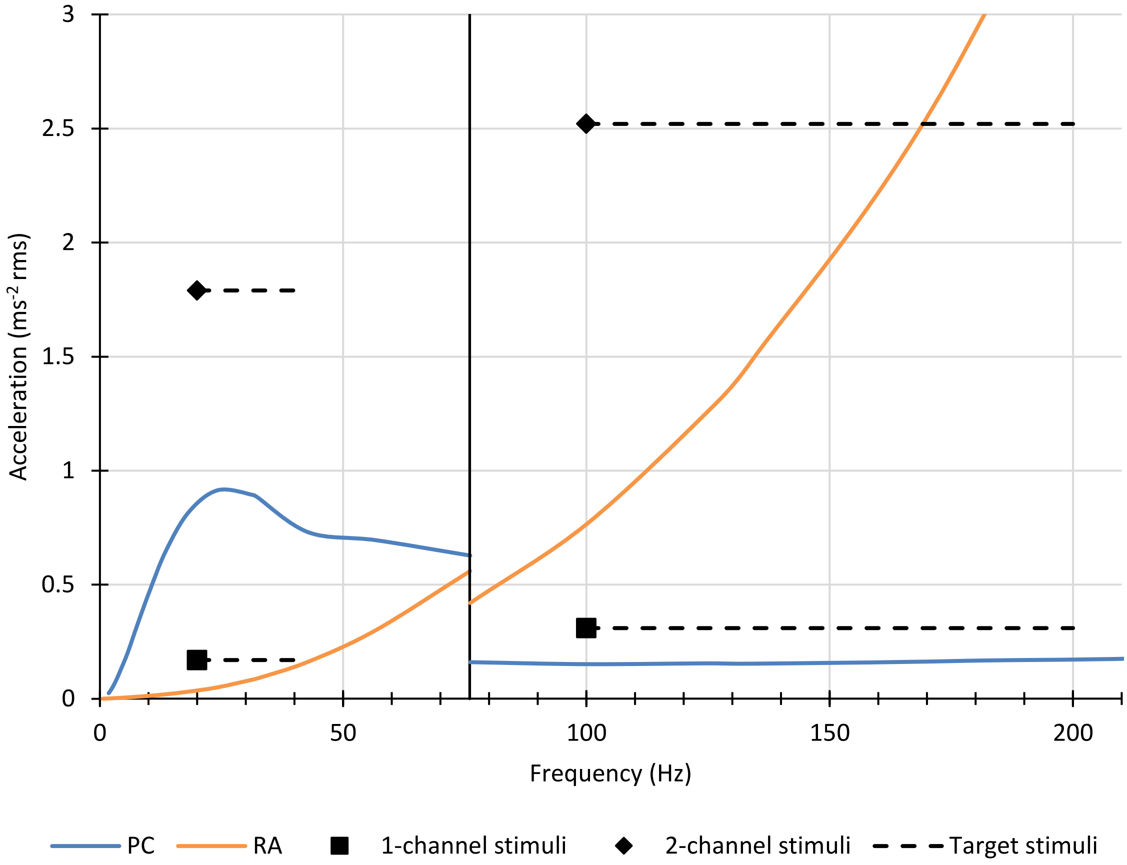

Figure 30. Estimates of tuning curves for PC and RA channels (solid coloured lines) in with the 1-mm contactor (left) and the 10-mm contactor (right), and the chosen stimulus magnitudes and frequency ranges for 1-channel and 2-channel activations (dashed lines). The vertical black line divides estimates of channel sensitivity for the contact conditions on the two contactors.

To determine the magnitudes of the stimuli in the frequency discrimination task, the sensitivity of the RA and PC channels was estimated based on tuning curves derived from previous research on vibrotactile thresholds (Verrillo, 1963; Bolanowski and Verrillo, 1982; Gescheider *et al.*, 1985; Verrillo and Bolanowski, 1986; Bolanowski *et al.*, 1988). Channel sensitivity varies systematically as a function of frequency and contactor size, among other factors. To estimate the sensitivity of the two channels in the conditions chosen for this experiment, the detection thresholds of 8 participants (5 male and 3 female, with a mean age of 25 [*SD* = 2.05]) were measured at 125 Hz with the same 10-mm diameter contactor as in the main experiment, using the von Békésy method of limits as defined in ISO 13091- 1:2001. The mean absolute threshold at 125 Hz was found to be 0.22 ms^{-2} r.m.s (SE = 0.06).

This value was used to estimate channel sensitivity across a broader frequency range when using the two contactors on the fingertip, by multiplying the historical tuning curves such that that they intersect with this experimentally determined threshold.

Stimuli were chosen for the 1-channel and 2-channel conditions to have magnitudes of double the expected absolute acceleration threshold for the relevant channel, in order to activate one or two target channels. All vibration stimuli therefore had an acceleration magnitude of either 0.31 ms^{-2} r.m.s. or 2.52 ms^{-2} r.m.s. on the 10-mm contactor, and acceleration magnitudes of either 0.17 ms^{-2} r.m.s. or 1.78 ms^{-2} r.m.s. on the 1-mm contactor. Figure 30 shows estimates of tuning curves for PC and RA channels in with the 1-mm contactor (left side of graph) and the 10-mm contactor (right), and the chosen stimulus magnitudes and frequency ranges for 1-channel and 2-channel activations.

5.3 Results

Performance in each of the six conditions was measured as the mean of the 5th through 10th reversals. To illustrate this process, Figure 31 shows completed staircases for participant 1. The full set of individual data is presented in this fashion in Appendix C.

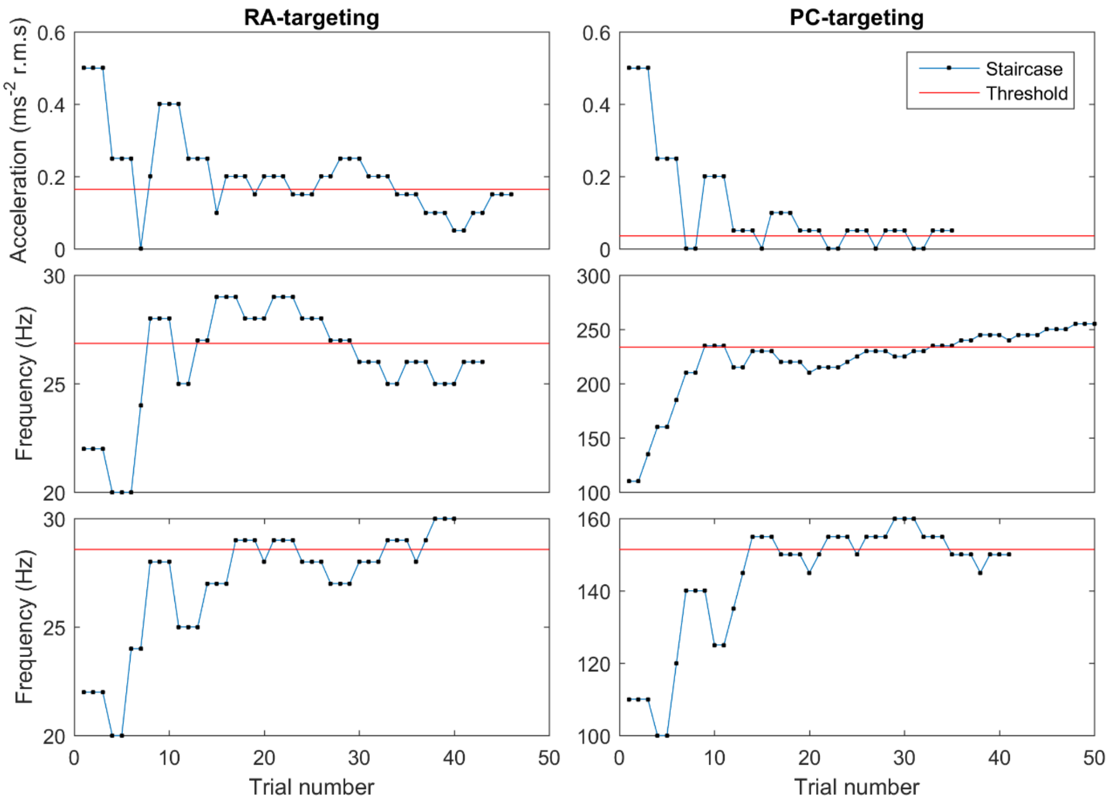

Figure 31. Completed staircase procedures in all 6 conditions for participant 1. The top two panels illustrate trials in the detection threshold task. The remaining panels illustrate performance in the frequency discrimination task, with the middle row representing performance in the 1-channel condition and the lower row representing performance in the two channel condition. For all panels the target value intersects with the x-axis, and test values vary depending on past performance following a 3-down 1-up procedure.

5.3.1 Detection Thresholds

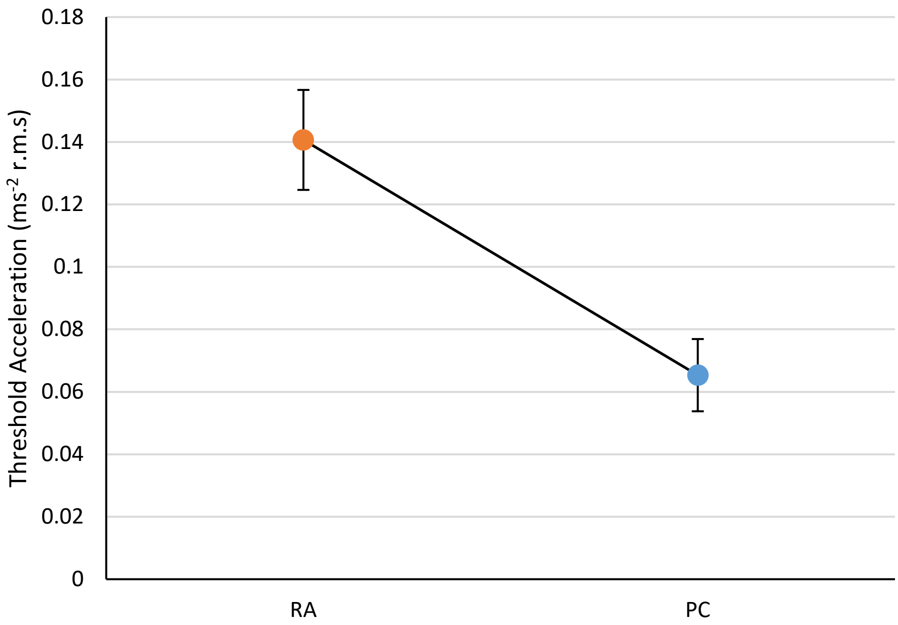

Figure 32. Mean detection thresholds in RA-targeting conditions (1-mm contactor, 31.5 Hz) and PC-targeting conditions (10-mm contactor, 125 Hz) expressed in acceleration magnitude. Error bars give the standard error of the mean.

A paired samples t-test was conducted to investigate differences in detection threshold in PC RA targeting conditions (1-mm contactor, 31.5 Hz) and PC-targeting conditions (10-mm contactor, 125 Hz). Thresholds were found to be significantly lower in the PC-targeting condition ($t(15) = 5.87$, $p < .001$). This difference is illustrated in Figure 32.

5.3.2 Frequency Discrimination

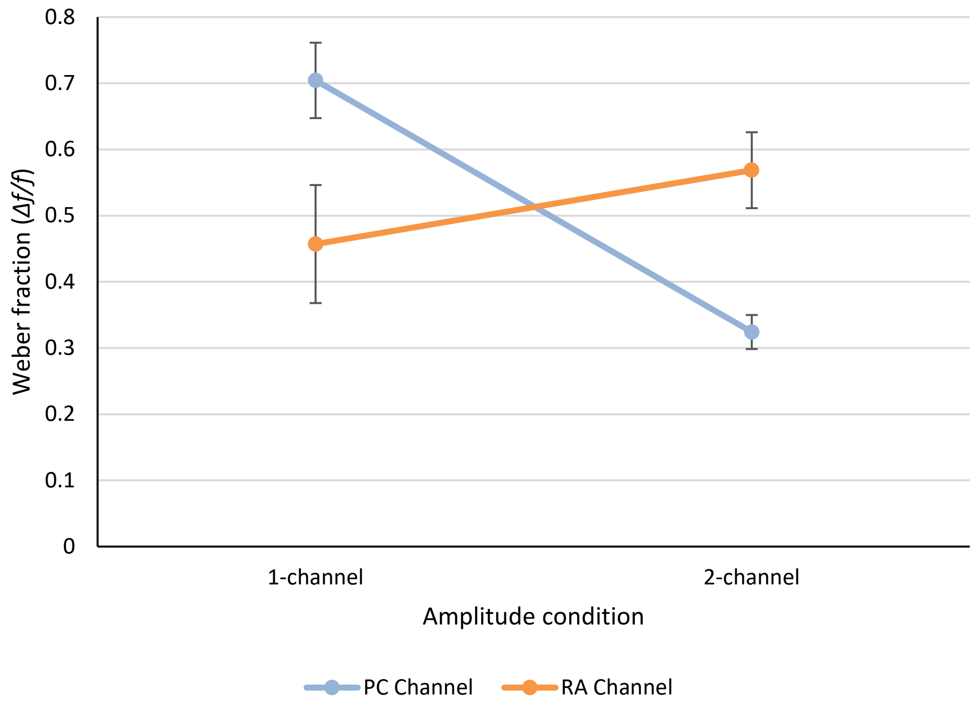

Figure 33. Mean weber fractions for vibrotactile frequency in two acceleration magnitude conditions. The RA channel targeting conditions used a 1-mm contactor and a 20 Hz standard frequency, and acceleration magnitudes were of 0.17 (1-channel) and 1.78 ms-2 (2-channel). The PC channel targeting conditions used a 10-mm contactor and a standard frequency of 100 Hz, and acceleration magnitudes were of 0.31 (1-channel) and 2.52 ms-2 (2-channel). Error bars give the standard error of the mean.

A 2x2 repeated measures ANOVA was conducted to investigate differences in weber fraction as a function of target channel (PC or RA; the most sensitive channel in the target conditions) and of amplitude condition (1-channel or 2-channel; whether the acceleration magnitude was sufficient to activate the target channel alone or both channels together). A significant main effect of amplitude condition was observed ($F(1,15) = 6.9$, $p = .019$, $\eta_p^2 = .314$) such that weber fractions for vibrations at an acceleration magnitude estimated to activate only the most sensitive channel were higher than weber fractions at acceleration magnitudes thought to activate both channels together. A significant interaction between amplitude condition and target channel was also observed ($F(1,15) = 35.4$, $p < .001$, $\eta_p^2 = .703$). This interaction was investigated using paired t-tests (with a Bonferroni corrected α of .0125). A significant difference was found between weber fractions for vibrotactile frequency in RA targeting conditions and PC targeting conditions in the 2-channel amplitude condition ($t(15) = 4.4$, $p = .001$), but not in the 1-channel amplitude condition ($t(15) = -2.5$, $p = .026$). A significant difference was also found between weber fractions for vibration frequency in PC channel targeting conditions in 1-channel amplitude conditions and 2-channel amplitude condition ($t(15) = 7.2$, $p < .001$), such that perception of frequency differences improved at the higher acceleration magnitude. No such difference in weber fraction was found between amplitude conditions in the RA channel targeting conditions ($t(15) = 1.5$, $p = .164$). These results are shown in Figure 33.

5.3.3 Post-hoc correlational analysis

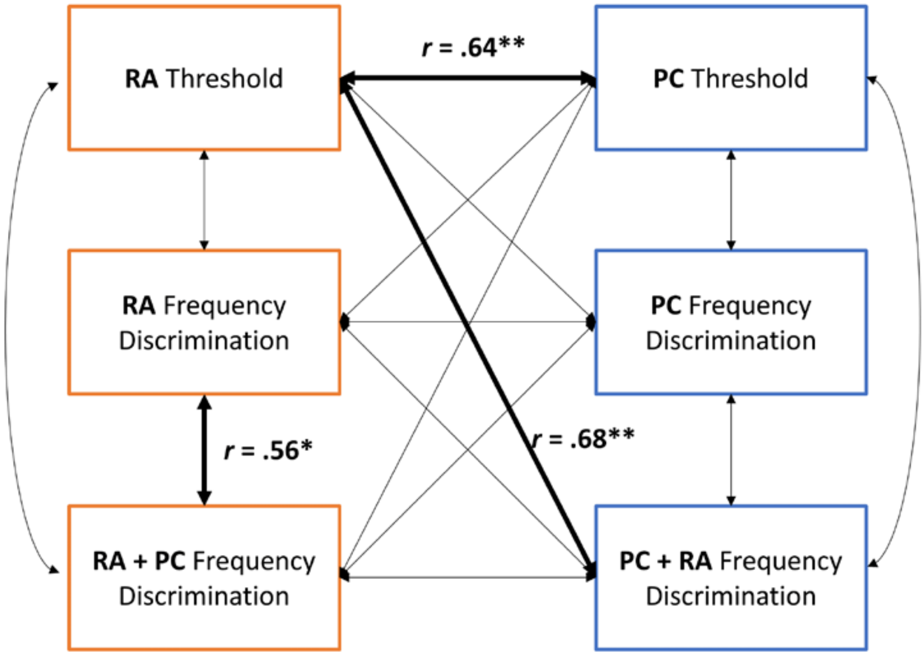

Figure 34. Correlations between performance in the 6 conditions across participants. Significant Pearson's correlations are printed in bold. The symbol * indicates significance at an alpha level of .05, ** indicates significance at the .01 level.

As an exploratory approach to investigate inter-subject variability in the study cohort across different experimental conditions, Pearson's product-moment correlation coefficients were calculated between all conditions. Significant correlations were revealed between: RA detection threshold and PC threshold ($r = .64$ $p = .004$), RA detection threshold and PC + RA mediated frequency discrimination ($r = .68$, $p = .008$), and RA mediated frequency discrimination and RA +PC mediated frequency discrimination ($r = .56$, $p = .025$). All other relationships were non-significant at the $\alpha = .05$ level. The correlations between performance in the 6 conditions are illustrated in Figure 34.

5.4 Discussion

In this study, Weber fractions for the perception of changes in vibrotactile frequency were found to be smaller in magnitude conditions thought to activate both the PC and RA channels than in conditions activating the PC channel alone. This is consistent with the belief that both of these channels are capable of encoding vibration frequency, and that highly discriminative touch depends on information from more than one channel in the tactile system.

Psychophysical investigations of touch perception have been largely dependent on absolute thresholds – the least amplitude of vibration that can be detected reliably. This approach has been effective at identifying the selectivity of the individual channels, and attributing the activation of particular channels to discrete functions (Johnson, 2001).

The results of this study showed that suprathreshold vibrations of parameters designed to activate the PC and RA channels alone and together result in different capacities to discriminate vibration frequency. This implies that as the number of recruited channels changes, the ability to discriminate vibration frequency at the finger also changes. This could be understood either as the takeover of the PC channel by the RA channel, which is more capable at frequency discrimination, or as the integration of two informative channels to provide a more accurate percept. Further research should be able to identify which of these mechanisms is more likely by extending our understanding of frequency discrimination in response to changes in frequency and amplitude across the sensitivity of the tactile channels.

The findings of this study have implications for the diagnosis of impaired tactile perception, which currently depends on absolute thresholds for the perception of vibration to identify the sensitivity of the PC and RA channels. This appears to be a useful part of a suite of diagnostic tools for identifying the sensorineural components of hand-arm vibration syndrome (e.g., Ye and Griffin, 2017). In day-to-day discriminative touch, however, the PC and RA channels are likely to be encoding the temporal properties of stimuli, rather than simply the presence or absence of vibration. More informative diagnostic tools would reflect changes not just in the absolute thresholds, but in the sensory processing that underlies feeling the texture of a surface or the manipulation and control of hand-held tools.

The results of this experiment go some way to explaining the highly varied frequency discrimination thresholds observed in previous studies. Those studies that used higher magnitude stimuli may have resulted in smaller Weber fractions for vibrotactile frequency because they recruited both the RA channel and the PC channel. Previous research has found difference limens for the perception of changes in frequency from 100 Hz as disparate as 3 Hz with a reported sensation level (SL) of 30 dB (Franzén and Nordmark, 1975), 21 Hz with 12 dB SL stimuli (Mahns *et al.*, 2006), and 118 Hz with 6 dB SL stimuli (Kuroki *et al.*, 2013). Differences in experimental design, contact area, and training may have influenced the previously reported thresholds, but it is likely that the stimulus magnitude was also a key factor influencing the large differences in vibrotactile frequency discrimination.

One question raised by the results of this experiment concerns vibration magnitude. Do the changes in weber fraction for vibration frequency that were observed in this study - whereby recruitment of an additional channel increases sensitivity to changes of the stimulus – also occur when the stimulus changes in its vibration magnitude rather than frequency. Because of the characteristic phase-locked response of the RA channel, it seems likely that recruitment of the RA channel may be especially able to enhance frequency but not magnitude discriminations. This hypothesis is addressed in Chapter 6.

In this experiment, the physical amplitude, rather than the subjective magnitude, of the vibration stimuli was controlled across subjects and frequencies. One possibility is therefore that the discriminations made by participants in this experiment were of changes in the subjective intensity of sensations elicited by vibrations of different frequency, rather than of changes in perceived 'pitch' or frequency. A good way to begin to address this question is to test participants ability to discriminate changes in acceleration magnitude in a closely comparable way.

One important limitation of this study is the failure to identify a notable pattern of correlations between performance in conditions thought to be mediated by distinct tactile channels. Part of the reason for this is a lack of variance in the measured thresholds across the participant cohort, which was likely caused by too large a step size in the staircase procedure. Chapter 6 builds on this methodology using a staircase procedure capable of greater precision.

5.5 Conclusions

The discrimination of changes in the frequency of vibration applied to the finger is more accurate when both the RA channel and the PC channel are activated than when only the PC channel is activated. This suggests that supra-threshold touch is supported by the joint action of the tactile channels, each with a different capacity to encode vibrotactile frequency. The findings emphasize the importance of the choice and control of the magnitude of vibration in psychophysical investigations of frequency discrimination, and have implications for psychophysical methods used in the diagnosis of impaired tactile perception. Subsequent research should address how this finding is paralleled in the discrimination of vibration magnitude, and examine the pattern of results in frequency discrimination in greater detail.

Chapter 6 Discrimination of the acceleration magnitude of vibration in the PC and RA channels

6.1 Introduction

To further investigate the validity of the threshold-based model of information processing in the tactile system, discrimination of suprathreshold acceleration magnitude will also be investigated in conditions mirroring those of experiment 2 – within and between the RA and PC channels. Unlike frequency, the 'intensity' of a vibration is thought to be encoded in the pattern of activity across channels, rather than in the temporal code of a single channel. This leads us to a set of parallel hypotheses, in which 1) the recruitment of further channels improves perception of amplitude differences, and 2) that concurrently measured thresholds predict amplitude discrimination difference limens.

In the previous studies, at high frequencies, weber fractions for vibrotactile frequency were significantly different at acceleration magnitudes designed to target either the PC-channel alone or both the PC and RA channel. It was found that a stimulus magnitude thought to additionally recruit the RA channel supported a significantly improved capacity to discriminate changes in frequency. This has the potential to facilitate a diagnostic method that assesses suprathreshold discrimination in the RA channel. One purpose of this study is to determine whether the capacity to discriminate changes in acceleration magnitude has a similar capacity to differentially measure the influence of the two channels.

In the previous experiment, the physical amplitude of the vibration stimuli was controlled across subjects and frequencies. One possibility is therefore that the discriminations made by participants were of changes in the subjective intensity of sensations elicited by vibrations of different frequency. The current study will begin to address this question by testing participant's ability to discriminate changes in acceleration magnitude in a closely comparable way and assessing whether weber fractions for frequency are smaller than for magnitude. This would suggest that there is a greater sensitivity to changes in frequency, implying that this is more likely to have driven better discrimination.

Like experiment 2 (Chapter 5), this study will recruit sufficient participants to investigate correlation between performances in different tasks, exploiting individual variability between participants as informative, rather than inconvenient. It uses an identical experimental design to control, as far as possible, for confounding factors of training, amplitude, response bias, and directional decisions. Illustrative data will be included to compare performance in frequency and amplitude discrimination for those participants who completed both tasks.

It was hypothesized that Weber fractions for vibrotactile magnitude would be smaller in the 2-channel magnitude condition than in the 1-channel magnitude condition. The effect of magnitude condition is expected to interact with the effect of target channel. This study also further advances experiment 1 and 2 by adapting the 3-interval 2AFC task to allow for the systematic variation of stimulus magnitude in an adaptive method of limits. The measurement of vibrotactile detection threshold into the 2-AFC task has been incorporated to be completed in parallel with the suprathreshold magnitude discrimination task and increases the precision of the threshold measure by reducing the size of the smallest step.

6.2 Methods

Amplitude difference limens were assessed in conditions targeting: the RA channel alone, primarily the RA channel with PC channel recruitment, the PC channel alone, and the PC channel plus RA recruitment. Detection thresholds were also measured in conditions targeting the PC channel and conditions targeting the RA channel. These conditions are summarised in Table 4. This experiment uses a similar procedure to experiment 2, with a 3-interval 2-AFC, 'odd one out' style procedure, and parallel 1-up 3-down staircase procedures for each condition.

6.2.1 Participants

Sixteen participants were recruited from the staff and students at the University of Southampton (9 male and 7 female, with an average age of 27.5 years [*SD* = 5.4). Six of the participants had previously participated in Experiment 2 (conducted approximately 2 months earlier), which followed an identical experimental procedure, and the remaining 10 participants were naive to the experimental procedure. All participants were naive to the aims and hypotheses of the experiment. On a screening questionnaire (Appendix A), the participants reported that they had no problems with their touch perception, and that they had not been exposed to vibration or taken medication that may have affected their sense of touch.

6.2.2 Apparatus

As in previous studies, vibration stimuli were delivered with two *HVLab* Tactile Vibrometers (VTT), having 10-mm diameter contactor and a 1-mm diameter contactors and rigid surrounds. The output of the VTT was calibrated using a Brüel and Kjaer calibration exciter (type 4294). During testing, participants maintained a constant 2N downward force on the contactor with the distal phalanx of their left middle finger using feedback from a force sensor. Pink noise was played to the participants over circumaural headphones at 75 dB to mask any auditory cues to the magnitude of the vibration stimuli. Visual cues to the timing of the presentation of the stimuli were shown on a computer monitor, and responses were made by clicking a mouse. All stimuli were controlled with custom MatLab software and monitored by the experimenter. Testing took place in a temperature-controlled room (21 ±1°C). The participants sat on one side of an opaque screen so that they could not see the experimenter or the control equipment.

6.2.3 Procedure

Participants completed a single two-alternative forced choice (2AFC) task that measured both weber fractions for discrimination of vibration magnitude and thresholds for the detection of vibration stimuli. Vibrotactile magnitude discrimination was measured in conditions designed to primarily activate two different tactile channels: a PC-targeting condition (10-mm contactor and 125 Hz stimuli) and an RA-targeting condition (1-mm contactor and 31.5 Hz stimuli). Performance in each condition was measured in two acceleration magnitude conditions (a 1-channel condition designed to activate only the target channel, and a 2-channel condition designed to activate both the target channel and the less sensitive channel). Vibrotactile detection thresholds were measured in two conditions, randomly interleaved into the magnitude discrimination task. As in Experiment 2, each trial type followed 3-down 1-up method of limits staircases, with the three staircases evolving in parallel.

The two frequency difference staircases had the initial magnitude of the 'target' plus 10%, and step sizes starting at 30% and decreasing in size by 5% with each reversal. The detection threshold staircase had the initial magnitude of the 'target' as 0.5 ms^{-2} r.m.s. with step sizes starting at 0.3 ms^{-2} r.m.s. and decreasing in steps of 0.05 ms^{-2} r.m.s with each reversal, and then the final reversal bringing the step size to a minimum of 0.01 ms^{-2} r.m.s. Each staircase was considered complete after 10 reversals or 60 trials. The difference limen was taken as the average of the 4th through to the 10th reversals.

The experimental protocol was approved by the University of Southampton Ethics Committee (ID: 41875).

6.2.4 Stimuli

As in Experiment 2, the standard stimuli were designed to exceed estimated thresholds for the relevant channels by 2x their acceleration (+6dB displacement). For two-channel discriminations, the target stimulus was of a lower acceleration magnitude than the standard stimuli, and for 1-channel discriminations the target stimulus was of a higher acceleration magnitude than the standards. This was to ensure than all stimuli were detectible (at low magnitudes) and unaffected by harmonic distortion in the waveform (at high magnitudes). All stimuli were 1-second long, with 0.05 second tapers at each end and 0.1 second ISIs. Example stimuli for the RA 1-channel amplitude discrimination and RA detection threshold task are shown in Figure 35.

Table 4. Summary of stimulus parameters. 'x+/-' indicates that this parameter of the stimuli is manipulated to find the minimum detectible change and the direction of that change. In practice most values will be just above x, and not exceed predefined limits of 5 ms^{-2}.

Description	Staircase #	Contactor	Frequency (Hz)	Amplitude (ms^{-2} r.m.s.)
RA channel threshold	1	1 mm	31.5	0+
1-channel (RA) amplitude discriminations	2	1 mm	20	0.17+
2-channel (RA+PC) amplitude discriminations	3	1 mm	20	1.78-
PC channel threshold	5	10 mm	125	0+
1-channel (PC) amplitude discriminations	6	10 mm	100	0.31+
2-channel (PC+RA) amplitude discriminations	7	10 mm	100	2.52-

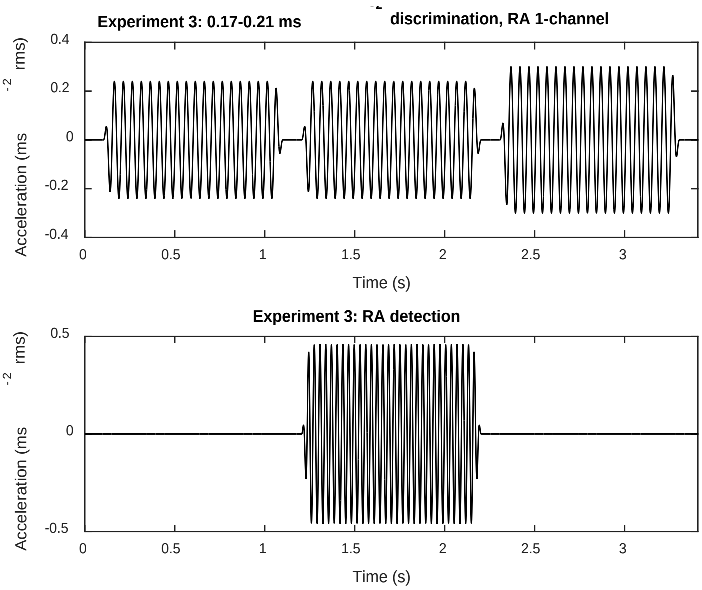

Figure 35. Top: example stimuli for the amplitude discrimination task in the RA only condition with the target stimulus in the 3rd interval, and a weber fraction of .25. Bottom: example stimuli for the detection task in the RA condition with the target stimulus in the 2nd interval

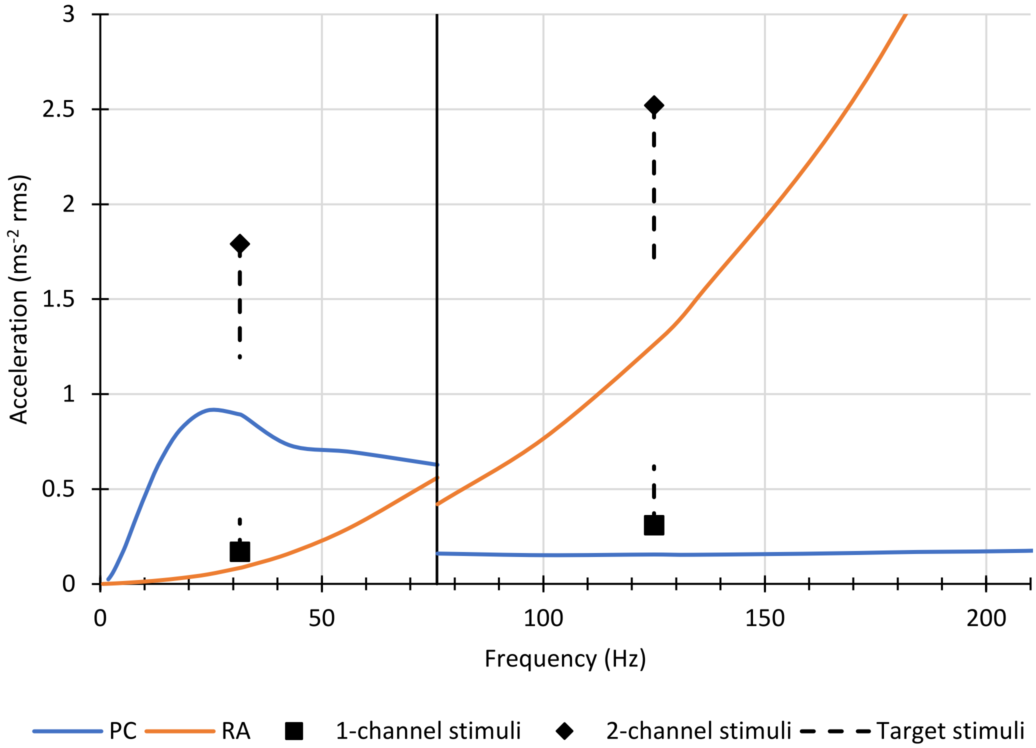

Figure 36. Estimates of tuning curves for PC and RA channels (solid coloured lines) in with the 1-mm contactor (left) and the 10-mm contactor (right), and the chosen stimulus magnitudes for standard stimuli (markers) and comparison stimuli (dashed lines) for 1-channel and 2-channel activations.

6.3 Results

Performance in each of the six conditions was measured as the mean of the 5th through 10th reversals. To illustrate this process, Figure 37 shows completed staircases for participant 1. The full set of individual data is presented in this fashion in Appendix D.

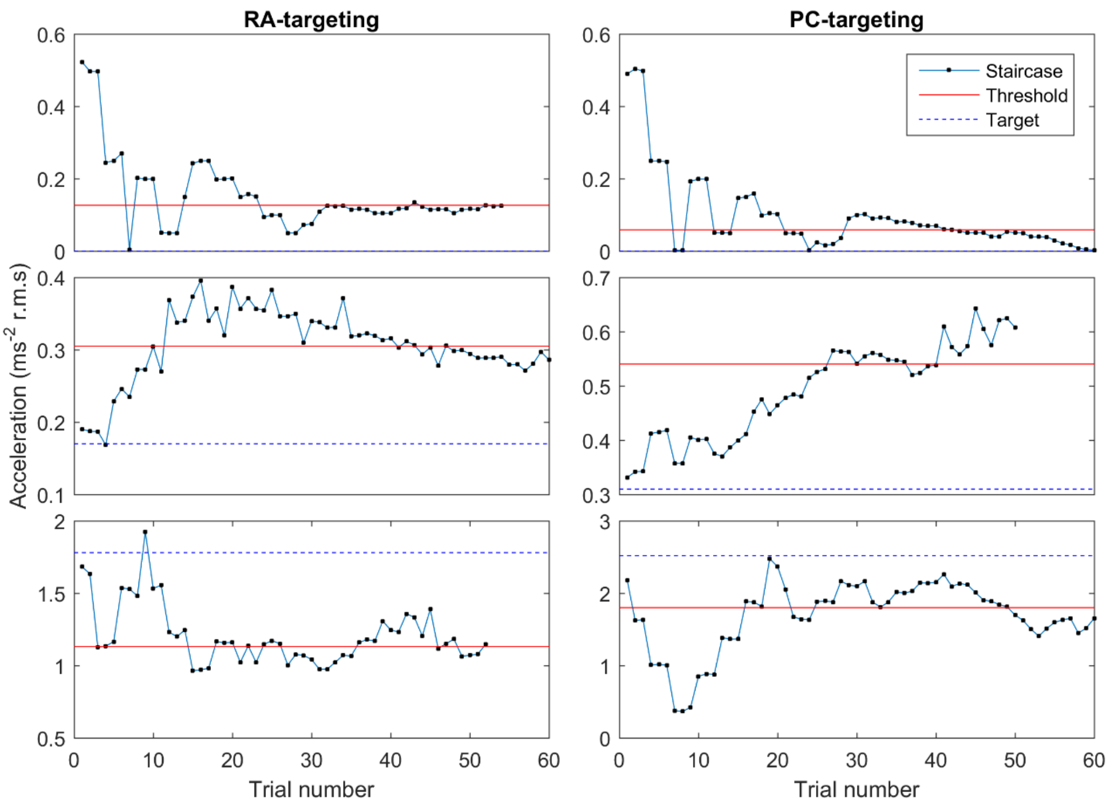

Figure 37. Completed staircase procedures in all 6 conditions for participant 1. The top two panels illustrate trials in the detection threshold task. The remaining panels illustrate performance in the frequency discrimination task, with the middle row representing performance in the 1-channel condition and the lower row representing performance in the two channel condition. For all panels the target value intersects with the x-axis, and test values vary depending on past performance following a 3-down 1-up procedure.

6.3.1 Detection Thresholds

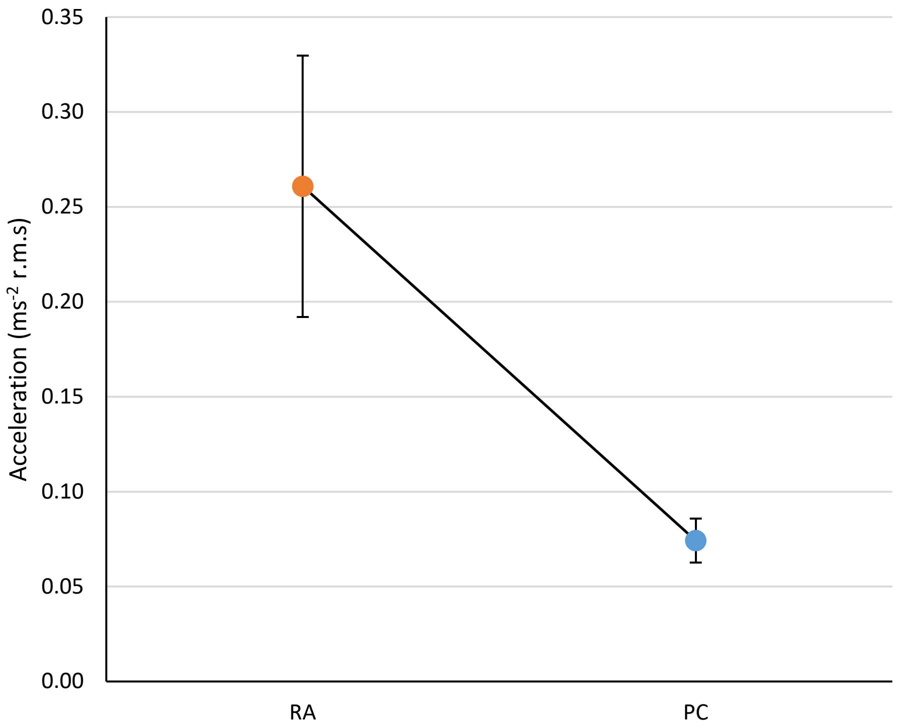

Figure 38. Mean detection thresholds in RA-targeting conditions (1-mm contactor, 31.5 Hz) and PC-targeting conditions (10-mm contactor, 125 Hz) expressed in acceleration magnitude. Error bars give the standard error of the mean.

As previously, a paired samples t-test was conducted to investigate differences in detection threshold in PC RA targeting conditions (1-mm contactor, 31.5 Hz) and PC-targeting conditions (10-mm contactor, 125 Hz). Similar to Experiment 2, thresholds were found to be significantly lower in the PC-targeting condition ($t(15) = 5.87$, $p < .001$). This is illustrated in Figure 38.

6.3.2 Vibration Magnitude Discrimination

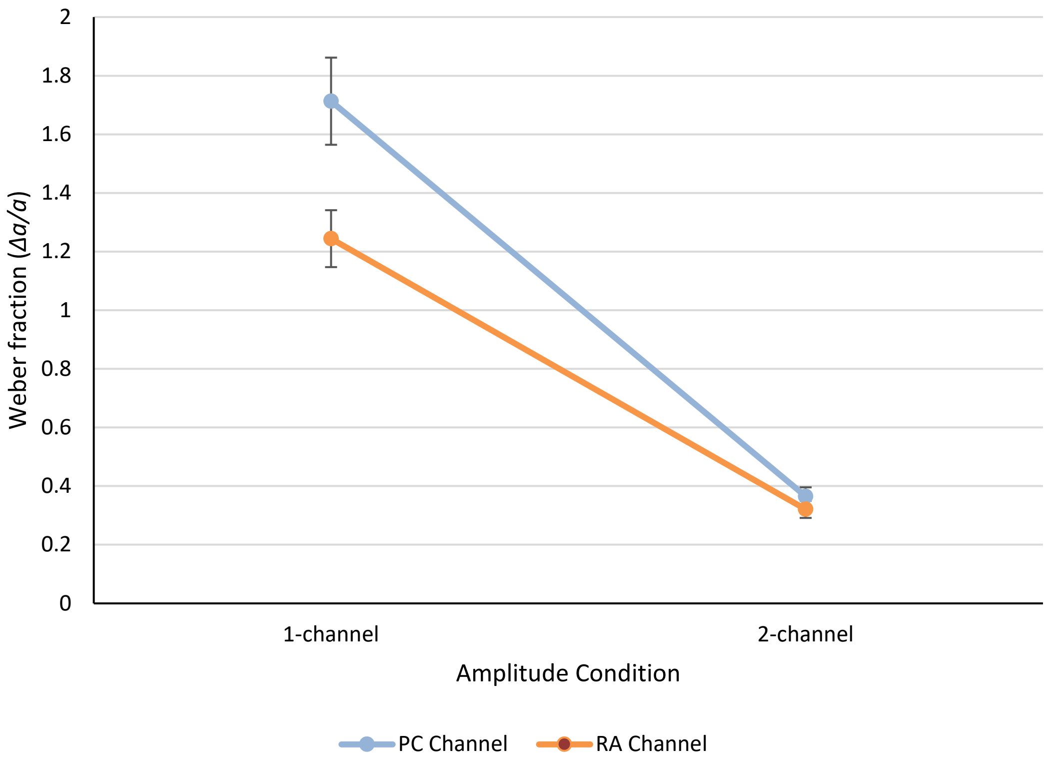

Figure 39. Mean weber fractions for vibration acceleration magnitude in two acceleration magnitude conditions. The RA channel targeting conditions used standard acceleration magnitudes of 0.17 (1-channel) and 1.78 ms^{-2} (2-channel) at 31.5 Hz and used a 1-mm contactor. The PC channel targeting conditions used standard acceleration magnitudes of 0.31 (1-channel) and 2.52 ms^{-2} (2-channel) at 125 Hz and used a 10-mm contactor. Error bars give the standard error of the mean.

A 2x2 repeated measures ANOVA was used to investigate differences in weber fraction for vibration acceleration magnitude with the factors target channel (RA or PC) and amplitude condition (1-chnnel or 2-channel). Significant main effects of target channel (F(1,15) = 12.8, p = .003, η_p^2 = .459) and amplitude condition (F(1,15) = 100.6, p < .001, η_p^2 = .870) were observed, as well as a significant interaction effect (F(1,15) = 9.3, p = .008, η_p^2 = .384). These effects were further investigated using paired t-tests (with a Bonferroni corrected α of .0125). This revealed that weber fractions were lower in the 2-channel amplitude condition for both RA targeting conditions (t(15) = 8.3, p < .001) and PC channel targeting conditions (t(15) = 8.9, p < .001). In the 1-channel amplitude condition, the weber fraction for the PC channel was significantly higher than for the RA channel (t(15) = 3.4, p = .004), but this was not the case in the 2-channel amplitude condition (t(15) = 1.1, p > .05).

6.3.3 Correlation analysis

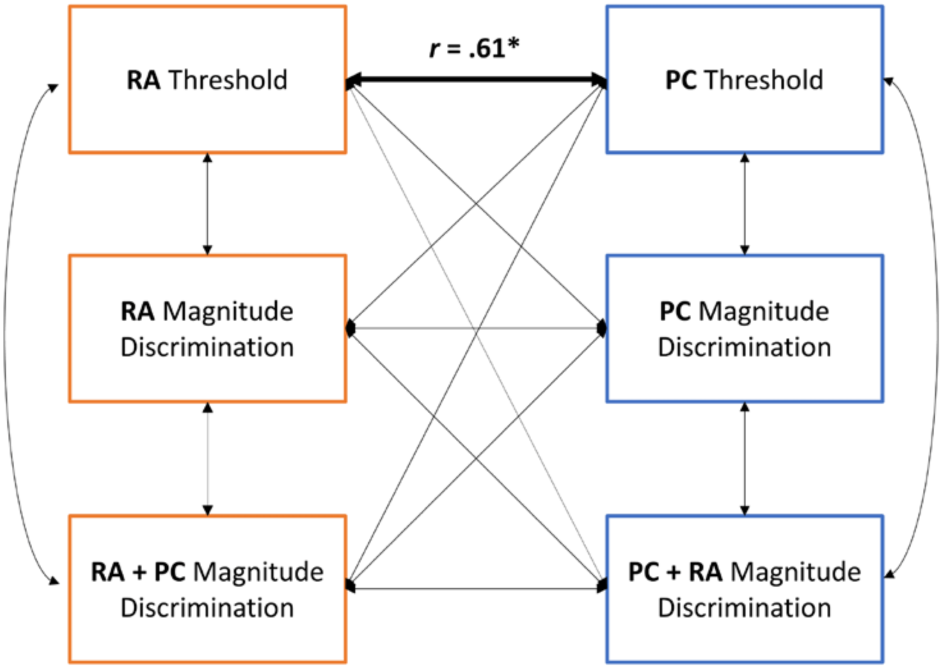

Figure 40. Correlations between performance in the 6 conditions across participants. Significant Pearson's correlations are printed in bold. The symbol * indicates significance at an alpha level of .05.

As in the previous experiment, exploratory analysis of correlations was conducted to investigate whether inter-subject variability varied systematically across experimental conditions, which could highlight shared variance in the results of the experiment as a function of target channel. Pearson's product-moment correlation coefficients were calculated between all conditions as an exploratory measure. Significant correlations were revealed between RA detection threshold and PC threshold (r = .61 p = .026). All other relationships were non-significant at the α = .05 level. The correlations between performance in the 6 conditions are illustrated in Figure 40.

6.3.4 Magnitude and Frequency Discrimination: Comparison with Experiment 2

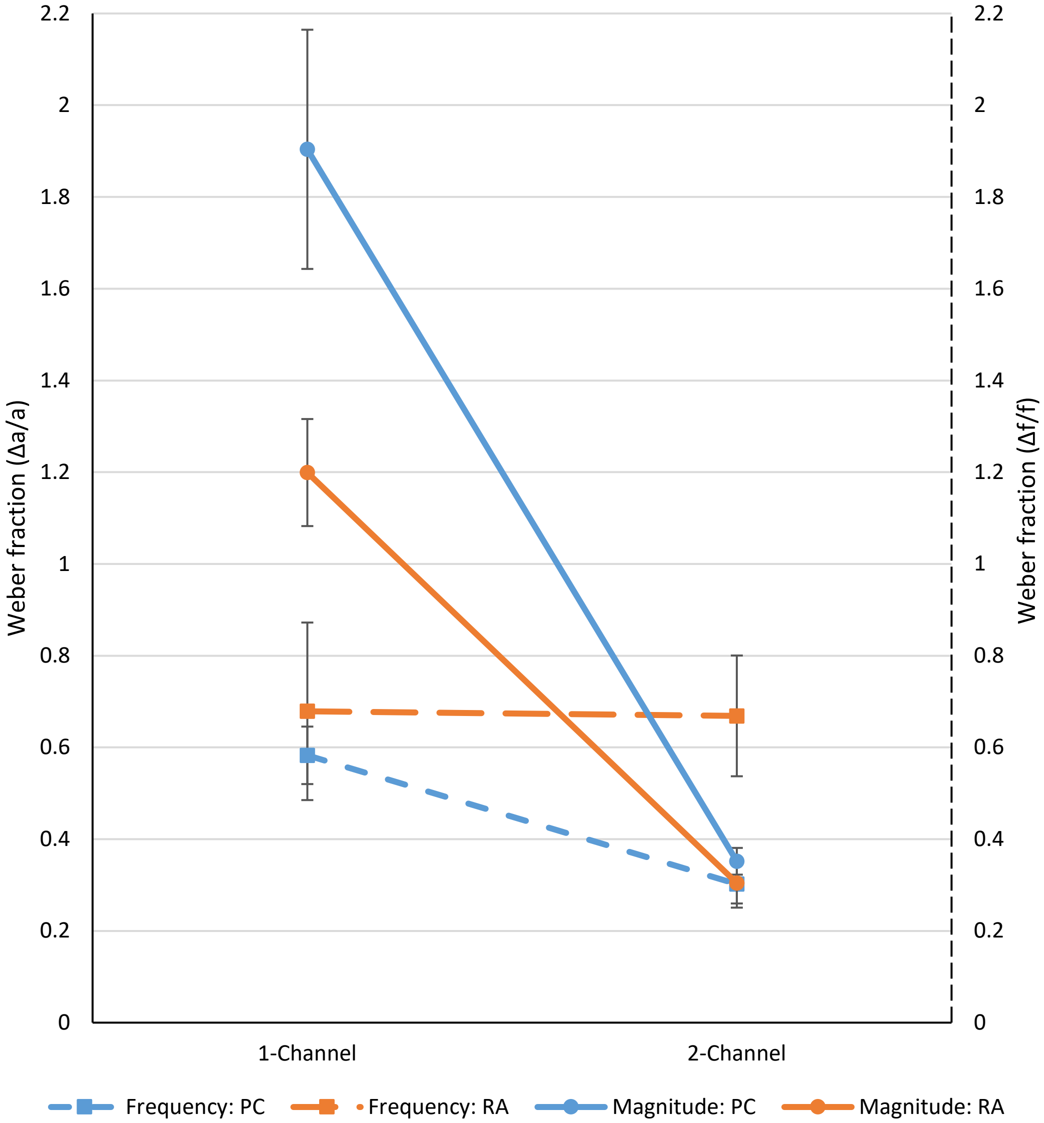

Figure 41. Mean weber fractions for vibration acceleration magnitude in two acceleration magnitude conditions (solid lines; this study) and mean weber fractions for vibration frequency discrimination in two acceleration magnitude conditions (dashed lines; study reported in chapter 5) in six participants who participated in both experiments. The RA channel targeting conditions used standard acceleration magnitudes of 0.17 (1-channel) and 1.78 ms^{-2} (2-channel) at a low frequency and used a 1-mm contactor. The PC channel targeting conditions used standard acceleration magnitudes of 0.31 (1-channel) and 2.52 ms^{-2} (2-channel) at a high frequency and used a 10-mm contactor. Error bars give the standard error of the mean.

Figure 41 shows the mean weber fractions for acceleration magnitude and frequency discrimination for the six participants who participated in both experiments. Because of the small sample size, this data is shown for illustrative, not statistical, purposes.

6.4 Discussion

In this study, Weber fractions for the perception of changes in vibrotactile acceleration magnitude were found to be smaller in magnitude conditions thought to activate both the PC and RA channels than in conditions activating the PC channel alone. This was the case at both low and high frequencies, with a very similar weber fraction being attained in both 2-channel conditions. These results are consistent with the theory that the encoding of magnitude differences depends largely on multi-channel activations. More generally this supports the idea that highly discriminative touch depends on information from more than one channel in the tactile system.

As previously, this study failed to identify correlations between performance in conditions thought to be mediated by distinct tactile channels. This was the case despite a smaller step size, and therefore greater precision, in the determination of detection thresholds compared to the previous study. It therefore seems likely that this design is unable to identify any systematic correlations between participants in the different conditions depending on the supporting tactile channels, and we are unable to reject the null hypothesis that there are no such relationships. It is possible that a much larger sample would be able to identify shared variance between conditions mediated by the same tactile channels.

Interestingly, in those participants who took part in both the previous study of frequency discrimination and the current study of magnitude discrimination, performance in the two-channel condition was remarkably similar at high frequencies. This may be due to similar cross-channel mechanisms in the discrimination of high magnitude stimuli. Importantly, weber fractions for frequency at low magnitudes were substantially smaller than for changes in acceleration magnitude, supporting the idea that the tactile system is far better specialised for discrimination of the temporal properties of low magnitude vibrations – as would be the case in the discrimination of fine surface texture – than of intensity.

One important limitation of this study is that the two-channel conditions had a different structure from the one-channel conditions. Because of the limitations of the vibrometer, it was necessary for test stimuli to be lower in magnitude than standard stimuli in the high-magnitude conditions, and higher than the standard stimuli in the one-channel conditions.

Although participants were naïve to which condition was which, and instead were instructed merely to identify an 'odd-one-out' stimulus, this difference may have induced systematic error into responses to these two conditions. This is a further reason to focus on frequency differences, that can be generated more reliably the magnitude differences within the range of human sensation by current equipment designed for diagnostic purposes.

An alternative approach to addressing the aims of this experiment could consist of a masking experiment (e.g. Geschieder & Verillo, 1983). Masking can be a powerful tool to reduce the activity of channel, to derive the activity of a less sensitive channel. This approach has been used to great effect in establishing the tactile channel model at threshold (Geschieder *et al.*, 2010), and could plausibly be applied to suprathreshold discrimination. However, this approach was considered inappropriate to the aims of this thesis due to: 1) the extensive testing involved to generate each data point, which would make the method difficult to adapt to a diagnostic application; similarly 2) the degree of participant training typically involved; 3) a severe lack of neurophysiological evidence regarding the effect of this form of stimulus on underlying mechanoreceptive systems. Together, these factors made a strong argument that the eventual use of these methods was outside the primary objectives of this thesis.

6.5 Conclusions

In this study, discrimination of vibrotactile acceleration magnitude exhibited a smaller weber fraction in a high baseline magnitude condition than at a lower baseline magnitude condition. This was the case at both low and high frequencies. This can be explained by more accurate perception of stimulus differences with the recruitment of an additional tactile channel.

Like magnitude discrimination, vibrotactile frequency discrimination exhibits a clear difference in weber fraction between discriminations mediated by one tactile channel and two channels . Importantly, this effect is only present when the second channel being recruited is the RA channel. This makes it a much better candidate for the development of a suprathreshold diagnostic procedure. Future studies should examine this change in weber fraction in more detail, identifying the frequency and magnitude of stimuli that recruit the RA channel, resulting in better discrimination of frequency.

Chapter 7 Discrimination of the frequency of vibration within and across the tactile channels

7.1 Introduction

The results of previous studies reported in this thesis have indicated that: 1) the tactile channels have different capacities to encode vibrotactile frequency, and 2) when frequency discrimination is supported by more than one tactile channel it results in smaller weber fractions. This experiment explores this effect in more detail by measuring the ability to discriminate frequency in a wide number of conditions, to identify whether crossing the boundary between one channel and more than one channel is marked by a concurrent improvement in frequency discrimination.

This experiment is a crucial step in the advancement of a model of vibrotaction in human glabrous skin that operates both at and above threshold. It builds on the idea of 'tactile channels' that are independent and selective, to identify whether these principles are robust above threshold to discriminative procedures. Specifically, this experiment builds on the results of experiment 2, as well as the other studies in this thesis, by: 1) adding further levels of acceleration and frequency to increase the precision of the findings, 2) investigating the prospect of a 'channel boundary' corresponding to the recruitment of a second tactile channel and associated with a 'step change' in weber fraction. Adding this knowledge will form a crucial part of the advanced model of suprathreshold discrimination in the tactile channels. Moreover, these ideas a central to the future development of a diagnostic tool that assessing tactile information processing within and across the tactile channels.

This experiment is directly relevant to the development of diagnostic tools for identifying impaired touch perception, as it provides a crucial foundation to the design of suprathreshold diagnostic tools. If this experiment is able to identify a clear difference between frequency discriminations mediated by the PC channel alone and by the additional action of the RA channel for example, this would allow us to design a test of whether - or at what magnitude - the RA channel is active and supporting frequency discrimination. Such a diagnostic tool would have a number of advantages over current methods that rely on vibrotactile detection thresholds. For instance, by being suprathreshold and discriminative, it has greater ecological validity. Importantly, because such a diagnostic tool would test the specialised function of the RA channel, rather than simply testing a measure of detection, this would a measure of relative impairment of the RA channel independently of the PC channel.

This experiment aims to build on and consolidate the results from the three previous studies by investigate the amplitude dependency of vibrotactile frequency discrimination. To do this, weber fractions for vibrotactile frequency were measured in 15 frequency-magnitude combinations, illustrated in Figure 42. These stimuli were chosen in order to investigate whether changing the number of recruited tactile channels affects weber fractions for vibrotactile frequency.

Previous studies in this thesis have provided evidence that the capacity to discriminate vibration frequency changes with stimulus magnitude and frequency. Therefore, for the initial analysis, it was hypothesized that:

- **H_1 1.0:** Amplitude affects weber fraction for frequency
- **H_1 2.0:** Frequency affects weber fraction for frequency
- **H_1 3.0:** Amplitude affects weber fraction for frequency differently as a function of frequency

These changes can be interpreted in terms of the changing combinations of tactile channels supporting suprathreshold discrimination. Therefore, for the 'channel-boundary' analysis, it was further hypothesized that:

- **H_1 1.1:** With changes in the magnitude of vibration, Weber fractions for frequency discrimination change when there is a change in the channel (PC or RA) mediating sensation. i.e. Mean weber fraction at a lower magnitude than the channel boundary is different from mean weber fraction at a higher magnitude than the channel boundary
- **H_1 2.1:** With changes in the frequency of vibration, Weber fractions for frequency discrimination change when there is a change in the channel (PC or RA) mediating sensation. i.e. Mean weber fraction at a lower frequency than the channel

boundary is different from mean weber fraction at a higher frequency than the channel boundary

7.2 Methods

7.2.1 Participants

Twelve participants (7 male and 5 female; with a mean age of 24.5 years [SD=2.29]) participated in this experiment. They were recruited from the staff and students of the University of Southampton. On a screening questionnaire (Appendix A), the participants reported that they had no problems with their touch perception, and that they had not been exposed to vibration or taken medication that may have affected their sense of touch. Each participant attended three experimental sessions of 1-hour duration on separate days, with no more than five days between the first and last sessions.

7.2.2 Apparatus

Vibration stimuli were delivered with a single *HVLab* Tactile Vibrometers (VTT) with a 1-mm diameter contactors and rigid surround. The output of the VTT was calibrated using a Brüel and Kjaer calibration exciter (type 4294). During testing, participants maintained a constant 2N downward force on the contactor with the distal phalanx of their left middle finger using feedback from a force sensor. Pink noise was played to the participants over circumaural headphones at 75 dB to mask any auditory cues to the magnitude of the vibration stimuli. Visual cues to the timing of the presentation of the stimuli were shown on a computer monitor, and responses were made by clicking a mouse. All stimuli were controlled with custom MatLab software and monitored by the experimenter. Testing took place in a temperature-controlled room (21 ±1°C). The participants sat on one side of an opaque screen so that they could not see the experimenter or the control equipment.

7.2.3 Procedure

In the first session, participants completed 7 vibrotactile detection threshold tracks using the von Bekesy algorithm described previously (section 3.7). This consisted of a 31.5, 40, 50, 80, 100 and 125 Hz sinusoidal vibration that steadily increased in amplitude (5 dB/second) until the participant responds by pressing and holding a button with their right thumb, at which point they gradually decrease at 3 dB/second until the participant released the button because they could no longer perceive the vibration, at which point the amplitude began to increase again. After 6 reversals, the mean of the peaks was taken as an estimate of threshold amplitude. This value did not determine the magnitude of any stimuli for the discrimination task but was instead employed at the analysis stage to categorize stimuli as 1- or 2-channel targeting.

For the remainder of the study, participants completed a single two-alternative forced choice (2AFC) task that measured both weber fractions for discrimination of vibration magnitude and thresholds for the detection of vibration stimuli. Vibrotactile frequency discrimination was measured in conditions across the frequency and amplitude range of interest. In previous experiments, each trial type followed 3-down 1-up method of limits staircases, with the staircases evolving in parallel and randomly interleaved. Each participant completed 15 staircases in total, with 5 selected at random for each session. Six participants also completed a randomly selected repetition of a staircase at the end of the final session, in order to measure test-retest reliability. The frequency difference staircases had the initial frequency of the 'target' plus 10%, and step sizes starting at 30% and decreasing in size by 5% with each reversal.

The experimental protocol was approved by the University of Southampton Ethics Committee (ID: 45174).

7.2.4 Stimuli

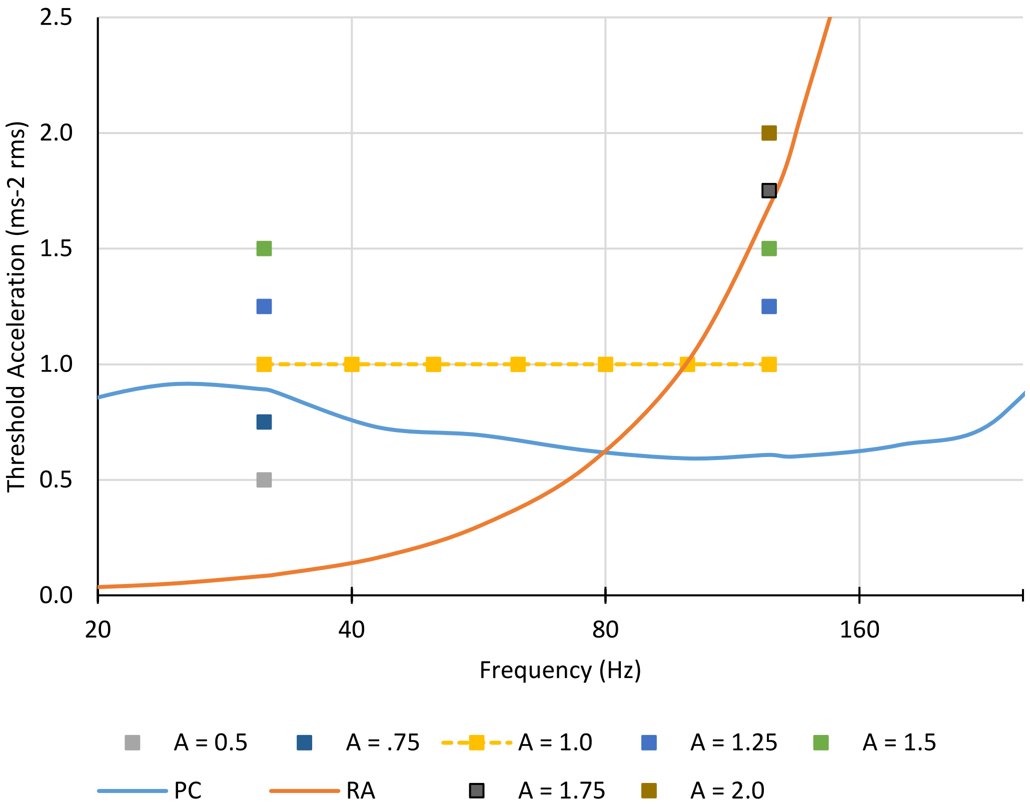

Figure 42. Summary of vibration stimuli and anticipated tuning curves for the PC and RA channels (based on historic data; Bolanowski *et al.*, 1988). Experimental stimuli were selected at 15 combinations of frequency and magnitude such that they are likely to cross the threshold of the less sensitive channel. The threshold for the PC channel will be crossed when magnitude is increased at 31.5 Hz, and the RA threshold will be crossed as magnitude is increased at 125 Hz, and as frequency is decreased at a constant magnitude (1ms^{-2} RMS). A = acceleration magnitude in ms^{-2} RMS.

The frequency and amplitude values of the test stimuli were chosen such that frequency discrimination is sampled across all 4 combinations of channels. By choosing sensation levels of between 0.25 and 1.25 ms^{-2} RMS above the participants thresholds, and measuring at half octaves between 31.5 and 125 Hz. This combination spans the 4 channel conditions.

7.3 Results

7.3.1 Initial analysis

Weber fractions for vibration frequency were measured at 31.5 and 125 Hz in 5 acceleration magnitude conditions (see Figure 43). A (5x2) repeated measures analysis of variance (ANOVA) was conducted, with the factors Frequency Condition (2 levels) and Magnitude Condition (5 levels). Individual data is presented in Appendix E. There was a significant within subjects interaction effect ($F(4,8) = 3.46$, $p = .015$, $\eta_p^2 = .24$), such that magnitude affects weber fractions differently at 125 Hz but not at 31.5 Hz, consistent with experimental hypothesis H_1 3.0. Main effects of Frequency Condition and Amplitude Condition were non-significant ($p > .05$).

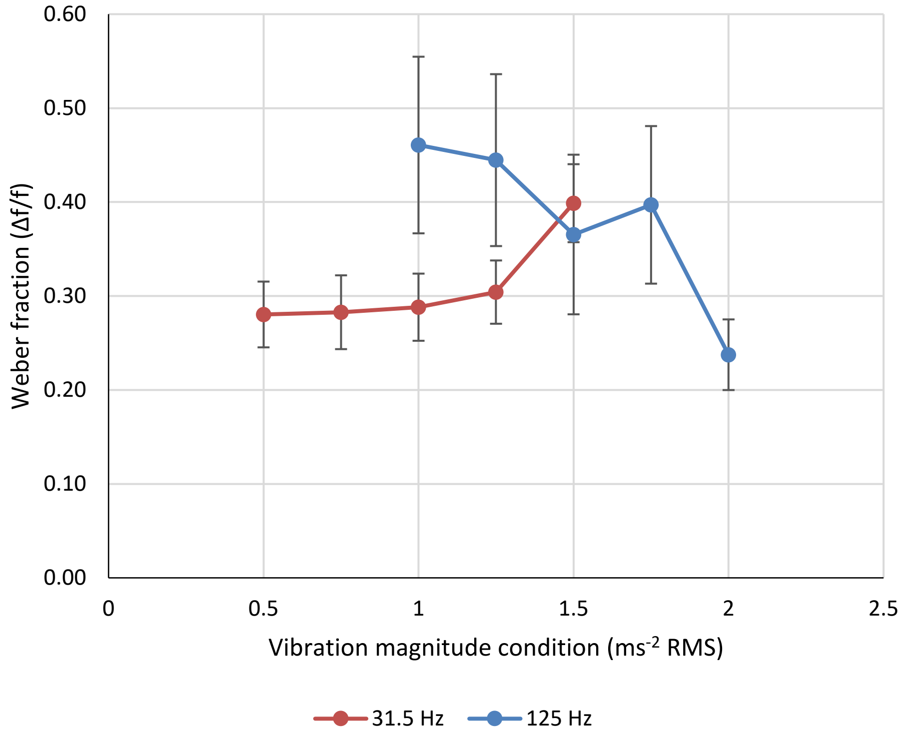

Figure 43. Weber fractions for vibration frequency at 2 frequencies (31.5 and 125 Hz) and 5 vibration magntide conditions at each frequency.

Weber fractions for vibration frequency were also measured at 1ms^{-2} RMS in 7 frequency conditions from 31.5 Hz to 125 Hz (see Figure 44). A (1x7) repeated measures ANOVA was conducted with the factor Frequency Condition. The data did not meet an assumption of sphericity ($\chi^2(20) = 47.3$, $p = .001$), so degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity ($\varepsilon = 0.41$). This analysis revealed a significant within subjects effect of frequency condition ($F(1,11) = 13.81$, $p < .001$, $\eta_p^2 = .56$), consistent with experimental hypothesis H_1 1.0.

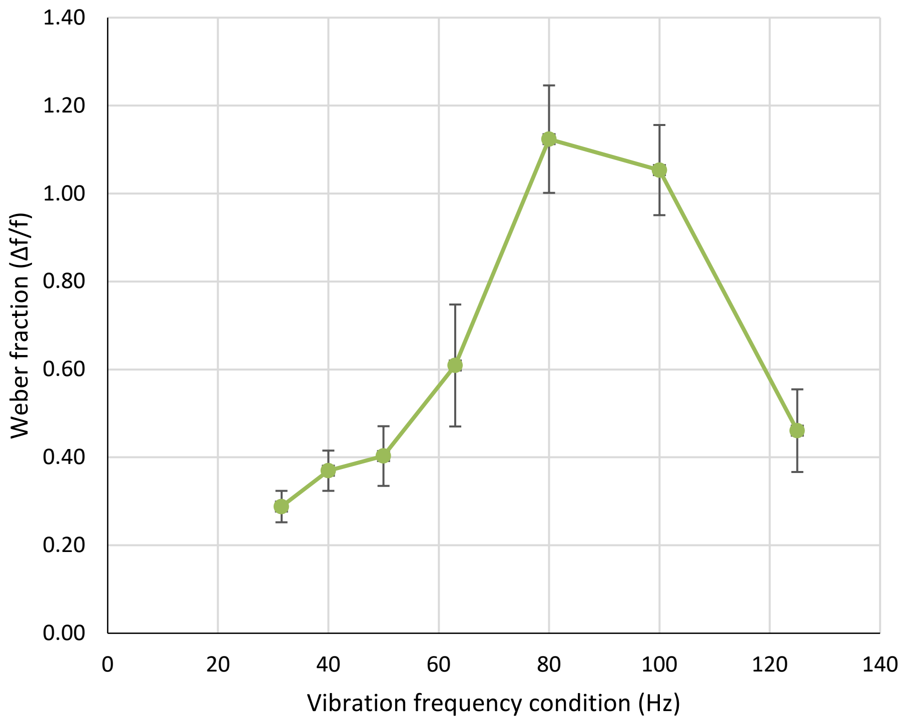

Figure 44. Weber fractions for vibration frequency for stimuli at 7 frequencies delivered at a vibration magnitude of 1 ms^{-2} RMS.

7.3.2 Channel-boundary analysis

Channel boundary analysis comprised comparison of weber fractions for vibration frequency between stimuli in 1-channel conditions compared with stimuli in 2-channel conditions, where 1-channel/2-channel status was based on whether the stimulus exceeded an estimate of the channel threshold for the less sensitive channel at that frequency.

To investigate whether weber fractions for vibration frequency vary depending on whether they are on different sides of a channel threshold, historic tuning curves for the PC and RA channels (from Bolanowski *et al.*, 1988) were first fitted to detection threshold measurements for each participant. Mean weber fractions above and below PC and RA curves for each participant are illustrated in Figure 45.Figure 45. A constant was applied to the RA curve to achieve a best fit with measurements at 31.5, 40 and 50 Hz – at which we assume the RA channel is the most sensitive, and mediates detection. The same process was applied to the PC curve to fit detection threshold measurements at 100 and 125 Hz – at which the PC channel is assumed to be the more sensitive channel, mediating detection. The fit of tactile channel tuning curves to individual threshold data is illustrated in Figure 105 through Figure 116. Weber fraction measurements were then categorized as belonging to 1-channel or 2-

channel conditions depending on whether the magnitude of the target stimulus was below or above the threshold for the secondary channel respectively. Specifically:

- At 31.5 Hz, weber fractions were categorized as being below or above the estimated sensitivity of the PC channel at that frequency.
- At 125 Hz, weber fractions were categorized as being below or above the estimated sensitivity of the RA channel at that frequency.
- At 1ms^{-2} RMS weber fractions were categorized as being below or above the estimated sensitivity of the RA channel at each of the 7 frequency points.

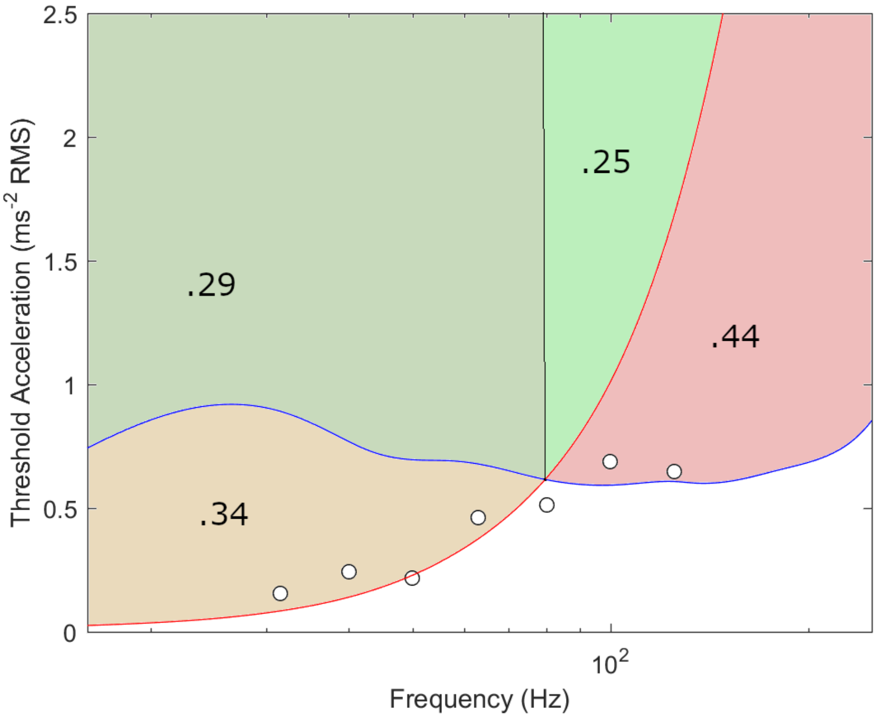

Figure 45. Mean weber fractions for vibrotactile frequency in 1-channel and 2-channel conditions. PC and RA curves were fitted to the detection thresholds (open circles) for each participant, although for this figure they are fitted to mean detection thresholds.

Mean weber fractions for vibration frequency in 1-channel and 2-channel conditions were then compared (see Figure 46) using paired samples t-tests. A significant difference was found between participants' mean weber fractions in 1-channel and 2-channel conditions at 125 Hz ($t(11) = 2.58$, $p = .026$, $d = .64$), such that weber fractions measured above the predicted PC threshold - i.e. the 2-channel condition - were significantly smaller than those below the PC threshold, consistent with experimental hypothesis H_1 1.1. No significant difference was found between mean weber fractions in 1-channel and 2-channel conditions at 31.5 Hz ($p > .05$). Note that 5 participants were excluded from this comparison either because none of their data points exceeded the PC threshold (P2 and P4) or all of their data points exceeded the PC threshold (P1, P3 and P5). There was also no significant difference between mean weber fractions for stimuli at 1 ms^{-2} RMS at frequencies where they exceeded both the RA threshold (2-channel condition) and frequencies where they fell below the RA threshold ($p > .05$), meaning that we cannot reject null hypothesis H_0 2.1.

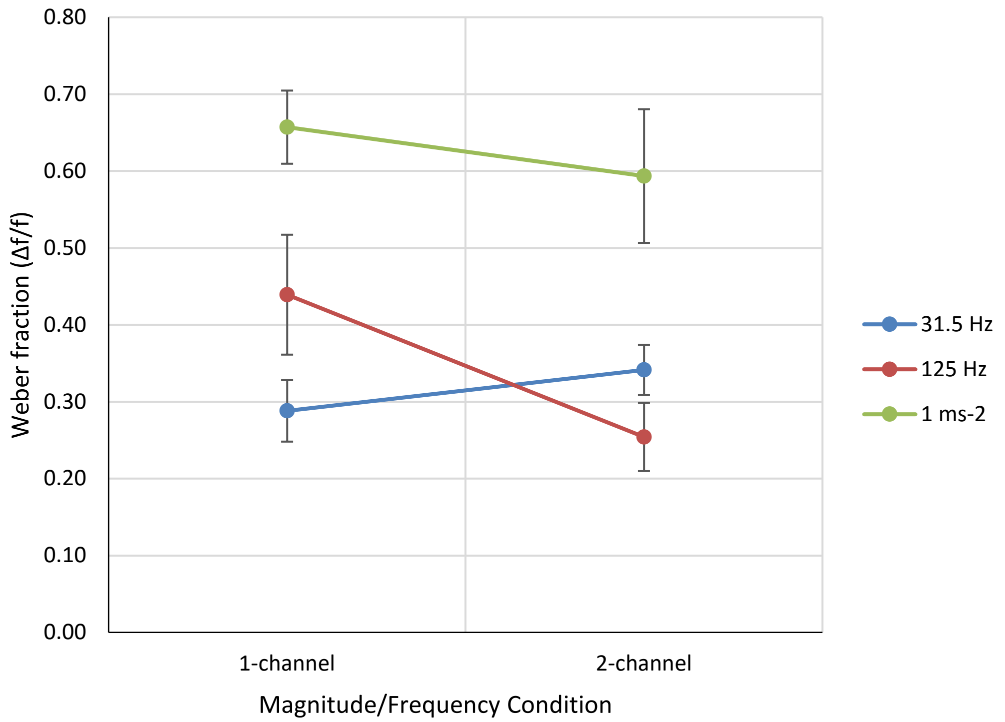

Figure 46. Weber fractions for vibration frequency in 1-channel and two-channel conditions. At 31.5 Hz the 1-channel condition is taken as the mean weber fraction for test conditions below the estimated PC channel.

7.3.3 Test-Retest Reliability

For 6 participants, an additional weber fraction was measured in order to assess test-retest reliability. A target stimulus was chosen randomly from the 16, and the additional staircase was conducted immediately after the completion of the main task. The mean time between completing the initial 'Test' of that staircase and the 'Retest' on the same stimulus was 1.5 days (SD = 0.96). The results from these staircases are presented in Table 5. Weber fractions determined at Test and Retest stages were found to be significantly correlated (R^2 = .89; p = .018), indicating high test-retest reliability.

Table 5. Summary of results for test and retest of a random staircase in 6 participants.

Participant	Staircase Conditions	Time between tests (days)	Test Weber Fraction	Retest Weber Fraction
7	125 Hz, 1.5 ms^{-2}	1	0.83	0.97
8	50 Hz, 1ms^{-2}	3	0.36	0.51
9	63 Hz, 1ms^{-2}	2	0.29	0.72
10	125 Hz, 1.5ms^{-2}	2	0.09	0.23
11	125 Hz, 1.75ms^{-2}	1	0.33	0.39
12	80 Hz, 1ms^{-2}	0	0.83	0.86
			R^2 = .89	

7.4 Discussion

Weber fractions for vibration frequency were also measured at 1ms^{-2} RMS in 7 frequency conditions from 31.5 Hz to 125 Hz. Analysis of these data revealed a significant within-subjects effect of frequency condition, consistent with the hypothesis that test frequency affects weber fractions for frequency. Weber fractions for vibration frequency were also measured at 31.5 and 125 Hz in 5 acceleration magnitude conditions. Magnitude was found to affect weber fractions differently at 125 Hz and 31.5 Hz. Crucially, a significant difference was found between participants' mean weber fractions in 1-channel and 2-channel conditions at 125 Hz such that weber fractions measured in the 2-channel condition were significantly smaller than those in the 1-channel condition.

At 31.5 Hz, weber fractions were that categorized as being below or above the estimated sensitivity of the PC channel did not significantly differ in weber fraction, which may indicate that the recruitment of the PC channel does not improve discriminations that are already mediated by the RA channel.

At seven frequencies from 31.5 to 125 Hz and 1 ms^{-2} RMS, weber fractions were that categorized as being below or above the estimated sensitivity of the RA channel not significantly differ in their weber fraction. On inspection, there appears to be an elevated weber fraction for frequency at 80 and 100 Hz compared to lower frequencies, but that this may have been mitigated by a relatively low weber fraction at 125 Hz. It is not known why the stimulus at 1ms^{-2} RMS and 125 Hz resulted in a relatively low weber fraction consistently through the study, and it should be noted that this may not be consistent with the hypothesized two-channel model. These results may have been due to the specific choice of 1 ms^{-2} RMS across the frequency range, and could be explored through a study that collected data at a wider range of magnitudes and frequencies. This form of study was considered inappropriate for this project because of the duration of testing that would have been required from each participant. It may also be advantageous to incorporate further tactile channels into the model of frequency discrimination. Though the existing neurophysiological evidence does not support their sensitivity to changes of vibration frequency, they may have captured differences in concordant alterations in another stimulus parameter.

Collectively, this study supports the conclusion that the recruitment of the RA channel supports finer discrimination of frequency differences than the action of the PC channel alone. This detectable change in sensitivity to frequency differences at high frequencies as a function of acceleration magnitude has a number of important implications for our model of the tactile channels, as well as for how we measure the sensitivity of the channels for the diagnosis of impaired touch perception.

There is substantial evidence that both the PC and RA channels are encoders of vibrotactile frequency, contributing extensively to texture perception and tool use (e.g. Johnson, 2001). However, the action, and interaction, of these tactile channels suprathreshold has not previously been well characterized. Gescheider, Bolanowski & Verrillo (2004) wrote that:

> *"… fundamental questions remain concerning the nature of how these channels, with their individual properties, operate together in the perception of tactile stimuli encountered in the natural environment. We hypothesize that suprathreshold stimulation of a sufficiently high intensity level to activate all of the channels is associated with tactile perceptions that result from an integration in the central nervous system of the activities of the separate channels."* (Gescheider *et al.*, 2004: pg.39)

The results of this study provide some evidence that the recruitment of the RA channel in addition to the PC channel at a higher acceleration magnitude directly supports finer discrimination of frequency differences at a behavioural level. Future work across a wide variety of disciplines might characterise this effect in detail across the full frequency-magnitude space to which the tactile system is sensitive, characterise the neural mechanisms of this recruitment and summation, and determine whether this effect is reflected in the behaviours of "active touch" (Lederman & Klatzky, 1987).

Equally, this finding has important implications for diagnostic methods. A practical, suprathreshold measure of channel sensitivity could allow offer a number of important insights into sensorineural disorders affecting the action of the tactile channels. It would allow, for example, for perception mediated by the RA channel to be distinguished from that mediated by the PC channel, which has a poorer capacity for frequency discrimination, and the Slow adapting (SA) channels which do not encode frequency. It would also have key advantages in reducing or eliminating response bias, and ensuring maximal ecological and face validity. These prospects are detailed in Chapter 8.

This study also served to confirm the reliability of the experimental procedure. For six of the participants, an additional weber fraction was measured at a second time point to assess test-retest reliability. Weber fractions determined at Test and Retest stages were found to be significantly correlated, indicating high test-retest reliability. It can therefore be considered likely that previous studies reported in this thesis—which used a very similar experimental paradigm and population—had similarly high levels of reliability.

7.5 Conclusions

In this study, vibrotactile frequency discrimination was found to exhibit a clear difference in weber fraction between discriminations mediated by one tactile channel and two channels. This result builds on the results of previous studies reported in this thesis to identify how this effect varies across the frequency and acceleration magnitude of the test stimuli. The results support the hypothesis that the recruitment of the RA channel results in a step change improvement in the capacity to discriminate vibrotactile frequency. This has important implications for diagnostic practice that aims to identify and measure impaired touch perception.

Chapter 8 General Discussion

This thesis has reported four psychophysical experiments that aimed to elucidate and evaluate suprathreshold information processing in the RA and PC tactile channels. The results of these studies are combined to advance a model of frequency discrimination in the tactile channels that can be used to further methods for the diagnosis of impaired touch perception by providing a measure of RA-mediated perception, differentiated from a detection threshold mediated by 'the most sensitive channel at that frequency' (per e.g. Gescheider 2010). Moreover, this model of information processing in the glabrous skin of the human hand has already been widely applied to haptic technology and the generation of augmenting signals for the perception of speech and spatial location by CI users (Chapter 9).

8.1 Frequency discrimination within and across the RA and PC channels

The first experiment (Chapter 4 instantiated a two-alternative forced-choice paradigm for vibrotactile frequency discrimination and investigated whether contact area affected the sensitivity of two tactile channels at two frequencies. Although mean weber fraction for frequency discrimination did not differ significantly on small and large contactors, the results from individual participants support the differential activation of target channels resulting in different WFs across conditions. This was supported by a correlational analysis that showed that probable PC-mediated frequency discriminations cross-correlated across conditions, whereas RA-mediated discriminations did not.

The second experiment (Chapter 5) built on this work to directly investigate the effect of recruiting additional channels on the sensitivity to frequency differences. Mean weber fractions for vibrotactile frequency discrimination were found to be significantly smaller at acceleration magnitudes designed to activate both the RA and PC channels than the PC channel alone. This supports the hypothesis that the RA channel had a greater sensitivity to vibration frequency, and provides evidence for the general thesis that cross-channel coding supports discriminative touch.

The third experiment (Chapter 6) investigated whether this finding was paralleled in the discrimination of acceleration magnitude. Again, the recruitment of a second tactile channel was found to support the discrimination of suprathreshold acceleration magnitude differences at a smaller weber fraction. Unlike the discrimination of frequency, this was found to be the case at both low and high frequencies, suggesting that the recruitment of an additional tactile channel – either the PC or RA channel – supported better discriminative performance than the other channel acting alone. Frequency was determined to be of greater diagnostic relevance than acceleration magnitude for this reason, as it theoretically allows for discretisation of PC- and RA-mediated discrimination. Post hoc correlational analyses

The fourth experiment (Chapter 7) investigated the channel dependency of frequency discrimination in more detail across a range of both frequency and magnitude. We found that, as the number of tactile channels recruited increased with magnitude to the point where the RA channel was recruited, this resulted in a step change in weber fractions for frequency discrimination. This supports the hypothesis that the recruitment of the RA channel corresponds to a substantial increase in the capacity to discriminate vibration frequency. This has clear implications for diagnosis of impaired touch perception, as it would allow the direct assessment of RA mediated frequency discrimination. This would have major advantages over the current methodology, as it would have greater ecological validity, closer correspondence to the normal action of the channels, and a clearer relationship to the purported action of the neurophysiological structures involved.

The results of these studies demand the development of a novel suprathreshold, diagnostic model of the tactile channels, which can be applied broadly to improve the effectiveness of vibrotactile applications in diagnostics d translational medical science.

8.2 Advancing a diagnosis model of the tactile channels suprathreshold

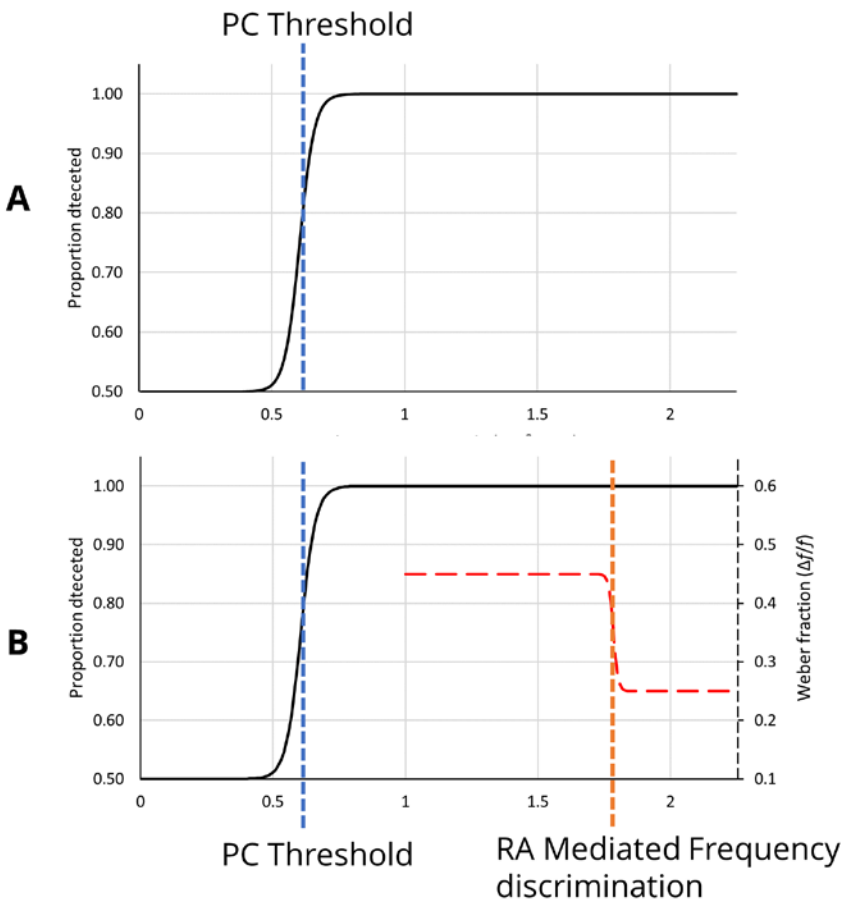

Figure 47. Panel A illustrates the existing threshold measure tool, in which a measured detection threshold provides an estimate of tactile sensitivity, and this threshold is ascribed to the absolute threshold of the most sensitive channel at that frequency. Panel B illustrates a two-level diagnostic psychophysical model, in which the activation of the most sensitive channel, and therefore detection of the stimulus, is supplemented by the measurement of an acceleration magnitude at which a particular weber fraction for vibration frequency is measured, which provides a metric of RA sensitivity.

The results of the studies reported in chapters 4-7 of this thesis provide strong evidence that, in healthy touch, the recruitment of the RA channels occurs at an acceleration magnitude somewhat above the PC threshold, and corresponds to a step change in weber fraction for frequency discrimination. This observation provides a measure of RA sensitivity that can be used in addition to a vibrotactile detection threshold (Figure 47). In the application of this diagnostic model, the standard high frequency vibrotactile detection threshold would be used to estimate the absolute sensitivity of the tactile system to 125Hz vibration, which would be taken to be the absolute sensitivity of the PC channel. By additionally measuring the acceleration magnitude at which the recruitment of the RA channel mediates a step increase in frequency weber fraction, we would also identify a measure of the sensitivity of the RA channel. This would not only serve to independently identify the sensitivity of two tactile channels, but also provide a crucial disambiguating measure when vibrotactile detection thresholds fail to identify, or misidentify, an underlying disorder of discriminative touch (this is illustrated in Figure 48 and Figure 49).

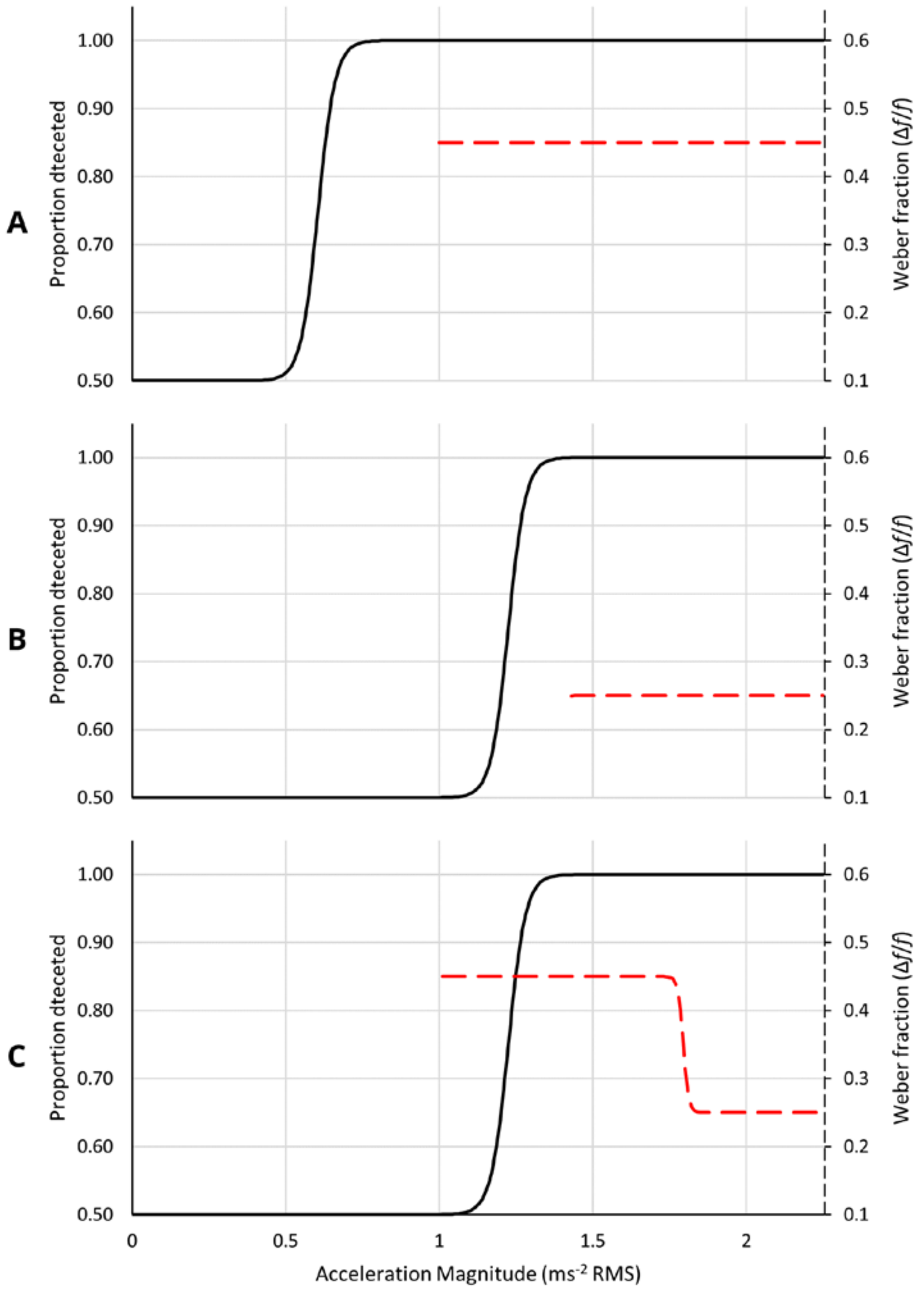

Figure 48. Examples of tactile threshold configurations in which a two-level diagnostic psychophysical model could provide nuance or further information to a diagnostic test battery. Panel A illustrates a scenario in which the participant exhibits a 'normal' absolute threshold, but exhibits no RA-mediated frequency step, suggesting that the RA channel

may be impaired. Panel B illustrates an elevated PC-mediated threshold but functioning RA response. Panel C illustrates an elevated threshold but normal suprathreshold frequency perception, which may indicate error or ambiguity in the measurement of the detection threshold.

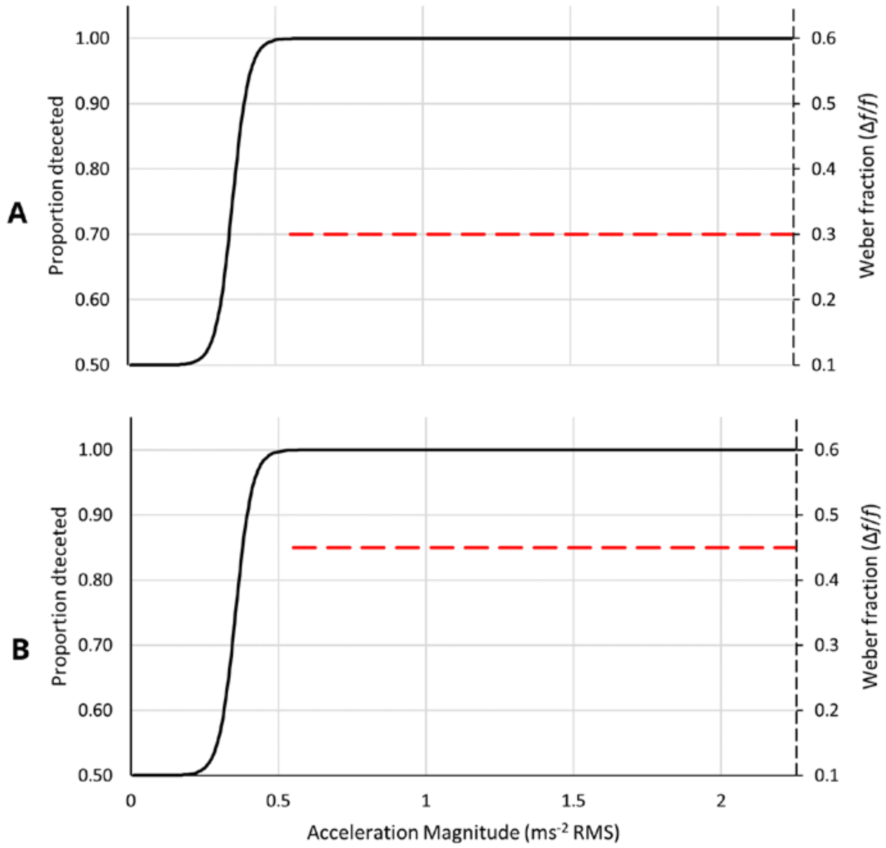

Figure 49. Examples of further two-level diagnostic psychophysical model results. Panel A illustrates RA-mediated detection and frequency discrimination. Panel B illustrates how the second level allows us to identify PC-mediated detection and frequency discrimination at 31.5 Hz, which would not be identifiable from detection thresholds alone.

8.3 Piloting a candidate suprathreshold test of RA activity

The model described here is based on the finding that the discrimination of fine (e.g. .3 WF) and coarse (e.g. .7 WF) frequency differences are dependent on the recruitment of the RA channel at an acceleration magnitude above the absolute threshold for vibration detection. It ought to be possible to create a psychophysical procedure that identifies this acceleration magnitude, thereby measuring the sensitivity of the RA channel suprathreshold. Such a procedure was piloted in the course of the research for this PhD, and is presented in brief here.

In the discrimination task the target was the interval in which a vibration of a different frequency was presented. In this version of the 2-AFC task used throughout the thesis, the staircase adaptively varies the acceleration of all three vibrations depending on whether frequency discriminations are made correctly. The staircase followed the same 3-down 1-up strategy as previous experiments; stimuli were 1-second sinusoids of 20, 60, 100 Hz; responses were made with a computer mouse; 75dB white noise was presented through close-backed circumaural headphones to eliminate subtle auditory cues to vibration frequency. It is anticipated that fine frequency differences will be reliably perceived at higher accelerations above threshold than coarse ones. Fine frequency differences will be reliably perceived at higher accelerations than coarse ones.

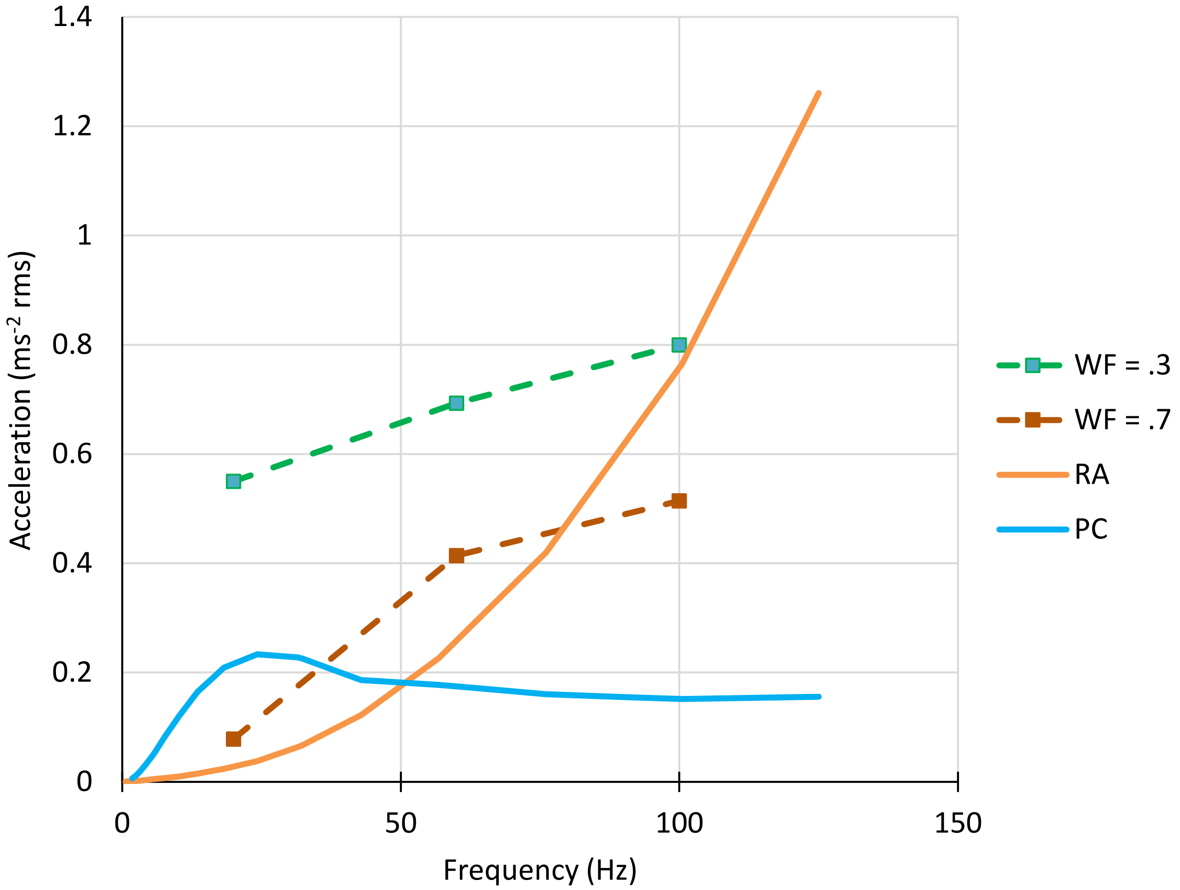

Figure 50. Data from one participant of 6 staircases that identified at what acceleration magnitude a fixed frequency difference could be discriminated. Data was collected at 3 frequencies and 2 weber fractions for frequency (points and dashed lines) and plotted with estimated tuning curves for the RA and PC channels on a 10mm contactor (solid lines).

Figure 50 shows pilot data for 6 staircases that identified at what acceleration magnitude a fixed frequency difference could be reliably discriminated. As data was collected from only one participant, statistical tests are not appropriate or informative, but preliminary data suggests that across the frequency range, a greater magnitude of vibration stimuli is required for smaller frequency differences to be reliably discriminated. Figure 51 shows the staircases from which these weber fractions were derived.

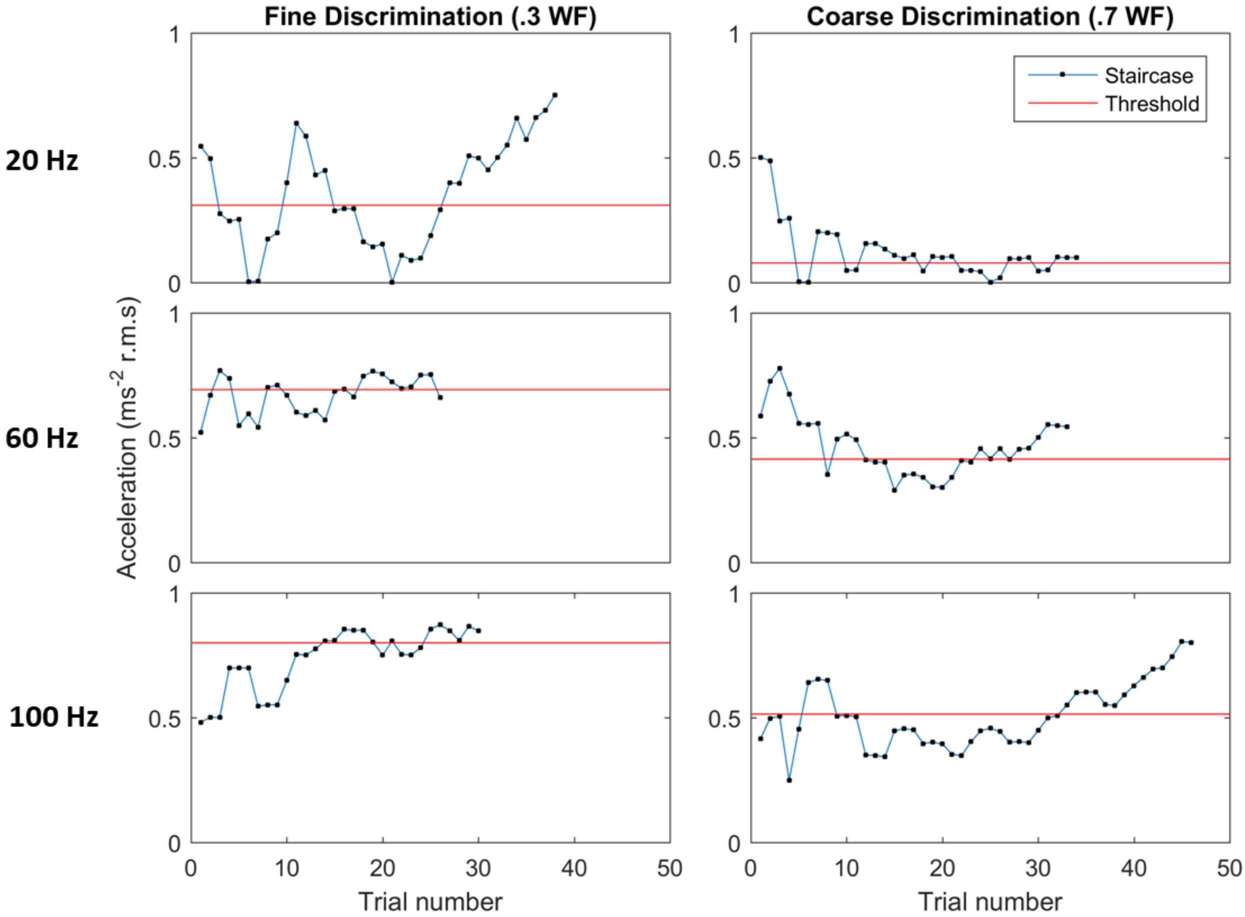

Figure 51. Completed staircases for one participant in a candidate diagnostic procedure.

8.4 Limitations of this research

All research has limitations in methodology, analysis and scope; the research reported here is certainly no exception. In addition to limitations specific to each experiment – which are reported in the discussion section of their respective chapters - the following key limitations should be considered in the interpretation of this research.

Suprathreshold discrimination of vibration properties was selected as an improvement over detection thresholds in that it more closely resembles the function of the tactile system in everyday touch. Nevertheless, a lack of **ecological validity** can be considered a limitation of this research, as it necessarily involves highly constrained experimental conditions, in artificial touch environments, that control for many of the factors present in normal touch. These variations might include hand and body movement, multi-sensory input, variations in temperature, and exposure to desensitizing or damaging vibration. Future research is required to expand the findings of the studies reported here to the real world, with all the challenges that entails.

The experimental methods used in this research project had the aim of reliably identifying 'thresholds' for perception, at which performance reaches a pre-specified level (e.g. 50%, 75%, or 79.6%). The final results generated are therefore somewhat vulnerable to particular patterns of **participant error** or **procedural limitations** caused by the need for rapid, reliable, testing of many conditions. Analysis of experiment 4 provided key evidence of high test-retest reliability, although caution must be taken in assuming a high-degree of other forms of reliability or validity beyond those for which the tasks were designed.

The **sample** sizes employed in this study were generated through power analyses in order to detect an effect of a pre-specified size. Power analyses necessarily rest on assumptions of the distribution of the study population, which may not be accurate. Moreover, the experiments reported in this thesis usually recruited a relatively small number of healthy people of a limited age range, and care should be taken in applying the findings presented here to the broader, more diverse, general population, and to populations of people with sensorineural impairments.

As is other studies of human vibrotactile sensation, the results of studies reported in this thesis were vulnerable to **high levels of variability**. Between subjects, substantial variability was observed between results in identical or closely related test conditions. Here, every effort was made to limit variability through experimental controls, and to identify if this inter-subject variability reflected true individual differences in sensitivity through exploratory analyses of correlations. However, it remains unclear what unobserved factor(s) caused these differences, or whether testing procedures were vulnerable to error. Intra-subject, a high degree of test-retest variability was observed, indicating the reliability of the testing methodology over short timescales.

Frequentist inferential statistics were employed throughout the thesis, in order to generate estimates of statistically significant effects. Effects sizes are also reported throughout. This has allowed the findings to be better understood by most researchers in relevant fields, and the harmonisation of the approach with the history of the subject. Nevertheless, the reporting of Bayes factors is considered by many researchers in psychology and neuroscience to be a preferred approach (Wagenmakers *et al.*, 2018), and future research may wish to re-examine the data or findings of this thesis in the light of probabilistic Bayesian statistics.

Many of these limitations are inherently linked to the historical and practical setting of **psychophysics** as a methodology for investigating sensory systems. The findings of this research will need to be cross-validated and interrogated through the use of a wide range of other approaches, including micro-neurography, neuro-imaging, prospective clinical trials, and approaches from the humanities.

The psychophysical approach employed here has rested on a set of **assumptions about the function of the tactile channels**. Many of these assumptions are long-standing principles in tactile neuroscience and the multi-channel model. These assumptions include: the independence and selectivity of the tactile channels, the recruitment of further channels with increasing magnitude of stimulation, and the ideas that the most sensitive channel in particular conditions mediates detection and that it is the later integration of the channels that drives everyday perception. Although these assumptions are fairly well evidenced, the possibility remains that some other approach provides a more parsimonious explanation for the observed phenomena, which in turn would have a significant bearing on the interpretation of the data collected in the experiments reported here.

One final key limitation of these studies is that they have been constrained to the experimental testing of the PC and RA channels, as these were selected on the basis of having a key involvement in the discrimination of vibration frequency, and therefore of the perception of surface texture. It was determined at an early stage that the selective stimulation of the SA1 and SA2 channels, as well as of **other sensorineural systems** within the skin (e.g. thermoception, nociception, and the action of tactile sensitive c-afferents) was beyond the scope of the project. More importantly, just because these sensory systems were not targeted, does not mean they were not active and contributing to the perceptual decisions made by participants.

8.5 Applications and further research

Gaining a deeper understanding of information processing in the tactile system, particularly the discriminability of vibratory stimuli, has a number of applications. A psychophysical approach can help describe how we feel objects and surfaces, how and why tactile perception fails and what can be done to treat it, and the encoding and delivery of information through the skin.

8.5.1 Perceptual research

By investigating the relationship between tactile perception at threshold and above threshold this research contributes to basic curiosity-driven questions in psychology and neuroscience. It may also provide a useful framework in which we can make links between information processing in different modalities – such as parallels between the psychophysics of touch and the psychophysics of visual perception – as well as in cross-modal perception.

8.5.2 Diagnostics and Biomedical Science

A robust model of information processing aids the understanding and treatment of diseases affecting the tactile system – if we see the conditions the system fails under, we may be able to identify the failed component part of a complex system.

Designing psychophysical procedures has a direct application in the accurate diagnosis and systematic description of sensorineural disorders. Hand-Arm Vibration Syndrome (HAVS), for example, is a collection of disorders associated with long-term exposure to vibration, and can present with numbness, tingling and loss of manual dexterity (Bovenzi, 1990; Griffin, 1990). Its sensorineural component can be assessed with vibrotactile thresholds (ISO 13091-1:2001), and thermo-tactile thresholds (detecting a change in temperature; e.g. Lindsell & Griffin, 1999). Currently, vibrotactile diagnostic procedures help identify impairment in two out of four separable neural systems. Robust psychophysical procedures which describe discriminability in the tactile system may complement, expand and reinforce these diagnostic procedures.

8.5.3 Haptics

By describing tactile perception in terms of the limits of information processing we can apply what we know to any application that relies on the encoding and presentation of tactile information. Notable possibilities include: new technologies for haptic interfaces with computers, advanced prosthetics which provide feedback through tactile stimulation or neural excitation, the creation and manipulation of virtual objects in computer simulations, and tele-robotics.

8.5.3.1 “Electro-Haptics”

A clear case where additional information provided through the tactile sense could have an enormous impact is that of CI users. CI users receive very limited sensory information through their CI, and this could be usefully complemented by a compact haptic device providing vibrotactile signals. A sophisticated research programme, the Electro-Haptics project, of which I am a founding member, is reported in the following chapter.

Chapter 9 Electro-Haptics

The experimental work of this thesis has examined the sensitivity of the tactile system to suprathreshold differences in vibration frequency and amplitude. Throughout, an emphasis has been placed on the accurate measurement of the human sensitivity to these differences as a way to establish methods for the measurement of the sensitivity of the component parts of the tactile system – the tactile channels. This then supports research and diagnostic tools. However, it quickly became clear that a sensitivity to changes in frequency and amplitude could also be applied more directly, to convey information about the world through the sense of touch by 'coding' it as fluctuations in the parameters of a vibration. Crucially, this could be used to compensate for an information deficit in another sense.

Cochlear Implants (CIs) are neural prostheses that restore the sensation of hearing to profoundly hearing-impaired people by electrically stimulating the auditory nerve. However, CIs have an extremely limited ability to convey crucial information about the world, such as speech in noisy situations, or the spatial origin of sounds. By augmenting the limited auditory information provided through the CI, we may be able to improve hearing outcomes for hundreds of thousands of CI users.

Importantly, it is necessary to design a vibration signal that:

1) Contains relevant parts of the audio signal that are not well conveyed by cochlear implants
2) Codes this information in such a way that the tactile channels sensitivity to frequency and amplitude fluctuations is able to capture the information present in the vibration
3) Could be readily delivered in real-time through a compact, wearable device

This chapter builds on the psychophysical work reported in this thesis design a signal that delivers information through the tactile system of cochlear implant users. Three experiments are reported investigating whether and how effectively missing auditory information provided through the sense of touch can be used to enhance CI listening. These experiments are as follows:

Electro-Haptics 1: Vibrotactile enhancement of speech intelligibility in multi-talker noise for simulated cochlear implant listening. This section reports experimental work investigating whether providing tactile cues to the fingertip of normal hearing subjects listening to a cochlear implant simulation enhanced their ability to understand speech in noise.

Electro-Haptics 2: Speech-in-noise performance in cochlear implant users is enhanced by tactile stimulation of the wrists. This section reports experimental work investigating whether providing tactile cues to the wrist of cochlear implant users enhanced their ability to understand speech in noise.

Electro-Haptics 3: Haptic enhancement of spatial hearing in cochlear implant users. This section reports experimental work investigating whether providing tactile cues to the wrist of cochlear implant users allowed them to better discriminate the spatial origin of a sound.

This was a collaborative project, with contributions from other authors. I jointly conceived and planned the project, wrote all three manuscripts, conducted statistical analyses for all three studies, designed and assembled the experimental set ups in electro-haptics 1 and electro-haptics 2, and ran participants for electro-haptics 1. Note that data from electro-haptics 2 were used in Ama Hadeedi' s masters dissertation (2018), and data from electro-haptics 3 were used in Robyn Cunningham's masters dissertation (2019). I wrote about some of this research for *The Conversation* (Mills & Fletcher, 2018, 2019); included in this thesis as Appendices F, G and H.

9.1 Electro-Haptics 1: Vibrotactile enhancement of speech intelligibility in multi-talker noise for simulated cochlear implant listening

9.1.1 Abstract

Many cochlear implant (CI) users achieve excellent speech understanding in acoustically quiet conditions, but most perform poorly in the presence of background noise. An important contributor to this poor speech-in-noise performance is the limited transmission of low-frequency sound information through CIs. Recent work has suggested that tactile presentation of this low-frequency sound information could be used to improve speech-in-

noise performance for CI users. Building on this work, we investigated whether vibro-tactile stimulation can improve speech intelligibility in multi-talker noise. The signal used for tactile stimulation was derived from the speech-in-noise using a computationally inexpensive algorithm. Eight normal-hearing participants listened to CI simulated speech-in-noise both with and without concurrent tactile stimulation of their fingertip. Participants' speech recognition performance was assessed before and after a training regime, which took place over three consecutive days and totalled around 30 minutes of exposure to CI simulated speech-in-noise with concurrent tactile stimulation. Tactile stimulation was found to improve the intelligibility of speech in multi-talker noise and this improvement was found to increase in size after training. Presentation of such tactile stimulation could be achieved by a compact, portable device and offer an inexpensive and non-invasive means for improving speech-in-noise performance in CI users.

9.1.2 Introduction

Many cochlear implant (CI) users achieve excellent speech understanding in acoustically quiet conditions (Fetterman and Domico, 2002; Zeng *et al.*, 2008), but most, even with state-of-the-art implants, perform poorly in the presence of background noise (Spriet *et al.*, 2007; Wouters and Van den Berghe, 2001). An important contributing factor to this poor speech-in-noise performance is the limited transmission of low-frequency sound information through CIs. This has been demonstrated by studies in normal-hearing subjects listening to CI simulations (NHCIs), which have shown that the addition of unprocessed low-frequency sound improves speech-in-noise performance (Chang, Bai, & Zeng, 2006; Qin & Oxenham, 2006). Studies have also shown improved speech-in-noise performance, as well as other benefits such as improved sound localization and music perception, in CI users who retain residual low-frequency acoustic hearing (O'Connell *et al.*, 2017). Unfortunately, few patients referred for CI fitting have usable residual hearing (Verschuur *et al.*, 2016).

The low-frequency sound that has been found to improve speech-in-noise performance in some CI users is within a frequency range of around 20-500 Hz (Verschuur *et al.*, 2016). This matches the frequency range in which the tactile system is most sensitive (Verrillo, 1963). Traditionally, researchers have used tactile aids to support speech perception in people with severe hearing impairment as an alternative to CIs, but with limited success (e.g., Sherrick, 1984 Hnath-Chisolm and Kishon-Rabin, 1988; Weisenberger, 1989). More recently, Huang *et al.* (2017) showed that speech-in-noise performance in CI users can be improved by presenting the fundamental frequency (F0) of the speech signal via vibro-tactile stimulation. However, some aspects of Huang *et al.*'s approach limit its real-world applicability, namely: (1) that the tactile signal was extracted from the clean speech rather than from the speech-in-noise signal, as would be required in a real-world application, and (2) that stationary background noise was used to assess speech-in-noise performance rather than multi-talker babble noise, in which CI users struggle most (Oxenham & Kreft, 2014; Zeng, Rebscher, Harrison, Sun, & Feng, 2008).

The primary aim of this study was to determine whether tactile stimulation can improve speech intelligibility in multi-talker noise for NHCIs, when the tactile signal is derived from the speech-in-noise signal. The signal processing approach used in this study extracted the temporal envelope and voicing information, which have been shown to provide similar benefit to F0 in acoustic presentation for NHCIs (Brown & Bacon, 2009; Kong & Carlyon, 2007). These were then used to modulate seven low-frequency carrier tones which were at frequencies where touch perception is most sensitive. The envelope modulations were amplified using an expander function, which was intended to increase the saliency of the speech envelope and reduce the contribution from background noise. The approach used in the current study is less computationally intensive than F0 extraction and may be more appropriate for real-time application. Furthermore, as discussed by Carroll *et al.* (2011), accurate real-time F0 extraction may not be feasible in real-world situations with multi-talker noise and recent work has shown that F0 extraction errors increase rapidly at SNRs below 10 dB (Jouvet & Laprie, 2017).

The secondary aim of this study was to establish whether any tactile enhancement of speech-in-noise performance increases with training. To establish this, speech-in-noise performance for NHCIs was measured with and without tactile stimulation both before and after a three-day training regime in which participants were exposed to concurrent speech-in-noise and tactile stimulation. An increase in tactile enhancement after training was anticipated, as previous studies using tactile aids to improve speech intelligibility in deaf and hearing-impaired individuals without a CI have found large increases in performance with training (Sherrick, 1984; Brooks *et al.*, 1986a; Brooks *et al.*, 1986b; Weisenberger *et al.*, 1987).

9.1.3 Methods

9.1.3.1 Participants

Table 6. Summary of participant characteristics. Individual data as well as the mean and standard error (SE) across participants are reported.

Participant	Gender	Age	Dominant hand	Vibro-tactile threshold at 31.5 Hz (ms^{-2} RMS)	Vibro-tactile threshold at 125 Hz (ms^{-2} RMS)
1	M	28	R	0.11	0.33
2	F	29	R	0.06	0.14
3	M	26	R	0.07	0.08
4	M	25	R	0.12	0.30
5	F	23	R	0.08	0.14
6	M	23	R	0.06	0.18
7	M	22	R	0.17	0.11
8	F	28	R	0.16	0.07
Mean		*25.5*		*0.10*	*0.17*
SE		*0.95*		*0.02*	*0.03*

Eight participants (5 male and 3 female, aged between 22 and 29 years old) were recruited from the staff and students of the University of Southampton, and from acquaintances of the researchers. Participants were not paid for their participation. All participants reported no hearing or touch issues on a screening questionnaire (see Appendix 1). They were also assessed by otoscopy and pure-tone audiometry. Participants had hearing thresholds not exceeding 20 dB hearing level (HL) at any of the standard audiometric frequencies between 0.25 and 8 kHz in either ear. Participants also had their vibro-tactile thresholds measured (see Procedure). All participants had thresholds below 0.3 ms^{-2} root-mean-square (RMS) at 31.5 Hz and 0.7 ms^{-2} RMS at 125 Hz, indicating normal touch perception (ISO 13091-2:2003). Participant characteristics are shown in Table 6.

9.1.3.2 CI simulation processing and tactile signal generation

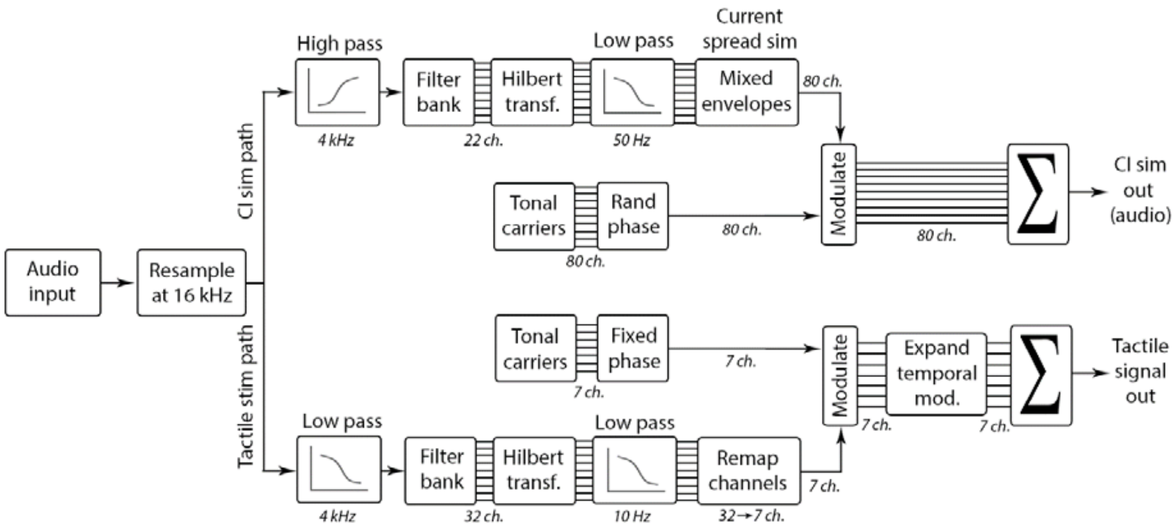

Figure 52. Schematic representation of the signal processing chain for the cochlear implant simulation (upper signal processing path) and tactile signal generation (lower signal processing path).

Acoustic signals processed with noise or tone vocoders have been proposed in several studies to simulate speech perception with CIs (Dorman *et al.*, 1998; Qin & Oxenham, 2006; Shannon *et al.,* 1995). In this study, we used the SPIRAL vocoder for CI simulation, which has recently been developed to achieve a more accurate simulation of the effects of current spread in the cochlea (Grange *et al.*, 2017). The speech reception scores for normal-hearing participants better match those of CI users when the SPIRAL vocoder is used than when a traditional noise-band vocoder is used (Grange *et al.*, 2017).

Figure 52 illustrates the signal processing chain. To generate the CI simulations, the audio signal was resampled with a sampling frequency of 16 kHz and then passed through a first-order high-pass filter with a cut-off frequency of 4 kHz, similar to the input filter characteristics applied in CI speech processors (Chung & McKibben, 2011). The signal was then passed through an FIR filter bank with 22 centre frequencies ranging from 250 to 8000 Hz, equally spaced on the equivalent rectangular bandwidth (ERB) scale (Glasberg & Moore, 1983). These 22 filter channels represent the 22 electrodes on an implanted electrode array in the inner ear of a CI user, with the number of simulated electrodes chosen to be the same as with implants produced by the manufacturer Cochlear Ltd. (Sydney, Australia). Following Grange *et al.* (2017), the envelopes of each channel of the filter bank were computed by calculating the Hilbert transform and applying a first-order low-pass filter with a cut-off frequency of 50 Hz. An envelope mixing function was then used to obtain a sum of weighted contributions from each simulated electrode channel to simulate the spread of excitation in the cochlea. Eighty tonal random-phase carriers were generated in the frequency range from 300 to 8000 Hz (with ERB spacing) and were modulated by the mixed envelopes. The envelope information was applied to the tonal carriers as a representation of the neural excitation patterns of electrically stimulated spiral ganglion cells. The default value of 8 dB per octave for the current decay slope was used, in line with tuning curve slopes measured using monopolar stimulation in CI users (Nelson *et al.*, 2011). The tonal carriers were then summed up to form the CI simulation output signal for acoustic presentation to the participant.

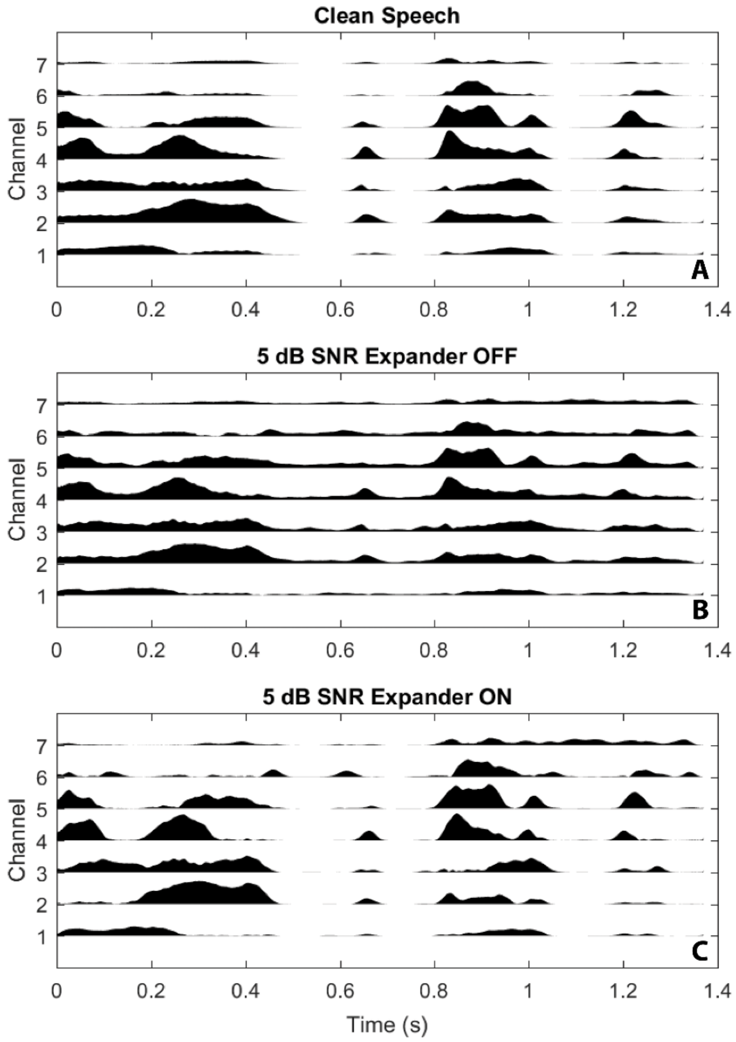

Figure 53. Illustration of the effect of the expander on the tactile signal. Panel A shows the tactile signal for clean speech (with the expander turned off), panel B shows the tactile signal for speech mixed with multi-talker noise (NAL) at an SNR of 5 dB (the lowest SNR used in the current study was 5.8 dB) with the expander turned off, and panel C shows the same signal as panel B, but with the expander turned on. The amplitude envelope for each of the 7 frequency channels of the tactile signal for the sentence "They moved the

furniture" spoken by a male speaker (BKB sentence corpus) are shown in each panel. The height of each channel waveform corresponds to the amplitude of the signal.

To generate the tactile signal, the audio input signal was resampled with a sampling frequency of 16 kHz and a first-order low-pass filter with a cut-off frequency of 4 kHz was applied. The low-pass filter was applied, firstly, to attenuate high frequency information that is efficiently transmitted by a CI and, secondly, to keep the signal in sync with the acoustic path by imposing the same processing delay. The signal was then passed through an FIR filter bank with 32 channels with centre frequencies ranging from 100 to 1000 Hz, equally spaced on the ERB scale, which yields a higher concentration of channels at lower frequencies. This frequency range was selected to include the frequencies most dominant in speech (Byrne *et al.*, 1994). For each channel of the filter bank, the Hilbert envelope was computed, and a first-order low-pass filter was applied with a cut-off frequency of 10 Hz. This low-pass filter limited the modulation frequency range to between about 1 and 30 Hz, which is the range most important for speech intelligibility (Drullman, Festen, & Plomp, 1994). The 32 channels were linearly remapped to 7 channels (by resampling in the frequency domain) and used to modulate the amplitude envelopes of seven tonal carriers with centre frequencies ranging from 30 to 300 Hz (a frequency range in which the tactile system is highly sensitive; Verrillo, 1963). The carriers had a 45 Hz frequency spacing and fixed phases. These carriers were chosen because they would be expected to be individually discriminable based on estimates of vibro-tactile frequency difference limens (Rothenberg *et al.*, 1977), although the results of some studies have suggested that information transfer for complex signals is more limited when these signals are summed and presented to a single site (Israr *et al.*, 2005; Rabinowitz *et al.*, 1987; Summers *et al.*, 1997, 2005). Each of the seven modulated carrier signals was individually passed through an expander function to amplify temporal modulations, and thereby increase the saliency of speech envelope information, and to reduce the contribution from the multi-talker background noise. Figure 53 illustrates the effect of the expander, with panel A showing the processed clean speech (without the expander) and panels B and C showing the processed speech in multi-talker noise at 5 dB SNR with and without the expander. The expander function applied additional gain to enhance fluctuations in the amplitude of each channel with a maximum amplification of 6 dB, attack and release times of 10 and 100 ms, a slope of 6 dB per octave, and a threshold set to the RMS level of the signal. The enhanced tonal carriers were then summed up to form the input signal for tactile presentation to the participant. The tactile signal was presented through a *HVLab* tactile vibrometer. The mean amplitude for a single sentence was 1.96 ms^{-2} RMS.

9.1.3.3 Speech and noise stimuli

Two different speech corpora were used in this study. The Bamford-Kowal-Bench (BKB) Institute of Hearing Research male sentence corpus was used for speech testing. Training and familiarization were conducted using speech material from the RealSpeech^{TM} (UK) content library (used with permission of Dr Ian Wiggins and Dr Mark Fletcher), which used different talkers than the BKB sentence corpus. RealSpeech material was recorded under near-anechoic conditions and comprises a set of narratives that cover a variety of general-interest topics. For both training and speech testing, a non-stationary multi-talker noise recorded by the National Acoustic Laboratories (NAL; Keidser *et al.*, 2002) was used. The noise was a real-world recording made at a party, with a spectrum that matched the international long-term average speech spectrum (Byrne *et al.*, 1994). All speech-in-noise material was processed for audio presentation using a CI simulation based on vocoder processing, and was also processed separately for tactile presentation.

9.1.3.4 Equipment

All stimuli were generated and controlled using custom MATLAB scripts (version R2016a, The MathWorks Inc, Natick, MA, USA). During pure-tone audiometry, participants were seated in a sound-attenuated booth with a background noise level conforming to British Society of Audiology (2017) recommendations. Acoustic stimuli were generated by a laptop located in a separate observation room, and played out via an RME Babyface Pro soundcard (sample rate of 96 kHz and bit depth of 24 bits) and Sennheiser HDA 200 circumaural, closed-back headphones. The stimuli were calibrated using a Brüel and Kjaer (B&K) artificial ear (type 4152) with a flat-plate adaptor (DB0843). For calibration, the two earphones were separated by approximately 145 mm, as specified in ISO 389-5:2006 and the headband tension complied with the requirement of ISO 389-5:2006. Vibro-tactile threshold measurements were made using a *HVLab* Vibrotactile Perception Meter with a 6-mm contactor with a rigid surround and a constant upward force of 2N, following the specifications of ISO 13091-1:2001. The tactile system for the testing and training sessions and for vibro-tactile threshold measurements was calibrated using a B&K calibration exciter (type 4294).

In testing and training sessions, stimuli were played out via an RME Fireface UC soundcard (Haimhousen, Germany) and ER-2 insert earphones (Etymotic, IL, USA). Stimuli were calibrated using a B&K 2260 Investigator and 4157 occluded ear coupler (Royston, Hertfordshire, UK). The experiment took place in a quiet room. The experimenter sat behind a screen with no line of site to the participant and listened to the signal that was delivered to the participant using

Sennheiser HD 380 Pro circumaural, closed-back headphones in order to mask any auditory cues that might unblind the experimenter to the experimental condition. The vibration signal was delivered to the participant via a *HVLab* Tactile Vibrometer with a 10-mm contacting probe to the distal phalanx of the index finger of the participant's right hand (which in all cases was their dominant hand) with an upward force of 2N.

9.1.3.5 Procedure

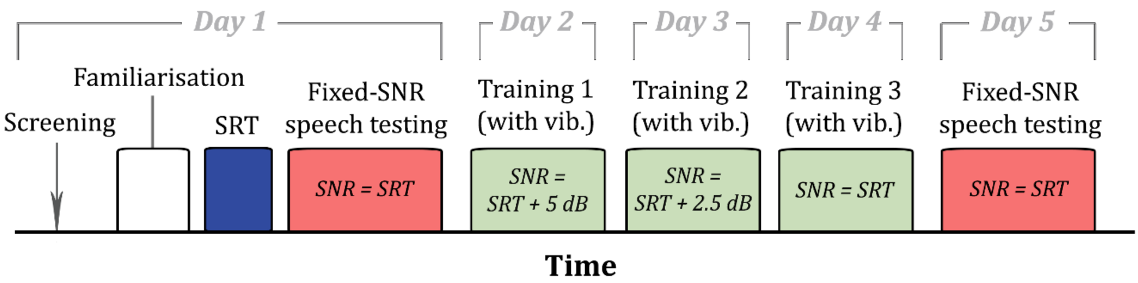

Figure 54. Schematic (not to scale), showing the timeline of the experiment.

Figure 54 shows a schematic illustrating the experimental procedure. On the first of five consecutive days, participants were screened, and were then familiarized with speech in quiet processed using the CI simulator without concurrent tactile stimulation. Each participant's speech reception threshold (SRT; the SNR at which 50% performance is obtained) was then measured without tactile stimulation. This SRT was then used as the SNR for speech-in-noise testing in conditions with and without tactile stimulation. On each of the following three days, participants were trained with concurrent tactile stimulation, at SNRs that decreased each day. On the fifth day, the speech-in-noise testing was again conducted with and without tactile stimulation, with the SNR fixed to the SRT measured on day one. Two different speech corpora were used, one for the familiarization and training phases, and one for the SRT and speech testing.

In the screening phase, pure-tone audiometry was conducted following the recommended procedure of the British Society of Audiology (British Society of Audiology, 2017). Vibro-tactile detection thresholds were measured using conditions and criteria specified in ISO 13091-1:2001 and ISO 13091-2:2003. These thresholds were estimated for sinusoidal vibrations of 31.5 and 125 Hz using the von Bekesy method of limits. In this procedure, the amplitude of the stimulus increased until the participant pressed a button to indicate they could feel the vibration, at which point the amplitude decreased until the participant could no longer feel the vibration. The amplitude changed by 5 dB/s for the first two reversals, and then by 3 dB/s for the remaining eight reversals that made up the threshold track. The threshold was taken as the average of the last six reversals. For each frequency, the procedure was conducted twice, and the mean taken as the threshold.

Following the screening phase, participants were familiarized with CI simulated speech (in quiet and with no tactile stimulation) using a 5-minute speech segment from a male talker from the RealSpeech content library. Participants were given a transcript of the speech with some sections of the text blacked out, and were asked to report to the experimenter what was said in the missing sections. This phase allowed participants to become comfortable with the unusual sound of the CI simulated speech.

After the familiarization phase, each participant's SRT was measured using a single BKB sentence list (containing 15 sentences) mixed with multi-talker noise. The SNR of the first trial was 5 dB. The sentence used in the first trial was repeated, with the SNR increased by 2 dB after each repeat, until the participant got at least 2 out of 3 keywords correct. A one-up one-down adaptive tracking procedure (Levitt, 1971) with a step size of 2 dB was then followed for the remaining 14 sentences (tracking 50 % correct performance). The speech signal was always presented at a level of 65 dB SPL LAeq. The SRT was calculated as the mean of the last 6 reversals. Two SRT estimates were made for each participant. The average SRT across participants was 7.9 dB (ranging from 5.8 to 14 dB), which is similar to the mean and range typically seen in CI users (e.g. Goehring *et al.*, 2017).

In the speech testing phases before and after the training, the percentage of keywords correctly reported was measured. Two sets of eight BKB sentence lists were used. Which of the sets was used for pre-training and which for post-training was counterbalanced across participants. In each speech testing phase, four of the sentence lists were used to measure performance in the condition with tactile stimulation, and four in the condition without tactile stimulation. The two conditions were alternated in an A-B-A-B pattern across the lists. Whether tactile stimulation was applied in condition A or B was counterbalanced across participants, such that half of the participants had tactile stimulation in condition A and half in condition B for all testing sessions. The experimenter was blinded to whether the participant was receiving tactile stimulation to avoid experimenter bias (see following section). The participant was either instructed via a text display to place their finger on a shaker contact, with the message "Vibration enhancement ON. Audio enhancement OFF." displayed, or was instructed to put both hands on their lap, with the message "Vibration enhancement OFF. Audio enhancement ON." displayed. This latter message falsely stated that the audio signal had been enhanced in the condition without tactile stimulation. This false cue was included to control for effects of participant expectation that tactile stimulation was intended to improve performance. Performance was scored as the percentage of correctly reported keywords.

In the training sessions, the target speech consisted of six speech segments from the RealSpeech content library each lasting around five minutes, which were passed through the CI simulation. Half of the segments were read by female talkers and half by male talkers. The segments were split into single sentences and mixed with the NAL multi-talker noise. Participants were asked to repeat each sentence to the experimenter, after which the sentence text was displayed to the participant. In each session, two segments (totalling around 10 minutes) were presented. The order in which the speech segments were presented was randomized across participants. The task was made more difficult in each successive training session. In the first training session, the SNR was set at 5 dB above the participant's SRT, in the second at 2.5 dB above, and in the final session at the participant's SRT. For all training material concurrent tactile stimulation was provided.

The experimental protocol was approved by the University of Southampton Ethics Committee (ID: 30753).

9.1.4 Results

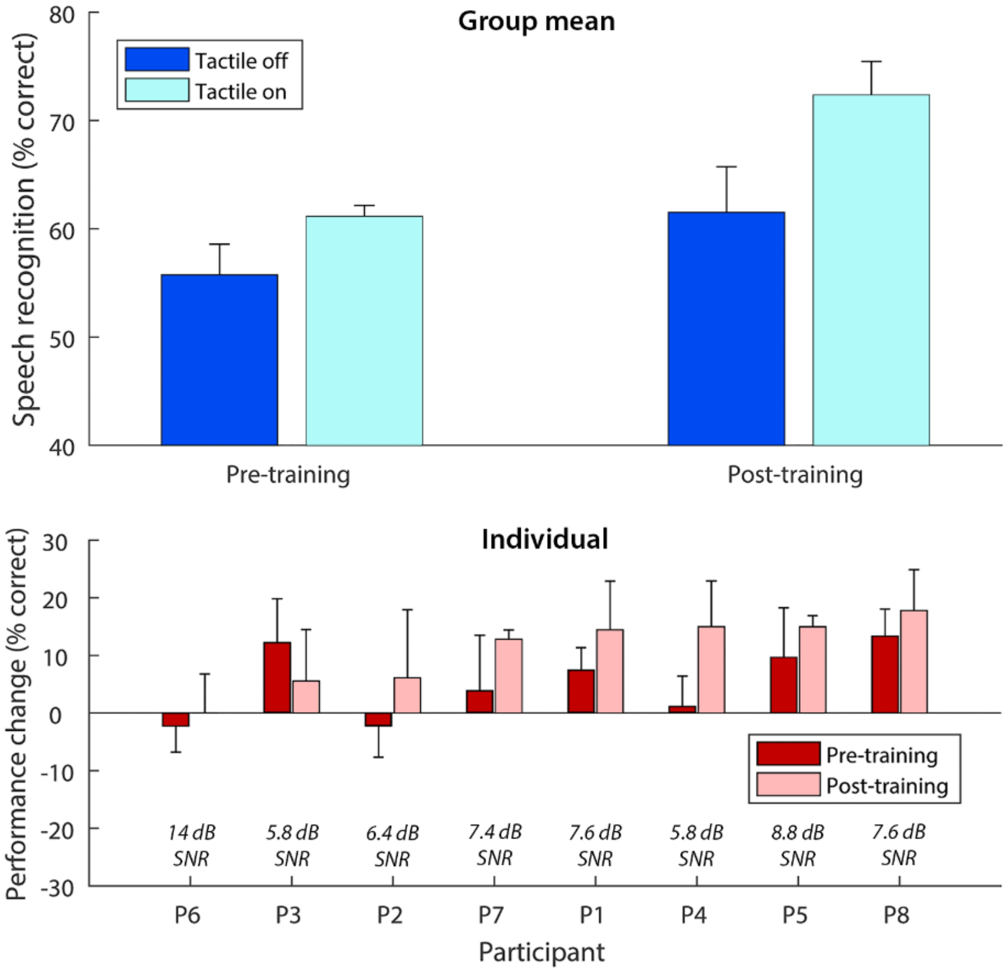

Figure 55. Mean speech-in-noise performance across all participants with and without tactile stimulation before and after training (top panel) and for each individual ordered by the size of their post-training performance change (bottom panel). The SNR at which speech-in-noise performance was measured is shown on the bottom panel for each individual. Error bars show the standard error of the mean.

Figure 55 shows the effect of tactile stimulation on speech-in-noise performance (the percentage of key words correctly identified) before and after training. The results were analysed using a repeated-measures ANOVA, with factors 'Session' (before or after training) and 'Condition' (with or without tactile stimulation). A significant main effect of Condition was measured ($F(1,7) = 18.0$, $p = .004$, $\eta_p^2 = .72$), such that a greater percentage of key words were correctly identified in the condition with tactile stimulation than without. A significant interaction between Session and Condition was found, indicating that the effect of tactile stimulation in the post-training session was significantly larger than in the pre-training session ($F(1,7) = 6.6$, $p = .037$, $\eta_p^2 = .48$). Paired t-tests (with a Bonferroni corrected alpha of .0125) revealed a significant effect of Condition in the post-training session ($t(7) = 5.0$, $p = .002$), but not the pre-training session ($t(7) = 2.5$, $p = .043$). The mean effect of tactile stimulation before training was 5.4% (improving from 55.7 % without tactile stimulation to 61.1 % with tactile stimulation; standard error of the mean: ± 2.2 %) and the mean effect of tactile stimulation after training was 10.8 % (improving from 61.5 % to 72.3 %; ± 2.2 %). The largest individual effect of tactile stimulation on performance was 17.8 % (P8, post-training) and the largest reduction in performance was 2.2 % (P2 and P6, pre-training). Evidence of an effect of Session was seen in the condition with tactile stimulation ($t(7) = 4.3$, $p = .004$) but not in the condition without tactile stimulation ($t(7) = 2.0$, $p = .082$). An overall effect of Session was also observed ($F(1,7) = 11.4$, $p = .012$, $\eta_p^2 = .62$).

9.1.5 Discussion

In this study, tactile presentation of envelope and voicing information was found to significantly improve the intelligibility of speech in multi-talker noise for NHCIs. After training, tactile stimulation improved the percentage of key words correctly reported for sentences in noise by 10.8 % on average. This is similar to the speech-in-noise performance benefit provided by residual low-frequency acoustic hearing in CI users (Gifford *et al.*, 2013, 2017). Our results build on the work of Huang *et al.* (2017), who found evidence that tactile stimulation could improve speech-in-noise performance for CI users. Like in the current study, Huang *et al.* found robust effects, though the size of the benefit is difficult to compare directly because of the different outcome measures and speech corpora used. Huang *et al.* presented tactile signals derived from clean speech, whereas in the current study the tactile signal was derived from speech-in-noise, as would be required in a real-world application. The current study also adds to the work of Huang *et al.*, who showed tactile benefit in stationary noise, by showing benefit in multi-talker noise, in which CI users struggle most (Zeng *et al.*, 2008; Oxenham and Kreft, 2014). Taken together, these findings indicate that tactile stimulation has strong potential as a means of improving speech-in-noise performance for CI listeners. It could offer a viable alternative for the majority of CI users who do not benefit from residual low-frequency hearing.

In the current study, tactile enhancement of speech-in-noise performance increased in size after just 30 minutes of exposure to speech-in-noise and tactile stimulation over three days. Over this short period, participants were trained by performing a speech-in-noise task while receiving additional speech information through vibration on the fingertip. Participants were trained in this condition only, which could have created a bias towards the condition with tactile stimulation. Further work is needed to establish the most effective training method and how much training is required for maximum performance to be achieved. Previous studies using tactile aids (with no accompanying CI signal) suggest a training period of several months or even years is required to achieve maximum benefit (e.g., Sherrick, 1984; Brooks *et al.*, 1986a,b; Weisenberger *et al.*, 1987). This raises the intriguing possibility that prolonged training could lead to even greater performance enhancements than were observed in the current study.

The robust improvement in speech intelligibility by tactile stimulation was achieved for speech in multi-talker noise, and with computationally non-intensive processing that could be applied in real time. Noise-reduction algorithms for CIs have facilitated substantial improvements in speech intelligibility in stationary noise. However, they have struggled to produce similar improvements for multi-talker background noise when no *a priori* information about the target speaker is available (Dawson *et al.*, 2011; Goehring *et al.*, 2017). These algorithms are typically computationally more intensive than the one proposed in this study and may require an increase in computational resources for integration into CI speech processors.

The effect of tactile stimulation on speech-in-noise performance was assessed at SNRs corresponding to typical SRTs for CI users, which are higher than those for hearing aid users or normal-hearing listeners. Drullman and Bronkhorst (2004) have shown that speech-in-noise performance for normal-hearing listeners can also be improved by tactile stimulation. They found benefits of tactile stimulation for speech with one or two interfering talkers, but not for speech with several interfering talkers. However, as in Huang *et al.* (2017), Drullman and Bronkhorst presented tactile signals derived from clean speech rather than from the speech-in-noise signal. Further work is required to establish whether the approach used in the current study is effective at lower SNRs.

An important limitation of the current study is that vibro-tactile stimulation was delivered to the fingertip, which may not be a suitable site for real-world application. Previously, researchers using tactile aids (with no accompanying CI signal) have successfully transferred complex auditory information at the wrist (Weisenberger, 1989), forearm (Hnath-Chisolm and Kishon-Rabin, 1988), and abdomen (Weisenberger, Broadstone, & Saunders, 1989). It is therefore considered likely that tactile enhancement of speech-in-noise performance for CI users can be achieved at sites other than the fingertip. The wrist is a particularly promising candidate for future research as, although it has higher vibro-tactile detection thresholds than the fingertip, researchers have shown that it has similar sensitivity to frequency and amplitude differences (Summers *et al.*, 2005). Tactile stimulation could be delivered via multiple contacts to maximize information transfer capacity, as has been done previously with tactile aids to transfer more spectral information and even to transfer spatial hearing cues (Richardson & Frost, 1979).

A second limitation was the use of NHCIs rather than actual CI users. CI simulations are an established way of presenting signals with a similar amount of usable information as is obtained by CI users. In the current study, the measured SRTs for NHCIs were well matched to those measured in real CI users (e.g. Goehring *et al.*, 2017). The CI simulation used here models channel interactions and current spread present in real CIs, making it more realistic than simple vocoder simulations (Grange *et al.*, 2017). This simulation reproduces the signal received by a CI user with an ideally fitted implant, for which all electrodes are functioning optimally, which is not always achieved in practice. It is possible that real CI users, who may receive more limited auditory information through their CI, will benefit more from the tactile stimulation used in this study.

There are a number of potential benefits of tactile stimulation to CI listening beyond improvements in speech-in-noise performance that should be explored in future work. These include the additional benefits that are provided by residual low-frequency acoustic hearing to CI users, such as enhanced music perception and spatial hearing (O'Connell *et al.*, 2017). Furthermore, previous studies have shown evidence that low-frequency auditory information is important for lip reading (Breeuwer & Plomp, 1984; Faulkner *et al.*, 1992). Studies of lip reading have found that tactile aids (with no accompanying audio) can improve the percentage of words correctly identified by around 9 % for postlingually deafened adults, and by around 7 % for normal-hearing listeners (Kishon-Rabin, 1996). These studies typically included extensive training, of up to 300 hours (Waldstein & Boothroyd, 1995). These findings indicate that another benefit of tactile stimulation in CI users may be enhanced lip-reading ability.

9.1.5.1 Conclusions

This study has shown that tactile presentation of envelope and voicing information can improve speech-in-noise performance for normal-hearing subjects listening to CI simulations. This tactile enhancement effect was shown to increase substantially after just 30 minutes of exposure to speech-in-noise material and tactile stimulation over three days. The tactile signal was extracted from the speech-in-noise and presented via a single, small vibrating contact after computationally non-intensive signal processing. Real-time presentation of such tactile stimulation could be achieved by a compact, portable device, and offer an inexpensive and non-invasive means for improving speech-in-noise performance in CI users.

9.2 Electro-haptics 2: Speech-in-noise performance in cochlear implant users is enhanced by tactile stimulation of the wrists

9.2.1 Abstract

When a sense is impaired and can only transmit limited information, the brain can extract missing information by relying more heavily on other senses. This plasticity could be exploited to enhance listening in cochlear implant (CI) users, who only receive limited sound information through their implant. Recent work has suggested that combining the electrical signal from the CI with a haptic signal that provides crucial missing sound information ("electro-haptic stimulation"; EHS) could improve speech-in-noise performance. The aim of the current study was to test whether EHS could enhance speech-in-noise performance in CI users using: (i) a tactile signal derived using an algorithm that could be applied in real time, (ii) a stimulation site appropriate for a real-world application, and (iii) a tactile signal that could readily be produced by a compact, portable device. We measured speech intelligibility in multi-talker noise with and without vibro-tactile stimulation of the wrist in CI users, before and after a short training regime. No effect of EHS was found before training, but after training EHS was found to improve the number of words correctly identified in multi-talker noise by an average of 8.3 %-points. The multi-sensory approach used in this study could offer an inexpensive and non-invasive means of improving speech-in-noise performance in CI users.

9.2.2 Introduction

When a sense is impaired or abolished, the brain adapts, relying more heavily on other senses to extract information (Isaiah, Vongpaisal *et al.*, 2014; Schorr *et al.*, 2005). This cross-modal plasticity could be exploited to enhance listening in deaf and hearing-impaired individuals fitted with a cochlear implant (CI). A CI is a neural prosthesis that bypasses the damaged or defunct outer and inner ear and electrically stimulates auditory nerve fibres to restore hearing. While, in normal-hearing individuals, speech information is transmitted to the brain by thousands of hair cells, in CI users it is transmitted through, at most, just 22 micro-electrodes. Because of this, much of the key information used to extract speech from a noisy background is not available. CI users therefore struggle to understand speech-in-noise much more than normal-hearing listeners (Spriet *et al.*, 2007; Wouters & Vanden Berghe, 2001). Results from previous studies suggest that speech amplitude envelope information is a crucial missing feature for CI users listening in noise(Brown & Bacon, 2009; Kong & Carlyon, 2007). We hypothesize that, given the brain's ability to extract missing information through another sense, speech-in-noise performance in CI users may be improved by providing speech envelope information through tactile stimulation. This haptic augmentation of these electrical signal from the CI will be referred to as "electro-haptic stimulation" (EHS).

Several studies have shown examples of sensory substitution, where information no longer transmitted through one sense is instead transmitted through another (Bach-y-Rita, 1972; Bach-y-Rita *et al.*, 1969; Capelle *et al.*,, 1998; Meijer, 1992). For example, researchers have shown that tactile aids (with no concurrent audio signal) can be used to transmit complex speech information (Brooks *et al.*,1983; Hnath-Chisolm & Kishon-Rabin, 1988; Thornton & Phillips, 1992). Similarly, when a sense is impaired and therefore all of the critical information cannot be transferred, missing information can be provided through another sense (Laurienti *et al.*, 2006; Schorr *et al.*, 2005; Sumby & Pollack, 1954). Two recent studies showed examples of this sensory augmentation for CI listening (Fletcher *et al.*, 2018; Huang *et al.*, 2017). We recently (Fletcher *et al.*, 2018) found that tactile presentation of speech envelope improved speech intelligibility for normal-hearing subjects listening to CI simulations (NHCIs; Fletcher *et al.*, 2018). We extracted their tactile signal from speech-in-noise and presented it to the index finger. Huang *et al.* found similar results for CI listening in noise when the fundamental frequency was presented to the finger (Huang *et al.*, 2017), but in their study the tactile signal was extracted from the clean speech, rather than from the speech-in-noise. In the current study, we used an approach that is suitable for a real-world application. Three key features of our approach were: (i) We extracted the speech envelope from the speech-in-noise signal using a signal processing approach that was computationally lightweight and appropriate for real-time processing; (ii) we delivered tactile stimulation to the wrist rather than the finger, which is a more suitable site for real-world use; and (iii) we used a vibration intensity that can be produced by a near-silent, inexpensive, compact device with low power consumption. The aim of the current study was to establish whether our approach can be used to improve speech-in-noise performance in CI users.

It is likely that a short training regime will increase the benefit of EHS to speech-in-noise performance. Fletcher *et al.* (2018) found that training was important; the benefit of tactile stimulation to speech recognition in noise was found to grow substantially after just 30 minutes of exposure to speech-in-noise and concurrent tactile stimulation. Fletcher *et al.* used NHCIs whereas, in the current study, CI users were tested. Evidence that CI users integrate auditory and lip-reading cues more effectively than NHCIs has been used to suggest that CI users are better at integrating multisensory information than normal-hearing listeners (Rouger *et al.*, 2007). It may therefore be expected that CI users will benefit more from tactile stimulation. However, it is possible that lip-reading represents a special case as lip-reading cues are often used to aid speech understanding in real-world situations, whereas speech envelope information is never presented through touch in real-world settings. The novelty of the tactile stimulus could be distracting at first or less readily integrated with auditory information. It is therefore possible that training or familiarisation will be required to facilitate the multisensory integration needed for CI users to benefit from EHS.

To investigate the effect of EHS, 10 CI users completed a speech testing session, followed by two training sessions, and then a final testing session. In the testing sessions, participants completed a speech-in-noise task, where the percentage of correctly identified keywords in noise was measured both with and without concurrent tactile stimulation of the wrists. Speech testing was conducted with multi-talker noise, in which CI users are known to struggle most (Oxenham & Kreft, 2014; Stickney *et al.*, 2004). In the training sessions, participants received speech-in-noise training with concurrent tactile stimulation. These training sessions used audiobook material with different talkers from the one used in the testing sessions. The two training sessions totalled just 20 minutes of exposure to speech-in-noise and tactile stimulation. It is anticipated that, after training, EHS will increase the percentage of keywords in noise that CI users are able to correctly identify.

9.2.3 Materials and Methods

9.2.3.1 Participants

Ten CI users (4 male, 6 female; mean age = 61.2 years, ranging from 41 to 70 years) were recruited through the University of Southampton Auditory Implant Service. Participants were only invited to take part in the experiment if they were: (i) native British English speakers, (ii) aged between 18 to 70 years old (inclusive), (iii) had been implanted at least 12 months prior to the experiment, (iv) had no EAS (i.e. no functional residual low-frequency hearing; >65 dB HL at 250 and 500 Hz), (v) had speech in quiet scores of at least 70% (for Bamford-Kowal-Bench sentences; BKB) measured at their most recent clinical appointment, and (vi) had the capacity to give informed consent. Table 1 details participant characteristics. All participants also reported on a screening questionnaire (see Fletcher *et al.*; 2018) that they had no medical conditions and were taking no medication that might affect their touch perception. Participants gave written informed consent and received an inconvenience allowance.

Vibro-tactile detection thresholds were determined for both the left and right index fingers for sinusoidal vibrations of 31.5 and 125 Hz, using conditions specified in ISO 13091-1:2001. Two participants (P2 and P3) had higher than normal thresholds (>0.7 ms^{-2} root mean square [RMS](International Organisation for Standardization, 2001) at 125 Hz on the index finger of their left hand, and two other participants (P1 and P7) had elevated thresholds at 125 Hz on the index finger of their right hand. All other measured thresholds at the index finger were at normal levels.

Table 7. Summary of participant information.

Participant	Gender	Age	Speech-in-quiet (% correct)	Type of implant	Time since implantation	Dominant hand
1	F	65	85	MEDEL Sonata	9.3	Right
2	M	56	89	AB Hi Res 90k	3.4	Right
3	M	69	99	AB Hi Res 90k	1.5	Right
4	F	68	98	Cochlear Nucleus 512 (CA) profile	3.7	Left
5	M	68	94	AB HiRes ultra	1.0	Right
6	F	70	96	Cochlear Nucleus 512 (CA) profile	2.7	Right
7	M	70	92	Cochlear Nucleus Freedom contour	9.1	Right
8	F	44	98	Cochlear nucleus 512 (CA) profile	1.6	Right
9	F	41	93	Cochlear nucleus contour (bilaterally)	7.7	Right
10	F	52	100	AB Hi Res 90k	10.9	Right
Mean		*60.3*	*94.4*		*5.1*	

9.2.3.2 Tactile Signal Processing

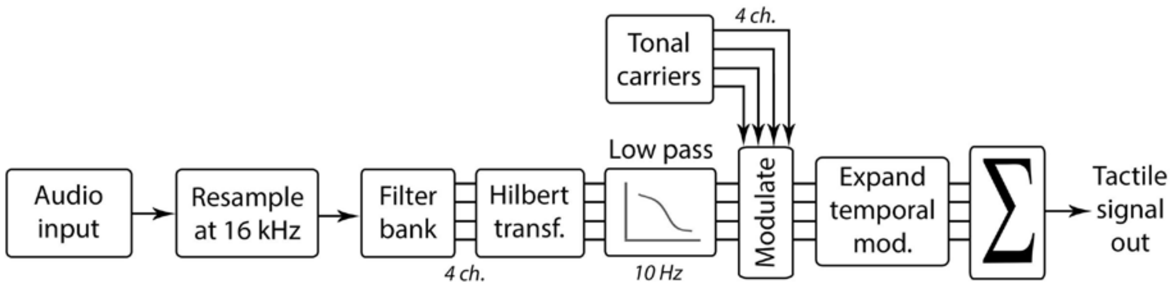

Figure 56. Schematic representation of the signal processing chain for the tactile signal generation.

Figure 56 shows a schematic representation of the signal processing chain that was used to convert the audio signal to a tactile signal. The signal processing approach is described in detail in Fletcher *et al.* (2018) and is summarized below. The parameters used in the current study were the same as in Fletcher *et al.*, except that a smaller number of tonal carriers were used over a reduced frequency range. The reduced frequency range of the tactile signal (50-230 Hz) means that it can be more easily produced by a low-power wearable device that is near-silent.

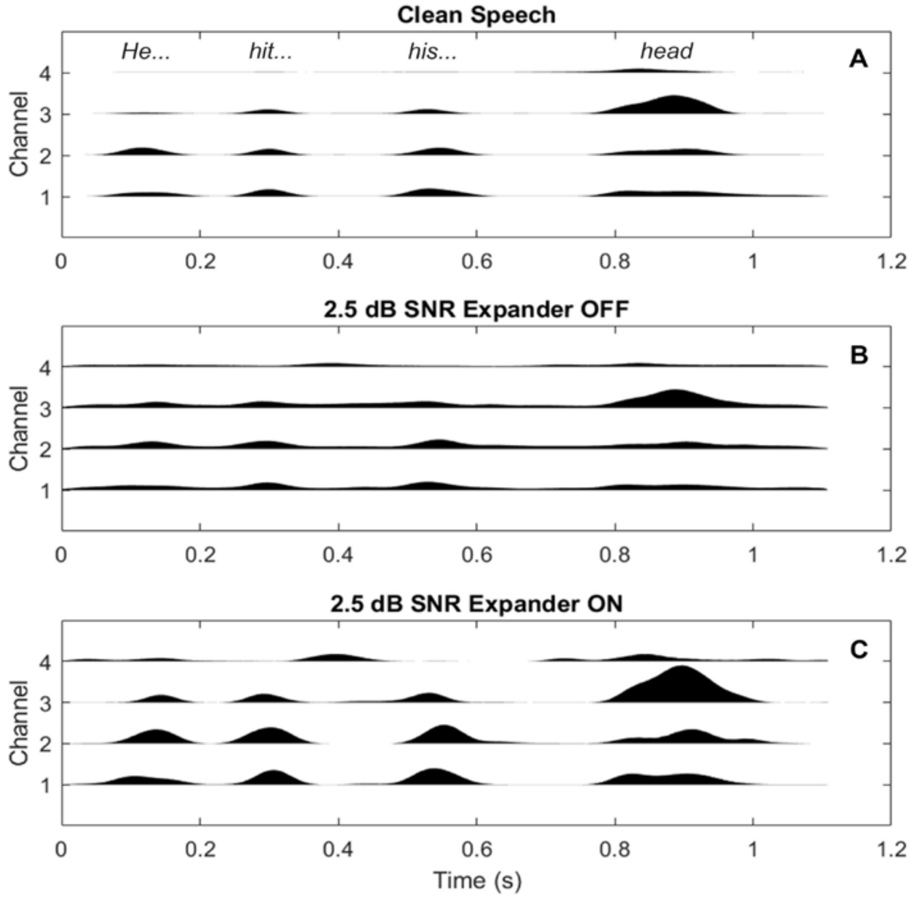

Figure 57. Illustration of the effect of the expander on the tactile signal amplitude for the sentence “He hit his head”. Panel A and B show the tactile signal for clean speech and for speech-in-noise (at 2.5 dB, the lowest SNR used in the study). Panel C shows the same signal as panel B, but with the expander on. The height of each channel waveform corresponds to the amplitude of the signal.

To generate the tactile signal, the audio input signal was first downsampled to a sampling frequency of 16 kHz. The signal was then passed through an FIR filter bank with 4 channels with centre frequencies ranging from 100 to 1000 Hz, equally spaced on the ERB scale. The Hilbert envelope for each channel was computed and a first-order low-pass filter was applied with a cut-off frequency of 10 Hz. The channels were then used to modulate the amplitude envelopes of four fixed-phase tonal carriers with center frequencies of 50, 110, 170, and 230 Hz (a frequency range in which the tactile system is highly sensitive; (Verrillo, 1963b)). Each of these carrier signals was individually passed through an expander function (as used in Fletcher *et al.*) to amplify temporal modulations and reduce the contribution from the background noise, thereby increasing the salience of speech envelope information. Figure 3 illustrates the effect of the expander by showing the same sentence as: processed clean speech without the expander (panel A), processed speech-in-noise at an SNR of 2.5 dB with the expander turned off (panel B), and the same speech-in-noise signal with the expander turned on (panel C). The enhanced tonal carriers were then summed to form the input signal for tactile presentation to the participant. A 10-ms delay was added, to keep the tactile signal approximately synchronized with the electrical signal from the CI. The tactile signal was presented through two *HVLab* tactile vibrometers. The mean acceleration magnitude of the vibration output for a single sentence was 1.84 ms^{-2} RMS.

9.2.3.3 Speech and Noise Stimuli

The speech signal was presented at a level of 65 dB SPL LAeq. Two different speech corpora were used in this study. The BKB Institute of Hearing Research male sentence corpus(MacLeod & Summerfield, 1990) was used for speech testing. This material was not familiar to participants as clinical audiology test procedures use a different BKB sentence corpus. Training was conducted using speech material from the RealSpeech™ (UK) content library (used with permission of Dr Ian Wiggins and Dr Mark Fletcher), which used two talkers (one male and one female) which are different from the talker used in the BKB sentence corpus. RealSpeech material comprises a set of narratives that cover a variety of general-interest topics recorded under near-anechoic conditions. A non-stationary multi-talker noise recorded by the National Acoustic Laboratories (NAL; Keidser *et al.*, 2002) was used in both training and speech testing. The noise was recorded at a party and had a spectrum that matched the international long-term average speech spectrum (Byrne *et al.*, 1994).

9.2.3.4 Apparatus

Participants were seated in a sound-attenuated booth with a background noise level conforming to the 2017 British Society of Audiology recommendations(British Society of Audiology, 2017). All stimuli were generated and controlled using custom MATLAB scripts (version R2016a, The MathWorks Inc, Natick, MA, USA). Acoustic stimuli were generated by a laptop located in a separate observation room and played out via an RME Babyface Pro soundcard (Haimhousen, Germany; sample rate of 44.1 kHz and bit depth of 24 bits) and a Genelec 8020C PM Bi-Amplified Monitor System positioned at head height 1.5 m from the participant. The acoustic stimuli were calibrated at the listening position using a Brüel & Kjær (B&K) G4 type 2250 sound level meter and B&K type 4231 sound calibrator.

Two *HVLab* tactile vibrometers were placed beside the participant's chair and were used to deliver the vibro-tactile signal to the participants' wrists. The vibrometers in this experiment were adapted by the substitution of the standard 6-mm probe with a 10-mm probe, and the removal of the rigid surround. These changes increased the area of skin excitation. A B&K type 4294 calibration exciter was used to calibrate the accelerometers, and the vibration signal was calibrated to provide equal amplitude across the frequency range. A further *HVLab* tactile vibrometer with a 6-mm probe and a rigid surround was used to measure vibro-tactile detection thresholds using *HVLab* diagnostic software.

During testing, the experimenter sat in the control room with no line of sight to the participant. The sentences spoken by the participants were captured using a Shure BG 2.1 dynamic microphone, amplified by a GSI-61 audiometer, and presented to the experimenter through the GSI-61 Operator's Headset.

9.2.3.5 Procedure

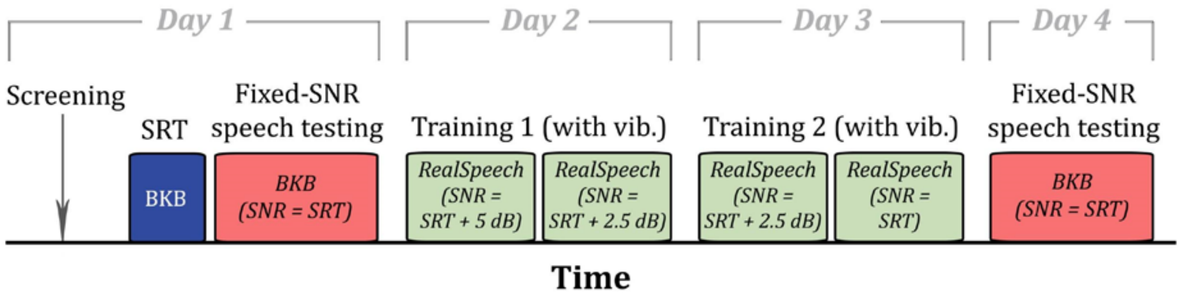

Figure 58. Schematic (not to scale) showing the timeline of the experiment. Speech material was either BKB sentences or audiobook material from RealSpeech.

Figure 58 shows a schematic illustration of the experimental procedure. Participants attended four sessions over a two-week period (mean period between first and last sessions = 5.4 days, ranging between 3 and 9 days, with an average gap between any two sessions of 1.8 days). The four sessions consisted of a speech testing session, followed by two training sessions, and then a final testing session. This procedure is similar to the one detailed in Fletcher *et al.* (Fletcher *et al.*, 2018), although here only 2 days of training were conducted, totalling around 20 minutes of exposure to speech in noise and concurrent tactile stimulation.

In the pre-training testing session, participants completed a screening questionnaire and had their vibro-tactile detection thresholds measured at the fingertip to check for normal touch perception. Detection thresholds were also measured for each wrist (where tactile stimulation was applied in this study) at 31.5 Hz (Mean = 0.79 ms^{-2} RMS) and 125 Hz (Mean = 0.68 ms^{-2} RMS). Each participant’s speech reception threshold (SRT) was then measured without tactile stimulation. Two SRT estimates were made, each using a single BKB sentence list (containing 15 sentences) mixed with multi-talker noise. Trials were marked as correct if participants correctly repeated at least 1 out of 3 keywords. For each SRT estimate, the SNR of the first trial was 5 dB. The sentence used in the first trial was then repeated, with the SNR increased by 2 dB after each repeat, until a trial was marked as correct. A one-up one-down adaptive tracking procedure(Levitt, 1971) with a step size of 2 dB was then followed for the remaining sentences for each SRT. The SRT was calculated as the mean of the last 4 reversals.

In both the pre- and post-training testing sessions, speech-in-noise performance was measured at an SNR equal to the mean of the two SRT estimates made in the first session. Speech testing was conducted with and without concurrent tactile stimulation. In both testing sessions, sentences were played to the participants and they were asked to repeat back what was said. Performance was measured as the proportion of key words that the participants correctly identified. The experimenter was able to use a text display to instruct participants to repeat their response if it was unclear. Sixteen BKB sentence lists were used in total, eight in each session. Half of the lists were played with concurrent tactile stimulation and half without. The two conditions were alternated in an A-B-A-B pattern across the lists and were counterbalanced across participants. The order of conditions was swapped between the pre- and post-training sessions (i.e. B-A-B-A). During the speech testing, participants were instructed via a text display to either place their wrists on the vibrometer contacts, or to place their arms on the armrests of the chair. The tactile signal was played through the vibrometers in both conditions. When participants had their wrists on the contacts, the message “Vibration enhancement ON. Audio enhancement OFF.” was displayed on the screen, and when they had their arms on the armrests the message “Vibration enhancement OFF. Audio enhancement ON.” was displayed. This latter message falsely stated that the audio signal had been enhanced in the condition without tactile stimulation. This deceptive cue was included to control for effects of participant expectation that tactile stimulation was intended to improve performance. The experimenter was blinded to which conditions contained tactile stimulation, in order to avoid experimenter bias.

The two training sessions consisted of target speech from the RealSpeech content library. In each session the participant listened to two speech segments, each lasting around five minutes. Half of the segments were read by a female talker and half by a male talker and were presented in a random order. The segments were split into single sentences and mixed with the NAL multi-talker noise. The first segment was presented at an SNR 5dB above the participants SRT, the second and third at 2.5 dB above, and the final segment at an SNR equal to the participant’s SRT. Participants were asked to repeat each sentence to the experimenter after which the correct sentence text was displayed on the screen. For all training material concurrent tactile stimulation was provided.

The experimental protocol was approved by the University of Southampton Ethics Committee (ERGO ID: 30753) and the UK National Health Service Research Ethics Service (Integrated Research Application System ID: 244309).

9.2.4 Results

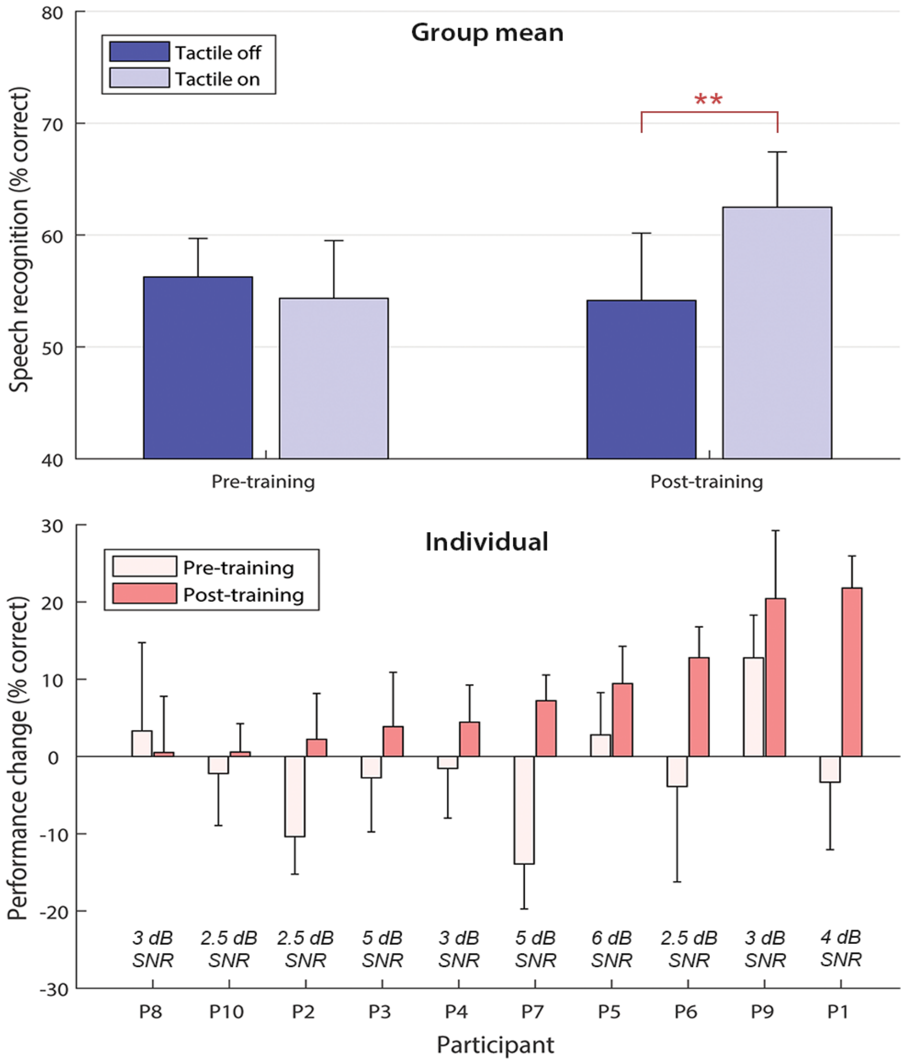

Figure 59. The top panel shows the mean speech-in-noise performance across all participants with and without tactile stimulation, both before and after training. The bottom panel shows the difference in performance with and without tactile stimulation for each individual, before and after training. A positive performance change indicates that performance was better with tactile stimulation. Participants are ordered by the size of their post-training performance change. The SNR (signal to noise ratio) at which speech-in-noise performance was measured for each individual is shown in the bottom panel. Note that the sentence lists used were fully counterbalanced across conditions, but not across sessions. Error bars show the standard error of the mean (SE).

Figure 59 shows the effect of tactile stimulation on speech-in-noise performance (the percentage of key words correctly identified) before and after training. The results were analysed using a repeated-measures ANOVA, with factors 'Session' (before or after training) and 'Condition' (with or without tactile stimulation). There was a significant interaction effect, indicating that the effect of tactile stimulation in the post-training session was significantly larger than in the pre-training session ($F(1,9) = 14.2$, $p = .004$, $\eta_p^2 = .917$). Main effects of Condition and Session were non-significant.

Paired t-tests (with a Bonferroni corrected alpha of .025), revealed a significant effect of Condition in the post-training session ($t(9) = 3.4$, $p = .008$, $d = 1.08$), but not in the pre-training session ($t(9) = .82$, $p = .43$). Before training, in 7 out of 10 participants performance was worse with tactile stimulation, and individual results were highly variable. The largest improvement in performance with tactile stimulation before training was 12.8 %-points (improving from 54.5 % to 67.2 %, *SE* = 5.5, P9), and the largest reduction in performance was 13.9 %-points (decreasing from 36.1 % to 22.2 %, *SE* = 5.8, P7). There was also substantial variability within participants, with the difference in performance across sentence lists within a single session and condition being as much as 44.4 %-points (vibration on, session 1 for P6). After training, all ten participants correctly identified more keywords with tactile stimulation, with the smallest improvement being 0.5 %-points (improving from 67.8 % to 68.3 %; *SE* = 7.3 %, P8) and the largest improvement being 21.8 %-points (33.8 % to 55.6 %, *SE* = 4.2 %, P1). The mean improvement with tactile stimulation after training was 8.3 %-points (improving from 54.3 % to 62.5 %; *SE* = 2.5 %). It should be noted that, while the order of the sentence lists used for the two conditions (with and without tactile stimulation) was counterbalanced across our 10 participants, the sentence lists used were not fully counterbalanced between the two sessions (before and after training).

9.2.5 Discussion

EHS was found to significantly improve speech-in-noise performance after a short training regime. The regime consisted of just 20 minutes of exposure to speech-in-noise material with concurrent tactile stimulation. Tactile stimulation increased the number of words correctly identified by 8.3 %-points on average compared to audio alone, with some individuals improving by more than 20 %-points and no individuals decreasing in performance. This benefit was observed for speech in multi-talker noise, where CI users are known to struggle most (Oxenham & Kreft, 2014; Stickney *et al.*, 2004), and in which noise reduction algorithms typically perform poorly (Dawson *et al.*, 2011; Goehring *et al.*, 2017). This multi-sensory approach represents a way to augment the limited signal from the CI by presenting speech information through tactile stimulation of the wrist. The tactile signal was delivered at a vibration amplitude that could readily be achieved by a low-cost wearable device after computationally non-intensive signal processing suitable for a real-time application.

Fletcher *et al.* (2018), who presented speech envelope through tactile stimulation to the index finger of NHCIs, found a slightly larger benefit of tactile stimulation for speech-in-noise performance (10.8 %-points compared to 8.3 %-points, on average). The current study deployed tactile stimulation to the wrist, rather than the fingertip. The wrist, while being a more practical site for real-world use, has higher vibro-tactile thresholds than the fingertip (Summers *et al.*, 2005) and a lower density of mechanoreceptors (Vallbo & Johansson, 1978). However, researchers have shown better perception of amplitude differences at the wrist than at the fingertip as well as similar gap detection and discrimination of frequency differences(Summers *et al.*, 2005). It is therefore possible that the wrist could be similarly capable of transferring speech information. Another difference between the studies was that the current study was conducted in CI users who were older than the NHCIs tested by Fletcher *et al.* (61.2 years on average compared to 25.5 years). Tactile sensitivity is known to be reduced in older adults (Verrillo, 1982; Verrillo, Bolanowski, & Gescheider, 2002) and age also affects integration of information from more than one sense (de Dieuleveultet *al.*, 2017). These limitations may reduce the benefit of EHS in older CI users. Finally, there was less training (20 minutes compared to 30 minutes) in the current study. Training has been found to be highly important in previous work in tactile aids (with no concurrent audio signal (Brooks *et al.*, 1983) and large training effects were found both in the current study and in Fletcher *et al.* It therefore seems likely that the smaller amount of training used here may have led to a smaller benefit from tactile stimulation. Another study, by Huang *et al.* (Huang *et al.*, 2017), reported robust benefits to speech-in-noise performance from EHS without training when the fundamental frequency of speech was derived from the clean speech signal and presented to the fingertip. However, the size of the benefit is difficult to compare directly to the current results because of the different outcome measures and speech corpora used.

There was a great deal of variation in the size of the EHS benefit between individuals, with the improvement in performance after training ranging from 0.5 to 21.8 %-points. It is important for future research to establish which factors are most important in determining how much a CI user will benefit from EHS. For example, it should be established whether EHS can provide benefit in congenitally deaf individuals and those who became deaf prelingually. Interestingly, there is evidence of enhanced tactile sensitivity in congenitally deaf individuals (Levänen &

Hamdorf, 2001) and that congenitally deaf individuals are able to effectively integrate audio and tactile information (Nava *et al.*, 2014), suggesting that this group may benefit from EHS. It will also be important to establish which factors influence how much training is needed for EHS to be effective. Before training, there was large variability in the effect of EHS, with most participants' performance decreasing with tactile stimulation (by more than 10 %-points in two participants; P2 and P7), and one participant's performance improving by 12.8 %-points (P9). Both of the participants who had substantial decreases in performance with tactile stimulation before training reported to the experimenter that they found tactile stimulation distracting in the pre-training session. Intriguingly, the participant who improved with tactile stimulation before training had previously learned to play the flute using vibration from the instrument when they had a severe hearing impairment and before they were implanted. This may suggest that learning to use tactile cues for auditory stimuli can generalize from one context (in this case music) to another (in this case speech) and that the ability to use tactile cues can be retained over many years.

In the current study, training consisted of just 20 minutes of exposure to speech-in-noise and concurrent tactile stimulation over the course of two one-hour sessions, and no exposure to speech-in-noise alone. It is possible that the absence of training with speech-in-noise alone created a bias in the post-training testing session towards the condition with EHS. Training without tactile stimulation was not included as an increase in number of visits, a substantial increase in the duration of each visit, or a decrease in the already small amount of training with tactile stimulation would have been required. An increase in the number of visits would have made recruitment of participants, who often live a significant distance from the research centre and must meet our strict inclusion criteria (see *Participants*), extremely difficult. An increase in the one-hour session time was not deemed appropriate as participants reported finding the training very tiring. It was felt that biasing towards the condition with EHS was unlikely to have occurred for three main reasons: (i) participants "train" extensively on speech-in-noise without tactile stimulation in their everyday life outside of the laboratory sessions using the same CI settings as in the experiment; (ii) participants trained with different talkers and different material from in the testing sessions, and so were unable to generate a content- or talker-specific bias for EHS; and (iii) participant expectation that EHS would be beneficial was controlled by falsely instructing the participants that the experiment compared "audio enhancement" with "vibration enhancement". This instruction was reinforced in each trial in the testing sessions and the experimenter received no indication that participants were sceptical about the truth of this statement. Furthermore, the experimenter remained blinded to whether EHS was being provided throughout the testing sessions to prevent experimenter bias. In future work, we plan to develop a remote training programme to increase the training time available and thereby allow for further control of bias effects.

Future research could also explore whether EHS can enhance spatial hearing. Spatial hearing is severely impaired in CI users, particularly in those with only one implant (Litovsky *et al.*, 2006; Verschuur *et al.*, 2005), who make up 93 % of users in the UK (British Cochlear Implant Group, 2018). As well as allowing CI users to better locate auditory objects in space, improved spatial hearing might increase the release from masking that occurs when speech is in a separate spatial location to a masking sound (Freyman *et al.*, 1999; Hirsh, 1950; Yost *et al.* 1996). Remarkably, it has been shown that, using only tactile stimulation, subjects are able to discriminate the location of concurrent sounds whose direction of origin is separated by less than 5° (Richardson *et al.,* 1978). Furthermore, other research suggests that the tactile system can make use of tactile intensity differences that originate from sounds whose intensities differ by as little as 1 dB (Richardson & Frost, 1979). Such a difference in sound level between the ears (interaural level difference) would correspond to a horizontal angle change of just a few degrees for sounds with frequency content above ~1 kHz (Feddersen *et al.,* 1957). The current study was conducted with tactile stimulation to both wrists, a set up that could easily be adapted to provide interaural level difference cues to improve spatial hearing in CI users.

9.3 Electro-Haptics 3: Haptic enhancement of spatial hearing in cochlear implant users

9.3.1 Abstract

Cochlear implants (CIs) are neural prostheses that enable profoundly hearing-impaired people to perceive sounds. Although they are an astonishing achievement of modern medicine, crucial limitations remain. For instance, CI users are often poor at locating sounds, which can lead to impaired threat detection as well as social and educational deficits. We tested whether augmenting the limited signal from the CI by providing missing sound information through haptic stimulation improved performance on a horizontal plane localization task. Haptic stimulation dramatically improved localization ability, both with and without concurrent audio. Importantly, a short training regime allowed participants to effectively integrate spatial information from across the two senses to improve their performance. This multisensory approach could allow CI users with one implant using a smart wearable device to perform similarly to users who have received a second CI, without the need for an expensive, invasive surgical intervention.

9.3.2 Introduction

Cochlear implants (CIs) are neural prostheses that enable profoundly hearing-impaired people to perceive sounds through electrical stimulation of the auditory nerve. The CI is one of the greatest achievements of modern medicine. However, recent decades have not been marked by the huge improvements in CI technology that were seen in the 1980s and 1990s (Wilson, 2015), and CIs still have significant limitations (Dorman *et al.,* 2016; McDermott, 2004; Spriet *et al.*, 2007). One of the primary limitations is that CI users often struggle to locate and segregate sounds (Verschuur *et al.*, 2005), impairing threat detection and the deconstruction of complex acoustic scenes. In normal hearing individuals, the origin of a sound is determined by exploiting differences in the intensity and arrival time of sounds between the ears (interaural level and time differences), as well as by the direction-dependent spectral filtering of sounds by the pinnae, head, and torso. CI users have limited access to interaural level difference (ILD) and interaural time difference (ITD) cues, particularly the around 95% that are implanted only in one ear (Peters *et al.,* 2010). Furthermore, because of the poor spectral resolution of CIs and the fact that CI microphones are mounted behind the ear, CI users often also have severely limited access to the spectral cues usually given by the pinnae. We propose a new approach of enhancing spatial hearing in CI users by providing missing spatial hearing cues through haptic stimulation of the wrists.

There are several existing approaches for improving spatial hearing in CI users, although each has substantial limitations. For example, preservation of residual low-frequency acoustic hearing after implantation can give considerable benefits to sound localisation (Dorman *et al.*, 2016). However, this is only possible for a small proportion of CI users (around 9%; Verschuur, Hellier, & Teo, 2016) and residual hearing deteriorates at a faster rate after implantation (Wanna *et al.*, 2018). Localisation can also be improved through the implantation of a second CI in the other ear (Dorman *et al.*, 2016; Verschuur *et al.*, 2005). However, this approach is expensive, poses a surgical risk, risks vestibular dysfunction and the loss of residual hearing, and limits access to future technologies and therapies. Our approach of using haptics could bring enhanced localisation to the majority of CI candidates who do not have residual low-frequency hearing without the need for an expensive, invasive surgery to fit a second CI.

Haptic cues for spatial hearing have not previously been used to augment CI listening. However, historically, a small number of studies have looked at whether spatial cues can be provided to the upper arms (v. Békésy, 1955) or fingertips (Frost & Richardson, 1976; Gescheider, 1970; Richardson & Frost, 1979, 1979) of young normal-hearing listeners. In 1955, Von Bekesy described subjective reports of people being able to learn to locate sounds with the upper arms (von Békésy, 1955), and later studies using the fingertips provided further support for the idea that it may be possible to transfer spatial hearing cues through the skin (Frost & Richardson, 1976; Richardson & Frost, 1979). Furthermore, recent work has shown that speech-in-noise performance in CI users can be improved using haptic stimulation (Fletcher *et al.,* 2019; Fletcher *et al.*, 2018; Huang *et al.*, 2017). Together, this research suggests that haptic stimulation may be able to augment the limited electrical signal from the implant to enhance CI spatial hearing.

In the current study, we investigated whether electro-haptic cues can improve CI users localization of sounds. We derived our haptic signal from the audio stimulus that would be received by microphones behind each ear to match the signal received by a CI. The haptic stimulus consisted of the amplitude envelope of the speech taken from bands in a frequency range where the ILD is largest. The stimulus from each ear was then delivered to each corresponding wrist, meaning that the intensity difference between the wrists matched the intensity difference between the ears. Our signal processing and haptic signal delivery was designed to be readily deliverable by a low latency, low power-consumption, smart, wearable device.

In this study, we tested three hypotheses: 1) that participants will utilize the additional spatial hearing cues available through the haptic signal to localise stimuli more accurately in the combined audio and haptic condition than in the audio-only condition; 2), given the evidence of substantial training effects in previous work with haptic (Brooks *et al.*, 1983) and audio-haptic (Fletcher *et al.*, 2019, 2018; Huang *et al.*, 2017) stimuli, that participants' ability to locate sounds will improve in the audio-haptic condition after training; and 3) that, with training, multi-sensory integration of the audio and haptic cues will occur, resulting in more accurate sound localisation in the audio-haptic condition than in the haptic only condition. Both unilateral CI users (one cochlear implant) and bimodal users (one cochlear implant and a contralateral hearing aid) were tested in this study, to reflect the variety of implant and hearing aid configurations present in the population (Neuman *et al.*, 2017; Yamaguchi & Goffi-Gomez, 2013). Participants were tested using their everyday CI and hearing aid configuration to maximize ecological validity.

9.3.3 Methods

9.3.3.1 Participants

Twelve CI users (4 male, 8 female; mean age = 52.6 years old, ranging from 41 to 63 years old) were recruited through the University of Southampton Auditory Implant Service. All participants were native British English speakers, had been implanted at least 6 months prior to the experiment, and had the capacity to give informed consent. The participants completed a screening questionnaire, confirming that they had no medical conditions and were taking no medication that may affect their sense of touch. Table 1 details the characteristics of the participants who took part in the study. Participants were instructed to use their normal hearing set up and not to adjust their settings during the experiment, and included 7 unilateral users (a single implant), and 5 bimodal users (an implant and a contralateral hearing aid). One participant (P2) was categorized as having some residual hearing, defined here as having unaided thresholds at 250 and 500 Hz that are 65 dB HL or better in both ears.

Vibrotactile detection thresholds were measured at the fingertip and wrist at 31.5 Hz and 125 Hz following conditions and criteria specified in ISO 13091-1:2001. One participant (P7) had elevated thresholds at the fingertips of the left and right index fingers at 125 Hz. All others had vibrotactile detection thresholds within the normal range. The mean vibrotactile detection threshold at the skin of the wrist at 31.5 Hz (averaged across left and right wrists) was 0.65 ms^{-2} RMS, and at 125 Hz was 0.75 ms^{-2} RMS.

Table 8. Summary of participant characteristics. CI = Cochlear implant, HA = Hearing aid.

Participant	Gender	Age	Device Left	Device Right	Years since implantation
1	M	59	CI: Cochlear CP920	HA: ReSound	3.2
2	F	42	CI: Cochlear CP920	None	4.4
3	F	54	None	CI: MED-EL Rondo	4.3
4	F	50	HA: Danalogic	CI: Cochlear CP1000	5.6
5	M	44	CI: Advanced Bionics Nadia Q70	HA: Phonak [linked]	1.0
6	F	49	CI: Cochlear CP 1000	HA: Oticon	1.5
7	M	58	HA: Phonak [linked]	CI: Advanced Bionics Naida Q90	0.6

8	F	41	None	CI: Cochlear CP 1000	10.6
9	F	61	CI: Med-El Sonnet	None	2.4
10	M	63	None	CI: Advanced Bionics Q90	0.7
11	F	58	CI: Advanced Bionics Naida Q70	None	9.1
12	F	52	CI: Advanced Bionics Naida Q70	None	11.3

9.3.3.2 Stimuli

The speech stimulus consisted of recording of a female voice saying "*Where am I speaking from?*", recorded using a Rode M5 microphone in the small anechoic chamber at the Institute of Sound and Vibration Research (ISVR), UK. The speech signal was presented at a level of 65 dB SPL LAeq. The intensity of each presentation was roved randomly +/- 2.5 dB around 65 dB SPL to prevent participants learning to locate the speech based on absolute level cues. Each loudspeaker was calibrated at the listening position using a Brüel & Kjær (B&K) G4 type 2250 sound level meter (which was calibrated using a B&K type 4231 sound calibrator).

For the haptic signal, head-related transfer functions (HTRFs) were taken from The Oldenburg Hearing Device HRTF Database (Denk *et al.,* 2018) and applied to the speech signal separately for each loudspeaker position used in the experiment. The 3 microphone behind the ear ("BTE_MultiCh") HRTFs were used, in order to match a typical CI signal. The signal was the downsampled to a sampling frequency of 22050 Hz. Each channel of this stereo signal was then passed through an FIR filter bank with 4 frequency channels with center frequencies equally spaced on the ERB scale (Glasberg & Moore, 1990) so that the edge of the bands were between 1,000 and 10,000 Hz, a frequency range that contains the most speech energy (Byrne *et al.*, 1994) and large ILDs (Feddersen *et al.*, 1957). The Hilbert envelope for each frequency channel was calculated and a first-order low-pass filter was applied with a cut-off frequency of 10 Hz to extract the speech envelope. These signals were then used to modulate the amplitude envelopes of four fixed-phase tonal carriers with center frequencies of 50, 110, 170, and 230 Hz. These were then summed for presentation via the vibrometer. Haptic stimuli were presented at a maximum acceleration magnitude of 1.84 ms^{-2} RMS. The vibrometers were calibrated using a B&K type 4294 calibration exciter.

9.3.3.3 Apparatus

Participants were seated in the centre of the ISVR small anechoic chamber. Eleven Genelec 8020C PM Bi-Amplified Monitor System loudspeakers were positioned in an arc in front of the participant, from -75° to 75° arc, with 15° spacing between the loudspeakers. The speakers were placed 2 m from the centre of the participants head, at approximately the same height as their ears in a sitting position (1.16 m). The speakers were labelled L5, L4...R5 as illustrated in Figure 60. An acoustically treated 20" wide-screen monitor for displaying feedback and giving instruction was positioned on the floor 1 m in front of the participant. Two *HVLab* tactile vibrometers were placed beside the participant's chair and were used to deliver the vibro-tactile signal to the participants' wrists via a rigid 10-mm nylon probe with no surround to maximise the area of skin excitation. All stimuli were controlled using a custom MATLAB script (MATLAB 2018b) via a RME M-32 DA 32-Channel digital to analog converter.

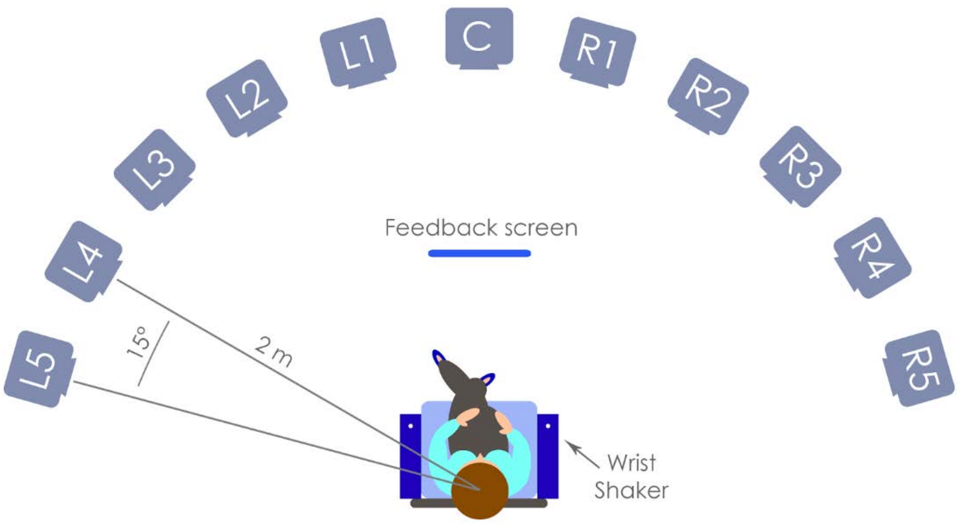

Figure 60. Schematic illustration of the experimental set up. On each trial the audio stimulus was presented through one of the 11 loudspeakers, positioned at points between 75° to the left and 75° to the right of the centre.

During testing, the experimenter sat in a separate control room. Participant verbal responses were monitored using a Shure BG 2.1 dynamic microphone placed low behind the participant's seat, amplified by a Creek OBH-21 headphone amplifier, and a pair of Sennhesier HD 380 Pro headphones. Participants were monitored visually using a Microsoft HD-3000 webcam.

9.3.3.4 Procedure

The experiment was conducted over two sessions not more than 5 days apart (average number of days = 1.58, *SE* = 0.38). In session 1, the participant first filled out a Health Questionnaire (Fletcher *et al.*, 2018) and had their vibrotactile thresholds measured following conditions and criteria specified in ISO 13091-1:2001. The task was then demonstrated to the participant by presenting the speech stimulus from speakers C (centre), L5 (hard left), and R5 (hard right). This demonstration was repeated for each of three conditions: Audio only, combined audio and haptic stimulation, and haptic stimulation only. At this stage, it was confirmed that the speech stimuli were clearly audible, and participants were given the opportunity to ask any questions.

A testing block of was then conducted, lasting around 20-25 minutes. In each trial the participant was instructed to fixate on the centre speaker (marked with a red cross), and to keep their head still. The speech stimulus was presented from one of the 11 loudspeakers, and the participant's task was to identify which one was the source. For each condition, the stimulus was presented from each speaker in a randomised order. This procedure was then repeated four times. Localization accuracy was calculated in terms of RMS error using the *D* statistic described by Rakerd and Hartman (1986). Chance performance level was estimated using a Monte Carlo simulation with 100,000 samples, assuming unbiased responses.

Responses were made verbally and recorded by the experimenter in the control room, who was blinded to the true source of the stimulus. The participant was monitored via webcam, to ensure that they did not move their head and were using the vibrators in the tactile stimulation conditions and removing their wrists in the audio only condition. The vibrators were near silent, but were left on in all conditions to control for any subtle audio cues.

After a break of at least 15 minutes, the participant completed a training block which was the same as the testing block except that stimuli were presented in a new randomised order and performance feedback was provided on the screen. The screen displayed an illustration of the speaker array. If the participant was correct, an illustration of the target speaker lit up green. If the participant was incorrect, an illustration of the their chosen speaker lit up red, and the target speaker lit up green.

In the second session, the participant completed a further training block, followed by a final testing block.

The experimental protocol was approved by the University of Southampton Ethics Committee (ERGO ID: 46201) and the UK National Health Service Research Ethics Service (Integrated Research Application System ID: 256879).

9.3.3.5 Statistics

Performance was calculated as root-mean-square (RMS) error from the target location in degrees arc for all trials in each condition within a session. Primary analysis of performance on the spatial hearing task consisted of a 3x2 repeated measures analysis of variance (ANOVA) with factors ‘Condition’ (Audio-only, Audio-haptic, or Haptic-only) and ‘Session’ (before or after training). Mauchly’s test indicated that the assumption of sphericity had been violated ($\chi^2(2) = 15.5$, $p < .001$), so degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity ($\varepsilon = 0.56$). The ANOVA used an alpha level of .05.

Post-hoc two-tailed t-tests were conducted to investigate these effects. Nine 2-tailed paired-samples t-tests (with a Bonferroni-Holm correction for multiple comparisons) were used to investigate performance across the three conditions and two sessions. Five 2-tailed independent samples t-tests (also with a Bonferroni-Holm correction) were conducted to analyse differences in performance between the seven unilateral and five bimodal CI users who took part in the study.

9.3.4 Results

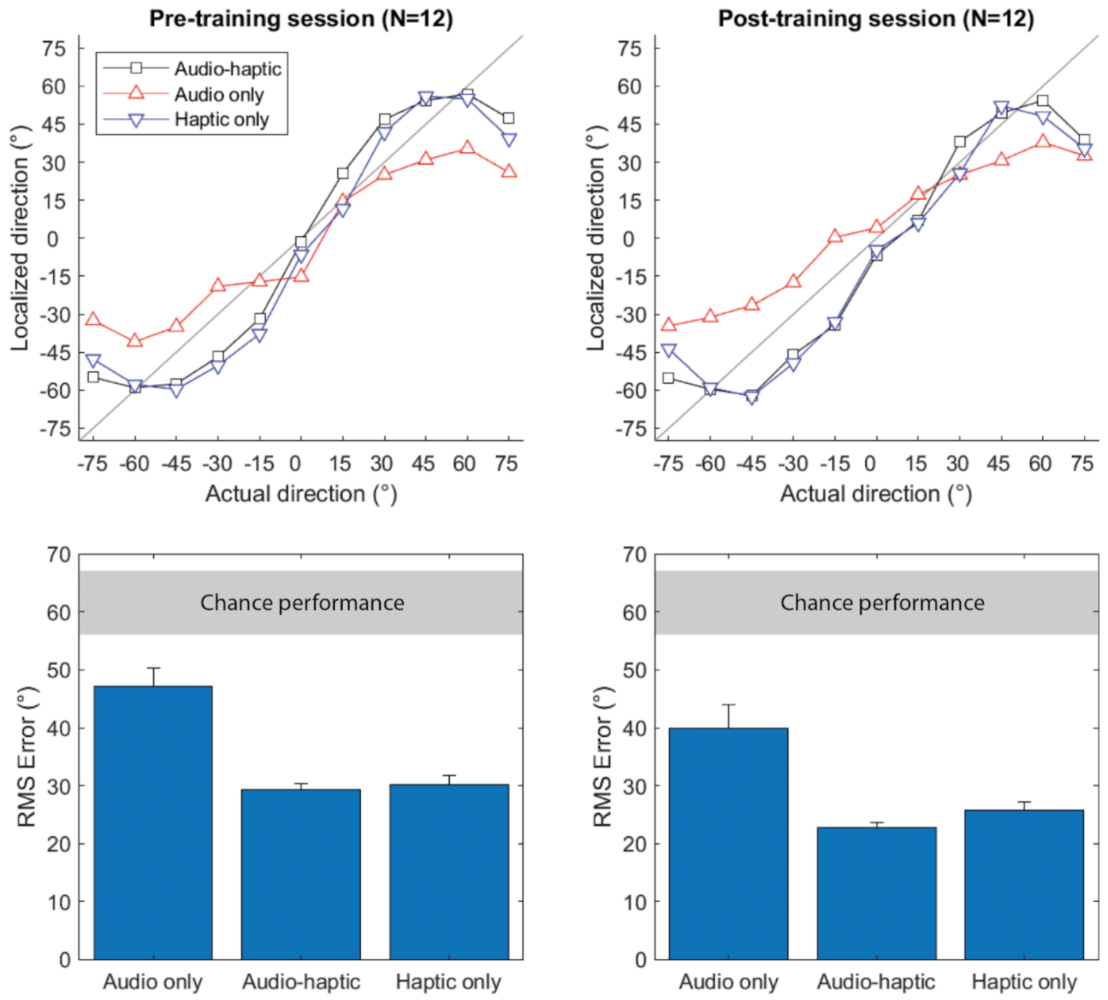

Figure 61. Performance in the horizontal plane localization task in Audio-only, Audio-haptic and Haptic-only conditions. The upper panels show mean response location against the actual source location of the target stimulus. The lower panels show RMS error for each condition before and after training, with the grey bar indicating chance performance (+/- 95 % confidence, assuming non-biased responses).

We tested 12 CI users' ability to localize a speech stimulus in the horizontal plane. Eleven loudspeakers were arranged in an arc around the participants from 75° to the left and right of centre, and participants were instructed to identify which loudspeaker a speech stimulus came from. We measured horizontal plane localization ability under three conditions: audio only, combined audio and haptic (Audio-haptic), and haptic only. Figure 61 illustrates these effects by showing localization performance across the three conditions before and after training (lower panels), as well as where participants perceived the source to be compared to true location of the speech stimulus (upper panels).

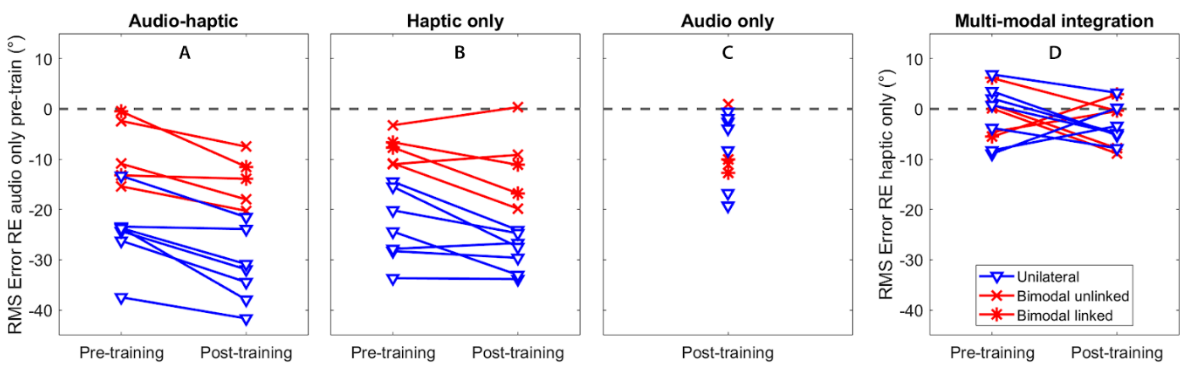

Figure 62. Individual performance enhancement (expressed as a reduction of RMS error) in the two sessions relative to performance in the audio-only condition in the pre-training session (panels A-C), and performance in the audio-haptic condition relative to the haptic-only condition (panel D). Users with unilateral device and bimodal configurations with and without linked devices are indicated by different lines and markers (see legend). All participants used their everyday settings for the task.

Primary analysis of the experimental results revealed that haptic stimulation enhanced localization performance for CI users ($F(1.2,12.3) = 25.3$, $p < .001$, $\eta_p^2 = .697$). We also found that localization performance improved between pre- and post-training testing sessions ($F(1,11) = 36.5$, $p < .001$, $\eta_p^2 = .768$). The interaction between these factors was non-significant ($F(1.9,14.6) = 1.0$, $p = .37$). To test the three hypotheses of the study, we first investigated whether participants were able to utilize the additional spatial hearing cues available through the haptic signal to localise stimuli more accurately. We found that RMS error was significantly lower in the Audio-haptic condition compared to the Audio-only condition both before training ($t(11) = 5.9$, $p < .001$, $d = 1.69$) and after training ($t(11) = 4.3$, $p = .005$, $d = 1.24$). Before training, root-mean-square (RMS) error reduced by 17.9°, from 47.2° to 29.3° on average (*SE* = 3.05). After training, RMS error reduced by 17.2° from 39.9° to 22.7° on average (*SE* = 4.0). All our participants performed better in the Audio-Haptic condition than the Audio-only condition in both sessions, with the benefit ranging from a 0.5° (P7, bimodal linked, pre-training) to a 37.7° reduction in RMS error (P8, unilateral, post-training). Figure 62 shows individual performance enhancement (expressed as a reduction of RMS error) in the two sessions relative to the Audio-only condition (panels A-C), and performance in the audio-haptic condition relative to the Haptic-only condition (panel D).

Next, we investigated our second hypothesis that completing a short training regime would allow participants to improve their ability to localise sounds using combined audio and haptic stimulation. Performance in the Audio-Haptic condition was found to be significantly better in the post-training session than in the pre-training session ($t(11) = 5.8$, $p < .001$, $d = 1.68$). With training, RMS error reduced by 6.6°, from an average of 29.3° to an average of 22.7°, in the Audio-Haptic condition (*SE* = 1.13).

Finally, we investigated our third hypothesis. We looked at whether completing the training regime allowed participants to integrate information from the audio and haptic stimulation to enhance localization performance. Although there was no difference in performance in the Haptic-only and Audio-haptic conditions in the pre-training session ($p = .566$), in the post-training session our CI users were able to locate sounds more accurately (a 3.1° enhancement) with Audio-haptic stimulation than with only haptic stimulation ($t(11) = 2.6$, $p = .048$, $d = .66$).

In further exploratory analysis, we found that even without audio cues, haptic stimulation was sufficient to discriminate spatial location. Localization performance was better in the Haptic-only condition than in the Audio-only condition, performing with a significantly smaller RMS error both before ($t(11) = 6.00$, $p < .001$, $d = 0.740$) and after training ($t(11) = 3.89$, $p = .012$, $d = 1.123$). We also observed that most participants were able to improve in the Audio-only condition between sessions, with RMS error reducing from an average of 47.2° to 39.9° (*SE* =1.95; $t(11) = 3.70$, $p = .012$, $d = 1.07$).

One factor that may have affected performance in the task is the hearing device configurations that our participants used. We measured performance in seven unilateral and five bimodal CI users. Two bimodal users were using a 'linked' configuration, in which a a CI in one ear and a hearing aid in the other ear share audio processing to improve hearing. All participants completed the task using their normal settings in order to retain the ecological validity of the study. We observed that the participants with unilateral configurations had poorer performance with audio cues alone than bimodal users (54.3° and 37.2° respectively before training; ($t(10) = 4.18$, $p = .008$, $d = 2.44$), but both groups reached a similar level of performance with audio and haptic combined (22.6° and 23.0° respectively). As such, they had a greater enhancement in performance from haptic stimulation than bimodal users (see Figure 2). Unilateral users had a significantly greater difference between performance in the Audio-haptic condition and the Audio-only condition than bimodal users in both the pretraining (24.6° vs 8.5°; $t(10) = 3.99$, $p = .009$, $d = 2.35$) and post-training sessions (24.1° vs 7.5°; $t(10) = 2.48$, $p = .034$, $d = 1.52$). They also had a significantly greater performance enhancement in the Haptic-only condition than bimodal users in both the pretraining ($t(10) = 4.54$, $p = .005$, $d = 2.83$) and post-training sessions ($t(10) = 2.85$, $p = .034$, $d = 1.68$).

9.3.5 Discussion

The vast majority of CI users are implanted in only one ear and are very poor at locating sounds. In this study, we tested whether CI users' localisation could be improved by presenting spatial hearing cues through haptic stimulation on the wrists. Auditory localisation accuracy improved substantially when auditory stimulation was combined with haptic stimulation. Even with no training, adding haptic stimulation reduced the RMS error from 47.2° to 29.3° on average. This performance is similar to the performance achieved by CI users with implants in both ears (~27°; Dorman *et al.*, 2016), or users with a CI in one ear and healthy hearing in the other (~28°; Dorman *et al.*, 2016). After a short training regime, participants' average RMS error with audio and haptic stimulation combined was reduced to just 22.7°, which is comparable to the performance of bilateral hearing aid users (~19°; Dorman *et al.*, 2016; Jousmäki & Hari, 1998) . These results suggest that haptic stimulation can be used to substantially improve localisation for CI users with one implant, without the need for expensive and invasive surgery to fit a second implant.

The size of the improvement given by adding haptic stimulation depended on participants' hearing device configuration. Our participants either had a CI in one ear and no device in the other (a unilateral configuration) or a CI in one ear and a hearing aid in the other (a bimodal configuration). Unilateral users had poorer localisation with audio only than bimodal users (54.3° and 37.2° respectively, before training), which is consistent with previous studies (Dorman *et al.*, 2016) and the fact that bimodal users are likely to have better access to spatial hearing cues. Despite this difference with audio only, both groups reached a similar level of performance with audio and haptic stimulation combined (22.6° and 23° after training, respectively). Therefore, as might be expected, combined audio and haptic stimulation appears to give the largest gains in performance for CI users who struggle most with audio only. After training, four out of seven unilateral participants performed more than 30° better with audio and haptic combined than with audio only. These large effects are particularly encouraging given that the authors know of no established alternative approach for improving localisation in CI users with a single device.

Importantly, a short training regime allowed participants to effectively combine spatial information from audio and haptic stimulation. We found that, after training, our participants performed better with audio and haptic stimulation together than with either audio only (17.2° better) or haptic stimulation only (3.1° better). In this study, both the audio and haptic signals were speech stimuli consisting of temporally complex amplitude modulations, rather than more simple stimuli (such as tones or noises). Recent work has provided strong evidence of the fundamental role of correlation detection in multisensory integration, and the importance of the temporal properties of the signals and their complexity[34–38]. Our use of more complex stimuli may have facilitated effective integration between information transmitted through the two senses. This multisensory enhancement in performance may also be expected based on previous psychophysical, physiological, and anatomical findings. Researchers have shown illusions demonstrating both that auditory stimuli can affect the perception of haptic stimuli (Jousmäki & Hari, 1998) and that haptic stimuli can affect the perception of auditory stimuli (Gick & Derrick, 2009). Multisensory interactions have also been been shown in the core auditory cortices of ferrets, where substantial populations of neurons that respond to auditory stimulation are modulated by tactile stimulation (Meredith & Allman, 2015). Furthermore, anatomical studies have shown the convergence of somatosensory input at many stages along the ascending auditory pathway, from the cochlear nucleus (the first node in the ascending auditory pathway) to core auditory cortices (Aitkin *et al.,* 1981; Allman, Keniston, & Meredith, 2009; Caetano & Jousmäki, 2006; Foxe *et al.*, 2000; Gobbelé *et al.*, 2003; Kanold *et al.*, 2010; Meredith & Allman, 2015; Shore *et al.*, 2003; Shore *et al.*, 2000). Collectively, these studies provide compelling evidence of strong links between audition and touch an offer a plausible neural basis for our finding that information from auditory and haptic stimulation can be effectively combined to improve behavioural performance.

The future development of a remote training system would allow us to study haptic enhancement of spatial hearing over longer time periods, using different training regimes. In general, previous work suggests that participants continue to improve their ability to extract information presented through tactile stimulation after many hours of training (Brooks *et al.*, 1983; Saunders *et al.*,1976; Sparks *et al.*, 1978; Weisenberger, 1986). In one study, a training regime was conducted in which two participants learned to identify words using only tactile stimulation (Brooks *et al.*, 1983). One participant trained for 40.5 hours in total, and learned 70 words in this time, and the other trained more rapidly, and after 55 hours, had learned 150 words. In both participants, training continued to substantially increase the number of words they were able to identify. There is also evidence that tactile stimulation can support lip-reading after an extensive training regime (Kishon-Rabin, Boothroyd, & Hanin, 1996). In the current study, we saw significant training effects in the Audio-haptic, Haptic-only, and Audio-only conditions. Some of the observed performance improvement over time could due to participants being able to better exploit spatial hearing cues for specific loudspeaker positions used in the experiment. However, previous work suggests that subjects can become more sensitive spatial hearing cues with training (Wright & Fitzgerald, 2001), which may suggest that these benefits can be generalized beyond the experimental procedure.

It will also be necessary to investigate ways of optimizing and improving the algorithms that generate the haptic signal. The haptic signal designed for use in this study exploited differences in intensity between the ears (ILDs), and presented this as differences in the intensity of the haptic signals between the wrists. Tactile sensitivity to temporal differences has not been as well characterized as intensity, and more research is needed before it can be determined if ITDs are also effective in conveying spatial information through haptic stimulation. Compression could also be applied to take into account individual vibrotactile thresholds, delivering haptic stimulation within a personalised dynamic range for each participant. Although this study shows that CI localization performance can be enhanced using haptic stimulation, it is important to note that the task took place under simplified acoustic conditions where participants identified the location of a single speech stimulus in the horizontal plane. Future work should therefore seek to expand this finding to more complex phenomena such as spatial release from masking, and how this could be improved through the application of noise reduction algorithms.

Future work should also build on the current results by investigating the advantages gained to spatial hearing performance from allowing head movement. Early research in young, normal-hearing listeners receiving haptic stimulation to the fingertip found that RMS error more than halved when head movement was allowed (Frost & Richardson, 1976; Richardson & Frost, 1979), and more recent work has provided evidence that head movement improved the spatial hearing of bilateral CI users using audio alone (Pastore *et al.*, 2018). This suggests that haptic stimulation based on the input from head mounted microphones could allow CI users to better localise and track moving sounds by moving their heads.

It will also be important to investigate whether the benefits to spatial hearing of training with haptic stimulation will persist when patients return to using a CI alone. Evidence from animal studies have suggested that multi-sensory training results in a long-standing improvement in performance in a single-sensory task (Meredith & Allman, 2015). Such an effect for CI users could be exploited to help recipients to adjust to their implant and improve their hearing outcomes over the long term.

Finally, future work might also build on the current study by assessing the effect of haptic stimulation on listening effort. CI users typically report high levels of listening effort and fatigue in everyday life (Alhanbali, Dawes, Lloyd, & Munro, 2017). The stress and fatigue associated with increased listening effort can lead to social and professional withdrawal (Kramer, Kapteyn, & Houtgast, 2006; Nachtegaal *et al.*, 2009), and could accelerate cognitive decline(Lin *et al.*, 2013). Anecdotally, it appears that haptic stimulation led to reduced listening effort in the current study. For example, one participant (P9) commented that “I was quicker and more comfortable giving an answer with both [audio and haptic stimulation]”. The idea that multisensory stimulation might reduce listening effort is supported by evidence that participants respond more quickly and accurately when they have multisensory stimulation than when the same stimuli presented to a sense in isolation (Hershenson, 1962; Kinchla, 1974). Future work could use existing psychophysical, psychophysiological or neuroimaging measures of listening effort to establish whether listening effort is reduced when haptic stimulation is provided to augment the CI signal.

In this study, we showed that providing spatial information to CI users through haptic stimulation substantially improves performance in a horizontal plane localization task. The haptic signal was delivered at a vibration amplitude that could readily be achieved by a low-cost, smart, wearable device after computationally non-intensive signal processing. This finding could have a huge clinical benefit to the vast majority of CI users with only one implant, without the expense and surgical risks associated with the implantation of a second cochlear implant. This multi-sensory approach represents a way to augment the limited signal from the CI, providing a much-needed new direction for CI research and treatment.

Chapter 10 Conclusions

The tactile system drives and informs our interactions with the surface of the world around us. Unfortunately, it is vulnerable to damage and degradation from illness or environmental exposure to vibration.

Our current methods for the diagnosis of impaired touch perception are marked by limitations in sensitivity, validity, and capacity to characterise the full action of the tactile channels. This thesis describes a research project that: 1) designed a vibrotactile psychophysical paradigm that measures the sensitivity of the tactile channels beyond the capacity of current methods, 2) extended the model of the tactile channels to a 2-level diagnosis model of the tactile channels. As this data emerged the opportunity arose to made links to applications of vibrotactile stimulation to the diagnosis and treatment of sensorineural disorders, especially in terms of providing haptic cues to CI users by exploiting the sensitivity of the skin to frequency and magnitude changes over time. This can be considered a related project that would not have been successful without the knowledge gained through the experiments conducted to advance the diagnostic model.

A series of psychophysical experiments were reported here. The first experiment instantiated and tested a two alternative forced choice paradigm for vibrotactile frequency discrimination and found that changes in contact area did not directly affect mean weber fractions for frequency, and suggested that acceleration magnitude was a key component in variation of weber fractions across participants and conditions. The second experiment builds on this work to evaluate the effect of recruiting additional channels on the sensitivity to frequency differences, finding that the recruitment of the RA channel results in a smaller weber fraction (better discrimination) of frequency differences than the PC channel alone, supporting the thesis that the specific function of the different tactile channels can be measured and assessed suprathreshold. The third experiment found that better discrimination of acceleration magnitude was also supported by cross-channel coding of suprathreshold vibrotactile input, but that this occurred irrespective of which channel was primary and which was secondary, making it a less useful metric of diagnostic channel identification. The fourth experiment measured the cross-channel coding of vibration frequency in far more detail, allowing us to inspect how weber fractions for vibration frequency undergo a step change with the recruitment of the RA channel at elevated acceleration magnitudes and at high frequencies. The results of these studies were then combined propose a suprathreshold, diagnostic model of the tactile channels, which could be used to augment current methods and may improve diagnostic and treatment outcomes.

These data have implications for other research disciplines. By considering the frequency and magnitude sensitivity of the tactile channels, we can generate vibration stimuli that are as 'rich' as possible in crucial information, which can be delivered and interpreted by the observer. A clear example of this is the case of CI users, who have a severely limited access to auditory information conveyed through their implant, particularly low-frequency information essential to perceiving speech in noise and spatial information. Part of an extensive research project is reported here, based on three peer-reviewed papers: Electro-haptics 1 reports a psychophysical experiment demonstrating that the provision of vibrotactile stimulation to the index finger substantially enhances speech-in-noise performance for normal hearing participants listening to CI simulations, and that this benefit increases with training; Electro-haptics 2 reports a second experiment, showing that similar stimulation provided to the skin of the wrist improves speech-in-noise performance for CI users after training; and Electro-haptics 3 reports an experiment showing that vibrotactile stimulation across the wrists dramatically enhances localization ability for CI users. The findings of this project provide a clear benefit, without any of the risk associated with the implantation of a second CI. As this approach becomes more closely integrated with tactile neuroscience, we would expect the size and utility of the electro-haptic effect to increase. Clear avenues for future research include the electro-haptic augmentation of music for CI users, and the effects of long-term training with custom smart wearable devices.

10.1 Key limitations

The following key limitations should be considered in interpreting the results of this research project.

- Although suprathreshold discrimination of vibration properties more closely resemble everyday touch in comparison to vibrotactile detection thresholds, a lack of ecological validity can be considered a limitation of this research, as it necessarily involves highly constrained experimental conditions.

- The general limitations of psychophysical methods should constrain interpretation of these data, including small sample sizes, limited participant populations, and vulnerability to procedural error.
- High degrees of variability were observed between participants' performance in the experiments. It remains unclear what factor(s) may have driven this variability.
- Statistical methodologies were chosen to maximise the accuracy and relevance of the experimental methods. Other methodologies may present advantages depending on the research context of future work.
- Similarly, space must be made for these results to be re-evaluated through other experimental methods, including neuroimaging and microneurography.
- The psychophysical approach employed here rested on a set of assumptions about the function of the tactile channels. Although these assumptions are reasonably founded on current understanding of perceptual psychology and neurophysiology, these assumptions must be continually challenged in order to advance psychophysical models and diagnostic methods.
- This thesis was limited by time and resources to the experimental testing of the PC and RA channels, selected on the basis of having a key involvement in the discrimination of vibration frequency. It is crucial that future research identify the function of further tactile channels in perception, and that these be practicably described by advanced diagnostic tools.
- The work to improve hearing for users of cochlear implants through vibrotactile stimulation (described here as 'electro-haptics') was founded on the knowledge gained in the larger part of the thesis. Nevertheless, this work will be improved in the future through a closer link to neurophysiological and psychophysical models of touch perception.
- Important limitations of this research included the site of vibrotactile stimulation and the general limitations of psychophysical research. Future research to expand these encouraging results to real world use of wearable devices will be crucial.

10.2 Contributions of this thesis

In summary, the experiments reported in this thesis have added knowledge about the function of the tactile system, established key methodological suggestions for the diagnosis of impaired touch perception, and made multi-sensory advances that could improve hearing outcomes for CI users.

List of References

Aaserud, O., Juntunen, J., & Matikainen, E. (1990). Vibration sensitivity thresholds: Methodological considerations. *Acta Neurologica Scandinavica*, *82*(4), 277–283.

Aitkin, L. M., Kenyon, C. E., & Philpott, P. (1981). The representation of the auditory and somatosensory systems in the external nucleus of the cat inferior colliculus. *Journal of Comparative Neurology*, *196*(1), 25–40.

Alhanbali, S., Dawes, P., Lloyd, S., & Munro, K. J. (2017). Self-reported listening-related effort and fatigue in hearing-impaired adults. *Ear and Hearing*, *38*(1), e39–e48.

Allman, B. L., Keniston, L. P., & Meredith, M. A. (2009). Adult deafness induces somatosensory conversion of ferret auditory cortex. *Proceedings of the National Academy of Sciences*, *106*(14), 5925–5930.

Bach-y-Rita, P. (1972). *Brain mechanisms in sensory substitution*. Academic Press Inc.

Bach-y-Rita, P., Carter C. Collins, Saunders, F. A., White, B., & Scadden, L. (1969). Vision Substitution by Tactile Image Projection. *Nature*, *221*(5184), 963–964. https://doi.org/10.1038/221963a0

Bensmaia, S. (2016). Texture from Touch. In T. Prescott, E. Ahissar, & E. Izhikevich (Eds.), *Scholarpedia of Touch* (pp. 207–215). https://doi.org/10.2991/978-94-6239-133-8_16

Bensmaia, S. J. (2008). Tactile intensity and population codes. *Behavioural Brain Research*, *190*(2), 165–173. https://doi.org/10.1016/j.bbr.2008.02.044

Bensmaïa, S. J., & Hollins, M. (2003). The vibrations of texture. *Somatosensory & Motor Research*, *20*(1), 33–43. https://doi.org/10.1080/0899022031000083825

Bensmaıa, S. J., & Hollins, M. (2000). Complex tactile waveform discrimination. *The Journal of the Acoustical Society of America*, *108*(3), 1236–1245.

Birznieks, I., Jenmalm, P., Goodwin, A. W., & Johansson, R. S. (2001). Encoding of direction of fingertip forces by human tactile afferents. *Journal of Neuroscience*, *21*(20), 8222–8237. Retrieved from Scopus.

Birznieks, Ingvars, Macefield, V. G., Westling, G., & Johansson, R. S. (2009). Slowly Adapting Mechanoreceptors in the Borders of the Human Fingernail Encode Fingertip Forces. *The Journal of Neuroscience*, *29*(29), 9370–9379. https://doi.org/10.1523/JNEUROSCI.0143-09.2009

Birznieks, Ingvars, Wheat, H. E., Redmond, S. J., Salo, L. M., Lovell, N. H., & Goodwin, A. W. (2010). Encoding of tangential torque in responses of tactile afferent fibres innervating the fingerpad of the monkey. *The Journal of Physiology*, *588*(7), 1057–1072. https://doi.org/10.1113/jphysiol.2009.185314

Bisley, J. W., Goodwin, A. W., & Wheat, H. E. (2000). Slowly Adapting Type I Afferents From the Sides and End of the Finger Respond to Stimuli on the Center of the Fingerpad. *Journal of Neurophysiology*, *84*(1), 57–64.

Blake, D. T., Hsiao, S. S., & Johnson, K. O. (1997). Neural Coding Mechanisms in Tactile Pattern Recognition: The Relative Contributions of Slowly and Rapidly Adapting Mechanoreceptors to Perceived Roughness. *The Journal of Neuroscience*, *17*(19), 7480–7489.

Bolanowski Jr, S. J., Gescheider, G. A., Verrillo, R. T., & Checkosky, C. M. (1988). Four channels mediate the mechanical aspects of touch. *The Journal of the Acoustical Society of America*, *84*(5), 1680–1694.

Bolanowski, S. J. (1984). Intensity and frequency characteristics of pacinian corpuscles. III. Effects of tetrodotoxin on transduction process. *Journal of Neurophysiology*, *51*(4), 831–839.

Bolanowski, S. J., Gescheider, G. A., Verrillo, R. T., & Checkosky, C. M. (1988). Four channels mediate the mechanical aspects of touch. *The Journal of the Acoustical Society of America*, *84*(5), 1680–1694. https://doi.org/10.1121/1.397184

Bolanowski, S. J., & Verrillo, R. T. (1982). Temperature and criterion effects in a somatosensory subsystem: A neurophysiological and psychophysical study. *Journal of Neurophysiology*, *48*(3), 836–855.
Bolanowski, S. J., & Zwislocki, J. J. (1984a). Intensity and frequency characteristics of pacinian corpuscles. I. Action potentials. *Journal of Neurophysiology*, *51*(4), 793–811.
Bolanowski, S. J., & Zwislocki, J. J. (1984b). Intensity and frequency characteristics of pacinian corpuscles. II. Receptor potentials. *Journal of Neurophysiology*, *51*(4), 812–830.
Bolanowski, Stanley J., Gescheider, G. A., & Verrillo, R. T. (1994). Hairy skin: Psychophysical channels and their physiological substrates. *Somatosensory & Motor Research*, *11*(3), 279–290.
Bovenzi, M. (1990). Medical aspects of the hand-arm vibration syndrome. *International Journal of Industrial Ergonomics*, *6*(1), 61–73. https://doi.org/10.1016/0169-8141(90)90051-3
Breeuwer, M., & Plomp, R. (1984). Speechreading supplemented with frequency-selective sound-pressure information. *The Journal of the Acoustical Society of America*, *76*(3), 686–691.
Brisben, A. J., Hsiao, S. S., & Johnson, K. O. (1999). Detection of Vibration Transmitted Through an Object Grasped in the Hand. *Journal of Neurophysiology*, *81*(4), 1548–1558.
British Cochlear Implant Group. (2018). Annual UK update. Retrieved 5 November 2018, from https://www.bcig.org.uk/annual-uk-update/
British Society of Audiology. (2017). Recommended procedure: Pure-tone air-conduction and bone-conduction threshold audiometry with and without masking. *British Society of Audiology*, 1–36.
Brooks, P. L., Frost, B. J., Mason, J. L., & Gibson, D. M. (1983). Identification of words and manner features of speech by two profoundly deaf teenagers using a tactile vocoder. *The Journal of the Acoustical Society of America*, *74*(S1), S105–S105. https://doi.org/10.1121/1.2020706
Brown, C. A., & Bacon, S. P. (2009). Low-frequency speech cues and simulated electric-acoustic hearing. *The Journal of the Acoustical Society of America*, *125*(3), 1658–1665. https://doi.org/10.1121/1.3068441
Byrne, D., Dillon, H., Tran, K., Arlinger, S., Wilbraham, K., Cox, R., … Ludvigsen, C. (1994). An international comparison of long-term average speech spectra. *The Journal of the Acoustical Society of America*, *96*(4), 2108–2120. https://doi.org/10.1121/1.410152
Caetano, G., & Jousmäki, V. (2006). Evidence of vibrotactile input to human auditory cortex. *NeuroImage*, *29*(1), 15–28. https://doi.org/10.1016/j.neuroimage.2005.07.023
Capelle, C., Trullemans, C., Arno, P., & Veraart, C. (1998). A real-time experimental prototype for enhancement of vision rehabilitation using auditory substitution. *IEEE Transactions on Biomedical Engineering*, *45*(10), 1279–1293. https://doi.org/10.1109/10.720206
Capraro, A. J., Verrillo, R. T., & Zwislocki, J. J. (1979). Psychophysical evidence for a triplex system of cutaneous mechanoreception. *Sensory Processes*. Retrieved from http://psycnet.apa.org/psycinfo/1982-04824-001
Carroll, J., Tiaden, S., & Zeng, F.-G. (2011). Fundamental frequency is critical to speech perception in noise in combined acoustic and electric hearing. *The Journal of the Acoustical Society of America*, *130*(4), 2054–2062.
Cascio, C. J., & Sathian, K. (2001). Temporal Cues Contribute to Tactile Perception of Roughness. *The Journal of Neuroscience*, *21*(14), 5289–5296.
Chang, J. E., Bai, J. Y., & Zeng, F.-G. (2006). Unintelligible low-frequency sound enhances simulated cochlear-implant speech recognition in noise. *IEEE Transactions on Biomedical Engineering*, *53*(12), 2598–2601.
Charmaz, K., & Belgrave, L. L. (2007). Grounded theory. *The Blackwell Encyclopedia of Sociology*.
Chung, K., & McKibben, N. (2011). Microphone directionality, pre-emphasis filter, and wind noise in cochlear implants. *Journal of the American Academy of Audiology*, *22*(9), 586–600.

Cohen, B., & Kirman, J. H. (1986). Vibrotactile frequency discrimination at short durations. *The Journal of General Psychology*, *113*(2), 179–186.

Cohen, R. H., & Vierk, C. J. V. (1993). Relationships between touch sensations and estimated population responses of peripheral afferent mechanoreceptors. *Experimental Brain Research*, *94*(1), 120–130. https://doi.org/10.1007/BF00230475

Collins, D. F., Refshauge, K. M., & Gandevia, S. C. (2000). Sensory integration in the perception of movements at the human metacarpophalangeal joint. *The Journal of Physiology*, *529*(2), 505–515. https://doi.org/10.1111/j.1469-7793.2000.00505.x

Collins, David F., & Prochazka, A. (1996). Movement illusions evoked by ensemble cutaneous input from the dorsum of the human hand. *The Journal of Physiology*, *496*(Pt 3), 857.

Connor, C. E., & Johnson, K. O. (1992). Neural coding of tactile texture: Comparison of spatial and temporal mechanisms for roughness perception. *The Journal of Neuroscience*, *12*(9), 3414–3426.

Craig, J. C. (1980). Modes of vibrotactile pattern generation. *Journal of Experimental Psychology: Human Perception and Performance*, *6*(1), 151–166. https://doi.org/10.1037/0096-1523.6.1.151

Craig, J. C., & Sherrick, C. E. (1969). The role of skin coupling in the determination of vibrotactile spatial summation. *Perception & Psychophysics*, *6*(2), 97–101. https://doi.org/10.3758/BF03210689

Cunningham, R. (2019) *Electro-haptic enhancement of spatial hearing.* University of Southampton, Faculty of Engineering and Physical Sciences, Master's dissertation.

Darian-Smith, I., Davidson, I., & Johnson, K. O. (1980). Peripheral neural representation of spatial dimensions of a textured surface moving across the monkey's finger pad. *The Journal of Physiology*, *309*, 135–146.

Dawson, P., Mauger, S., & Herbasch, A. (2011). Clinical evaluation of signal-to-noise ratio–based noise reduction in Nucleus® cochlear implant recipients. *Ear & Hearing*, *32*(3), 382–390.

de Dieuleveult, A. L., Siemonsma, P. C., van Erp, J. B. F., & Brouwer, A.-M. (2017). Effects of Aging in Multisensory Integration: A Systematic Review. *Frontiers in Aging Neuroscience*, *9*. https://doi.org/10.3389/fnagi.2017.00080

Debord, G.-E. (1955). Introduction to a Critique of Urban Geography. *Les Lèvres Nues*, *6*. Retrieved from http://library.nothingness.org/articles/SI/en/display/2

Deco, G., Scarano, L., & Soto-Faraco, S. (2007). Weber's law in decision making: Integrating behavioral data in humans with a neurophysiological model. *The Journal of Neuroscience*, *27*(42), 11192–11200.

Denk, F., Ernst, S. M., Ewert, S. D., & Kollmeier, B. (2018). Adapting hearing devices to the individual ear acoustics: Database and target response correction functions for various device styles. *Trends in Hearing*, *22*, 2331216518779313.

Dorman, M. F., Loiselle, L. H., Cook, S. J., Yost, W. A., & Gifford, R. H. (2016). Sound Source Localization by Normal-Hearing Listeners, Hearing-Impaired Listeners and Cochlear Implant Listeners. *Audiology and Neurotology*, *21*(3), 127–131. https://doi.org/10.1159/000444740

Dorman, M. F., Loizou, P. C., Fitzke, J., & Tu, Z. (1998). The recognition of sentences in noise by normal-hearing listeners using simulations of cochlear-implant signal processors with 6–20 channels. *The Journal of the Acoustical Society of America*, *104*(6), 3583–3585.

Doya, K., Ishii, S., Pouget, A., & Rao, R. P. (Eds.). (2007). *Bayesian brain: Probabilistic approaches to neural coding.* MIT press.

Drullman, R., & Bronkhorst, A. W. (2004). Speech perception and talker segregation: Effects of level, pitch, and tactile support with multiple simultaneous talkers. *The Journal of the Acoustical Society of America*, *116*(5), 3090–3098.

Drullman, R., Festen, J. M., & Plomp, R. (1994). Effect of temporal envelope smearing on speech reception. *The Journal of the Acoustical Society of America*, *95*(2), 1053–1064.

Duclaux, R., & Kenshalo, D. R. (1972). The temperature sensitivity of the Type I slowly adapting mechanoreceptors in cats and monkeys. *The Journal of Physiology*, *224*(3), 647-664.1.

Eck, J., Kaas, A. L., Mulders, J. L., Hausfeld, L., Kourtzi, Z., & Goebel, R. (2016). The Effect of Task Instruction on Haptic Texture Processing: The Neural Underpinning of Roughness and Spatial Density Perception. *Cerebral Cortex*, *26*(1), 384–401. https://doi.org/10.1093/cercor/bhu294

Edin, B. B., & Johansson, N. (1995). Skin strain patterns provide kinaesthetic information to the human central nervous system. *The Journal of Physiology*, *487*(1), 243–251. https://doi.org/10.1113/jphysiol.1995.sp020875

Faulkner, A., Ball, V., Rosen, S., Moore, B. C., & Fourcin, A. (1992). Speech pattern hearing aids for the profoundly hearing impaired: Speech perception and auditory abilities. *The Journal of the Acoustical Society of America*, *91*(4), 2136–2155.

Feddersen, W. E., Sandel, T. T., Teas, D. C., & Jeffress, L. A. (1957). Localization of High-Frequency Tones. *The Journal of the Acoustical Society of America*, *29*(9), 988–991. https://doi.org/10.1121/1.1909356

Fletcher, M. D., Mills, S. R., & Goehring, T. (2018). Vibro-Tactile Enhancement of Speech Intelligibility in Multi-talker Noise for Simulated Cochlear Implant Listening. Trends in hearing, 22, 2331216518797838.

Fletcher, M. D., Hadeedi, A., Goehring, T., & Mills, S. R. (2019). Electro-Haptic Enhancement of Speech-in-Noise Performance in Cochlear Implant Users. Scientific Reports, 9(1), 1-8.

Fletcher, M. D, Cunningham, R.O., & Mills, S. R. (2020). Electro-Haptic Enhancement of Spatial Hearing in Cochlear Implant Users. Scientific Reports, 10(1), 1-8.

Forta, N. G., Griffin, M. J., & Morioka, M. (2012). Vibrotactile difference thresholds: Effects of vibration frequency, vibration magnitude, contact area, and body location. *Somatosensory & Motor Research*, *29*(1), 28–37. https://doi.org/10.3109/08990220.2012.662182

Foxe, J. J., Morocz, I. A., Murray, M. M., Higgins, B. A., Javitt, D. C., & Schroeder, C. E. (2000). Multisensory auditory–somatosensory interactions in early cortical processing revealed by high-density electrical mapping. *Cognitive Brain Research*, *10*(1), 77–83. https://doi.org/10.1016/S0926-6410(00)00024-0

Franzén, O., & Nordmark, J. (1975). Vibrotactile frequency discrimination. *Perception & Psychophysics*, *17*(5), 480–484.

Freeman, A. W., & Johnson, K. O. (1982). A model accounting for effects of vibratory amplitude on responses of cutaneous mechanoreceptors in macaque monkey. *The Journal of Physiology*, *323*, 43–64.

Freyman, R. L., Helfer, K. S., McCall, D. D., & Clifton, R. K. (1999). The role of perceived spatial separation in the unmasking of speech. *The Journal of the Acoustical Society of America*, *106*(6), 3578–3588. https://doi.org/10.1121/1.428211

Frost, B. J., & Richardson, B. L. (1976). Tactile localization of sounds: Acuity, tracking moving sources, and selective attention. *The Journal of the Acoustical Society of America*, *59*(4), 907–914.

Gescheider, A., Bolanowski, S. J., & Hardick, K. R. (2001). The frequency selectivity of information-processing channels in the tactile sensory system. *Somatosensory & Motor Research*, *18*(3), 191–201.

Gescheider, G. A. (1976). Evidence in support of the duplex theory of mechanoreception. *Sensory Processes*. Retrieved from http://psycnet.apa.org/psycinfo/1980-00159-001

Gescheider, G. A., Berryhill, M. E., Verrillo, R. T., & Bolanowski, S. J. (1999). Vibrotactile temporal summation: Probability summation or neural integration? *Somatosensory & Motor Research*, *16*(3), 229–242.

Gescheider, G. A., Bolanowski, S. J., Hall, K. L., Hoffman, K. E., & Verrillo, R. T. (1994). The effects of aging on information-processing channels in the sense of touch: I. Absolute sensitivity. *Somatosensory & Motor Research*, *11*(4), 345–357.

Gescheider, G. A., Bolanowski, S. J., & Hardick, K. R. (2001). The frequency selectivity of information-processing channels in the tactile sensory system. *Somatosensory & Motor Research*, *18*(3), 191–201. https://doi.org/10.1080/01421590120072187
Gescheider, G. A., Bolanowski, S. J., & Verrillo, R. T. (2004). Some characteristics of tactile channels. *Behavioural Brain Research*, *148*(1–2), 35–40. https://doi.org/10.1016/S0166-4328(03)00177-3
Gescheider, G. A., Frisina, R. D., & Verrillo, R. T. (1979). Selective adaptation of vibrotactile thresholds. *Sensory Processes*, *3*(1), 37–48.
Gescheider, G. A., & Joelson, J. M. (1983). Vibrotactile temporal summation for threshold and suprathreshold levels of stimulation. *Perception & Psychophysics*, *33*(2), 156–162.
Gescheider, G. A., Verrillo, R. T., & Van Doren, C. L. (1982). Prediction of vibrotactile masking functions. *The Journal of the Acoustical Society of America*, *72*(5), 1421–1426.
Gescheider, George A. (1970). Some comparisons between touch and hearing. *IEEE Transactions on Man-Machine Systems*, *11*(1), 28–35.
Gescheider, George A. (1976). *Psychophysics: Method and theory.* Retrieved from http://psycnet.apa.org/psycinfo/1976-21684-000
Gescheider, George A., Bolanowski, S. J., & Verrillo, R. T. (2004). Some characteristics of tactile channels. *Behavioural Brain Research*, *148*(1), 35–40.
Gescheider, George A., Fay, R. R., Lyons, C. H., & others. (1978). Psychophysical tuning curves in vibrotaction. *Sensory Processes*. Retrieved from http://psycnet.apa.org/psycinfo/1980-22565-001
Gescheider, George A., O'Malley, M. J., & Verrillo, R. T. (1983). Vibrotactile forward masking: Evidence for channel independence. *The Journal of the Acoustical Society of America*, *74*(2), 474–485.
Gescheider, George A., Sklar, B. F., Van Doren, C. L., & Verrillo, R. T. (1985). Vibrotactile forward masking: Psychophysical evidence for a triplex theory of cutaneous mechanoreception. *The Journal of the Acoustical Society of America*, *78*(2), 534–543.
Gescheider, George A., Wright, J. H., & Verrillo, R. T. (2010a). *Information-processing channels in the tactile sensory system: A psychophysical and physiological analysis*. Psychology press.
Gescheider, George A., Wright, J. H., & Verrillo, R. T. (2010b). *Information-Processing Channels in the Tactile Sensory System: A Psychophysical and Physiological Analysis*. Psychology Press.
Gibson, J. J. (1962). Observations on active touch. *Psychological Review*, *69*(6), 477.
Gick, B., & Derrick, D. (2009). Aero-tactile integration in speech perception. *Nature*, *462*(7272), 502.
Glasberg, B. R., & Moore, B. C. (1990). Derivation of auditory filter shapes from notched-noise data. *Hearing Research*, *47*(1–2), 103–138.
Gobbelé, R., Schürmann, M., Forss, N., Juottonen, K., Buchner, H., & Hari, R. (2003). Activation of the human posterior parietal and temporoparietal cortices during audiotactile interaction. *NeuroImage*, *20*(1), 503–511. https://doi.org/10.1016/S1053-8119(03)00312-4
Goble, A. K., Collins, A. A., & Cholewiak, R. W. (1996). Vibrotactile threshold in young and old observers: The effects of spatial summation and the presence of a rigid surround. *The Journal of the Acoustical Society of America*, *99*(4), 2256–2269.
Goehring, T., Bolner, F., Monaghan, J. J. M., van Dijk, B., Zarowski, A., & Bleeck, S. (2017). Speech enhancement based on neural networks improves speech intelligibility in noise for cochlear implant users. *Hearing Research*, *344*, 183–194. https://doi.org/10.1016/J.HEARES.2016.11.012
Goff, G. D. (1967). Differential discrimination of frequency of cutaneous mechanical vibration. *Journal of Experimental Psychology*, *74*(2p1), 294.
Goodwin, A. W., John, K. T., & Marceglia, A. H. (1991). Tactile discrimination of curvature by humans using only cutaneous information from the fingerpads. *Experimental Brain Research*, *86*(3), 663–672. https://doi.org/10.1007/BF00230540

Goodwin, A. W., Macefield, V. G., & Bisley, J. W. (1997). Encoding of Object Curvature by Tactile Afferents From Human Fingers. *Journal of Neurophysiology*, *78*(6), 2881–2888.

Grange, J. A., Culling, J. F., Harris, N. S. L., & Bergfeld, S. (2017). Cochlear implant simulator with independent representation of the full spiral ganglion. *The Journal of the Acoustical Society of America*, *142*(5), EL484–EL489. https://doi.org/10.1121/1.5009602

Green, B. G. (1977). The effect of skin temperature on vibrotactile sensitivity. *Perception & Psychophysics*, *21*(3), 243–248.

Green, D. M., & Swets, J. A. (1966). Signal detection theory and psychophysics. 1966. *New York*, *888*, 889.

Griffin, M. J. (1990). Handbook of human vibration. *London: Academic*.

Griffin, M. J. (2008). Measurement, evaluation, and assessment of peripheral neurological disorders caused by hand-transmitted vibration. *International Archives of Occupational and Environmental Health*, *81*(5), 559–573.

Güçlü, B., & Bolanowski, S. J. (2004). Probability of stimulus detection in a model population of rapidly adapting fibers. *Neural Computation*, *16*(1), 39–58.

Hadeedi, A. (2018) *Can vibro-tactile stimulation enhance speech-in-noise performance in cochlear implant users?* University of Southampton, Faculty of Engineering and Physical Sciences, Master's dissertation.

Harada, N., & Griffin, M. J. (1991). Factors influencing vibration sense thresholds used to assess occupational exposures to hand transmitted vibration. *British Journal of Industrial Medicine*, *48*(3), 185–192.

Harvey, M. A., Saal, H. P., Dammann, J. F., & Bensmaia, S. J. (2013). Multiplexing Stimulus Information through Rate and Temporal Codes in Primate Somatosensory Cortex. *PLoS Biology*, *11*(5). https://doi.org/10.1371/journal.pbio.1001558

Hellström, Å. (1985). The time-order error and its relatives: Mirrors of cognitive processes in comparing. *Psychological Bulletin*, *97*(1), 35–61. https://doi.org/10.1037/0033-2909.97.1.35

Hershenson, M. (1962). Reaction time as a measure of intersensory facilitation. *Journal of Experimental Psychology*, *63*(3), 289.

Hirsh, I. J. (1950). The Relation between Localization and Intelligibility. *The Journal of the Acoustical Society of America*, *22*(2), 196–200. https://doi.org/10.1121/1.1906588

Hnath-Chisolm, T., & Kishon-Rabin, L. (1988). Tactile presentation of voice fundamental frequency as an aid to the perception of speech pattern contrasts. *Ear and Hearing*, *9*(6), 329–334.

Hollins, M. (2001). Vibrotactile adaptation impairs discrimination of fine, but not coarse, textures. *Somatosensory & Motor Research*, *18*(4), 253–262.

Hollins, M., & Bensmaïa, S. J. (2007). The coding of roughness. *Canadian Journal of Experimental Psychology/Revue Canadienne de Psychologie Expérimentale*, *61*(3), 184–195. https://doi.org/10.1037/cjep2007020

Hollins, M., Goble, A. K., Whitsel, B. L., & Tommerdahl, M. (1990). Time course and action spectrum of vibrotactile adaptation. *Somatosensory & Motor Research*, *7*(2), 205–221.

Hollins, M., & Risner, S. R. (2000). Evidence for the duplex theory of tactile texture perception. *Perception & Psychophysics*, *62*(4), 695–705.

Hollins, M., & Roy, E. A. (1996). Perceived Intensity of Vibrotactile Stimuli: The Role of Mechanoreceptive Channels. *Somatosensory & Motor Research*, *13*(3–4), 273–286. https://doi.org/10.3109/08990229609052583

Horch, K. (1991). Coding of vibrotactile stimulus frequency by Pacinian corpuscle afferents. *The Journal of the Acoustical Society of America*, *89*(6), 2827–2836.

Huang, J., Sheffield, B., Lin, P., & Zeng, F.-G. (2017). Electro-Tactile Stimulation Enhances Cochlear Implant Speech Recognition in Noise. *Scientific Reports*, *7*(1), 2196. https://doi.org/10.1038/s41598-017-02429-1

Hunt, C. C. (1974). The Pacinian Corpuscle. In *The Peripheral Nervous System* (pp. 405–420). https://doi.org/10.1007/978-1-4615-8699-9_15

International Organisation for Standardization. (2001). Mechanical vibration: Vibrotactile perception thresholds for the assessment of nerve dysfunction. Part 1: Methods of measurement at the fingertips. *ISO 13091-1:2001*.

Isaiah, A., Vongpaisal, T., King, A. J., & Hartley, D. E. H. (2014). Multisensory Training Improves Auditory Spatial Processing following Bilateral Cochlear Implantation. *Journal of Neuroscience*, *34*(33), 11119–11130. https://doi.org/10.1523/JNEUROSCI.4767-13.2014

Israr, A., Tan, H. Z., & Reed, C. M. (2005). Tactual frequency and amplitude discrimination with fixed and roving background. *2006 14th Symposium on Haptic Interfaces for Virtual Environment and Teleoperator Systems*, 383–385. IEEE.

Jenmalm, P., Birznieks, I., Goodwin, A. W., & Johansson, R. S. (2003). Influence of object shape on responses of human tactile afferents under conditions characteristic of manipulation. *European Journal of Neuroscience*, *18*(1), 164–176. https://doi.org/10.1046/j.1460-9568.2003.02721.x

Johansson, R. S. (1978). Tactile sensibility in the human hand: Receptive field characteristics of mechanoreceptive units in the glabrous skin area. *The Journal of Physiology*, *281*, 101.

Johansson, R. S., & Flanagan, J. R. (2009). Coding and use of tactile signals from the fingertips in object manipulation tasks. *Nature Reviews Neuroscience*, *10*(5), 345–359. https://doi.org/10.1038/nrn2621

Johansson, R. S., Landström, U., Lundström, R., & others. (1982). Responses of mechanoreceptive afferent units in the glabrous skin of the human hand to sinusoidal skin displacements. *Brain Research*, *244*(1), 17–25.

Johansson, R. S., & Vallbo, \AA B. (1979). Tactile sensibility in the human hand: Relative and absolute densities of four types of mechanoreceptive units in glabrous skin. *The Journal of Physiology*, *286*(1), 283–300.

Johnson, K. (2001). The roles and functions of cutaneous mechanoreceptors. *Current Opinion in Neurobiology*, *11*(4), 455–461. https://doi.org/10.1016/S0959-4388(00)00234-8

Johnson, K. O., & Lamb, G. D. (1981). Neural mechanisms of spatial tactile discrimination: Neural patterns evoked by braille-like dot patterns in the monkey. *The Journal of Physiology*, *310*(1), 117–144. https://doi.org/10.1113/jphysiol.1981.sp013540

Johnson, K. O., & Phillips, J. R. (1981). Tactile spatial resolution. I. Two-point discrimination, gap detection, grating resolution, and letter recognition. *Journal of Neurophysiology*, *46*(6), 1177–1192.

Johnson, K. O., Yoshioka, T., & Vega–Bermudez, F. (2000). Tactile functions of mechanoreceptive afferents innervating the hand. *Journal of Clinical Neurophysiology*, *17*(6), 539–558.

Johnson, K. O. (2001). The roles and functions of cutaneous mechanoreceptors. *Current Opinion in Neurobiology*, *11*(4), 455–461. https://doi.org/10.1016/S0959-4388(00)00234-8

Jones, F. N. (1974). History of psychophysics and judgment. *Handbook of Perception*, *2*, 1–22.

Jousmäki, V., & Hari, R. (1998). Parchment-skin illusion: Sound-biased touch. *Current Biology*, *8*(6), R190–R191.

Jouvet, D., & Laprie, Y. (2017). Performance analysis of several pitch detection algorithms on simulated and real noisy speech data. *2017 25th European Signal Processing Conference (EUSIPCO)*, 1614–1618. IEEE.

Kanold, P. O., Davis, K. A., & Young, E. D. (2010). Somatosensory context alters auditory responses in the cochlear nucleus. *Journal of Neurophysiology*, *105*(3), 1063–1070.

Kayser, C., Petkov, C. I., Augath, M., & Logothetis, N. K. (2005). Integration of touch and sound in auditory cortex. *Neuron*, *48*(2), 373–384.

Keidser, G., Ching, T., Dillon, H., Agung, K., Brew, C., Brewer, S., … Storey, L. (2002). The National Acoustic Laboratories (NAL) CDs of Speech and Noise for Hearing Aid Evaluation: Normative Data and Potential Applications. *Australian and New Zealand Journal of Audiology, The*, *24*(1), 16.

Kinchla, R. A. (1974). Detecting target elements in multielement arrays: A confusability model. *Perception & Psychophysics*, *15*(1), 149–158.
Kishon-Rabin, L., Boothroyd, A., & Hanin, L. (1996). Speechreading enhancement: A comparison of spatial-tactile display of voice fundamental frequency (F 0) with auditory F 0. *The Journal of the Acoustical Society of America*, *100*(1), 593–602.
Kong, Y.-Y., & Carlyon, R. P. (2007). Improved speech recognition in noise in simulated binaurally combined acoustic and electric stimulation. *The Journal of the Acoustical Society of America*, *121*(6), 3717. https://doi.org/10.1121/1.2717408
Kramer, S. E., Kapteyn, T. S., & Houtgast, T. (2006). Occupational performance: Comparing normally-hearing and hearing-impaired employees using the Amsterdam Checklist for Hearing and Work. *International Journal of Audiology*, *45*(9), 503–512. https://doi.org/10.1080/14992020600754583
Kreidler, S. M., Muller, K. E., Grunwald, G. K., Ringham, B. M., Coker-Dukowitz, Z. T., Sakhadeo, U. R., … Glueck, D. H. (2013). GLIMMPSE: Online Power Computation for Linear Models with and without a Baseline Covariate. *Journal of Statistical Software*, *54*(10). Retrieved from https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3882200/
Kuroki, S., Watanabe, J., & Nishida, S. (2012). Dissociation of Vibrotactile Frequency Discrimination Performances for Supra-Threshold and Near-Threshold Vibrations. In P. Isokoski & J. Springare (Eds.), *Haptics: Perception, Devices, Mobility, and Communication* (pp. 79–84). https://doi.org/10.1007/978-3-642-31404-9_14
Kuroki, S., Watanabe, J., & Nishida, S. (2013). Contribution of within-and cross-channel information to vibrotactile frequency discrimination. *Brain Research*, *1529*, 46–55.
Lacour, J. p., Dubois, D., Pisani, A., & Ortonne, J. p. (1991). Anatomical mapping of Merkel cells in normal human adult epidermis. *British Journal of Dermatology*, *125*(6), 535–542. https://doi.org/10.1111/j.1365-2133.1991.tb14790.x
Lamoré, P. J. J., & Keemink, C. J. (1988). Evidence for different types of mechanoreceptors from measurements of the psychophysical threshold for vibrations under different stimulation conditions. *The Journal of the Acoustical Society of America*, *83*(6), 2339–2351.
LaMotte, R. H., & Mountcastle, V. B. (1975). Capacities of humans and monkeys to discriminate vibratory stimuli of different frequency and amplitude: A correlation between neural events and psychological measurements. *Journal of Neurophysiology*, *38*(3), 539–559.
LaMotte, Robert H., & Srinivasan, M. A. (1991). Surface microgeometry: Tactile perception and neural encoding. In *Information processing in the somatosensory system* (pp. 49–58). Retrieved from http://link.springer.com/chapter/10.1007/978-1-349-11597-6_4
Laurienti, P. J., Burdette, J. H., Maldjian, J. A., & Wallace, M. T. (2006). Enhanced multisensory integration in older adults. *Neurobiology of Aging*, *27*(8), 1155–1163.
Lederman, S. J., & Klatzky, R. L. (1987). Hand movements: A window into haptic object recognition. *Cognitive Psychology*, *19*(3), 342–368.
Lederman, S. J., & Klatzky, R. L. (1993). Extracting object properties through haptic exploration. *Acta Psychologica*, *84*(1), 29–40.
Lederman, S. J., Loomis, J. M., & Williams, D. A. (1982). The role of vibration in the tactual perception of roughness. *Perception & Psychophysics*, *32*(2), 109–116.
Levänen, S., & Hamdorf, D. (2001). Feeling vibrations: Enhanced tactile sensitivity in congenitally deaf humans. *Neuroscience Letters*, *301*(1), 75–77.
Levitt, H. (1971). Transformed Up-Down Methods in Psychoacoustics. *The Journal of the Acoustical Society of America*, *49*(2B), 467–477. https://doi.org/10.1121/1.1912375
Litovsky, R. Y., Johnstone, P. M., & Godar, S. P. (2006). Benefits of bilateral cochlear implants and/or hearing aids in children. *International Journal of Audiology*, *45*(sup1), 78–91. https://doi.org/10.1080/14992020600782956
Mackevicius, E. L., Best, M. D., Saal, H. P., & Bensmaia, S. J. (2012). Millisecond precision spike timing shapes tactile perception. *The Journal of Neuroscience*, *32*(44), 15309–15317.

MacLeod, A., & Summerfield, Q. (1990). A procedure for measuring auditory and audio-visual speech-reception thresholds for sentences in noise: Rationale, evaluation, and recommendations for use. *British Journal of Audiology*, *24*(1), 29–43.

Macmillan, N. A., & Creelman, C. D. (1991). Detection theory: A user's guideCambridge Univ. *Press, New York*.

Maeda, S., & Griffin, M. J. (1994). A comparison of vibrotactile thresholds on the finger obtained with different equipment. *Ergonomics*, *37*(8), 1391–1406. https://doi.org/10.1080/00140139408964917

Mahns, D. A., Perkins, N. M., Sahai, V., Robinson, L., & Rowe, M. J. (2006). Vibrotactile frequency discrimination in human hairy skin. *Journal of Neurophysiology*, *95*(3), 1442–1450.

Mancini, F., Sambo, C. F., Ramirez, J. D., Bennett, D. L. H., Haggard, P., & Iannetti, G. D. (2013). A fovea for pain at the fingertips. *Current Biology: CB*, *23*(6), 496–500. https://doi.org/10.1016/j.cub.2013.02.008

Marco, E. J., Hinkley, L. B., Hill, S. S., & Nagarajan, S. S. (2011). Sensory processing in autism: a review of neurophysiologic findings. *Pediatr Res*, 69(5 Pt 2), 48R-54R.

Marks, L. E. (1979). Summation of vibrotactile intensity: An analog to auditory critical bands? *Sensory Processes*, *3*(2), 188–203.

McDermott, H. J. (2004). Music Perception with Cochlear Implants: A Review. *Trends in Amplification*, *8*(2), 49–82. https://doi.org/10.1177/108471380400800203

Meijer, P. B. L. (1992). An experimental system for auditory image representations. *IEEE Transactions on Biomedical Engineering*, *39*(2), 112–121. https://doi.org/10.1109/10.121642

Meredith, M. A., & Allman, B. L. (2015). Single-unit analysis of somatosensory processing in the core auditory cortex of hearing ferrets. *European Journal of Neuroscience*, *41*(5), 686–698.

Mills, S. R., & Griffin, M. J. (2018) Discrimination of the Frequency of Vibration Applied to the Finger at Two Acceleration Magnitudes. 53rd UK Conference on Human Responses to Vibration, Ascot, UK.

Mills, S. R., & Griffin, M. J. (2017) The Touch Perception Puzzle: A Basis for Choosing Stimulus Parameters in Vibrotactile Psychophysics. 52nd UK Conference on Human Responses to Vibration, Cranfield Defence Academy, UK.

Mills, S. R., Morioka, M., & Griffin, M. J. (2016). Limitations of Vibrotactile Thresholds. 51st UK Conference on Human Responses to Vibration, Institute of Naval Medicine, Gosport, UK.

Mills, S. R. (2019). Feel. In P. Dobraszczyk (Ed.), *Manchester: Something Rich and Strange*. Manchester: Manchester University Press.

Mills, S. R., & Fletcher, M. (2018). Playing sound through the skin improves hearing in noisy places. *The Conversation*. Retrieved from http://theconversation.com/playing-sound-through-the-skin-improves-hearing-in-noisy-places-97033

Mills, S. R., & Fletcher, M. (2019). Here's what music sounds like through an auditory implant. *The Conversation*. Retrieved from http://theconversation.com/heres-what-music-sounds-like-through-an-auditory-implant-112457

Morioka, M., & Griffin, M. J. (2002). Dependence of vibrotactile thresholds on the psychophysical measurement method. *International Archives of Occupational and Environmental Health*, *75*(1–2), 78–84.

Morley, J. W., Goodwin, A. W., & Darian-Smith, I. (1983). Tactile discrimination of gratings. *Experimental Brain Research*, *49*(2), 291–299.

Morley, J. W., & Rowe, M. J. (1990). Perceived pitch of vibrotactile stimuli: Effects of vibration amplitude, and implications for vibration frequency coding. *The Journal of Physiology*, *431*(1), 403–416. https://doi.org/10.1113/jphysiol.1990.sp018336

Mowbray, G., & Gebhard, J. (1957). Sensitivity of the skin to changes in rate of intermittent mechanical stimuli. *Science*, 125(3261), 1297.

Muniak, M. A., Ray, S., Hsiao, S. S., Dammann, J. F., & Bensmaia, S. J. (2007). The neural coding of stimulus intensity: Linking the population response of mechanoreceptive afferents with psychophysical behavior. *The Journal of Neuroscience*, *27*(43), 11687–11699.

Nachtegaal, J., Kuik, D. J., Anema, J. R., Goverts, S. T., Festen, J. M., & Kramer, S. E. (2009). Hearing status, need for recovery after work, and psychosocial work characteristics: Results from an internet-based national survey on hearing. *International Journal of Audiology*, *48*(10), 684–691.

Nava, E., Bottari, D., Villwock, A., Fengler, I., Büchner, A., Lenarz, T., & Röder, B. (2014). Audio-Tactile Integration in Congenitally and Late Deaf Cochlear Implant Users. *PLoS ONE*, *9*(6). https://doi.org/10.1371/journal.pone.0099606

Nelson, D. A., Kreft, H. A., Anderson, E. S., & Donaldson, G. S. (2011). Spatial tuning curves from apical, middle, and basal electrodes in cochlear implant users. *The Journal of the Acoustical Society of America*, *129*(6), 3916–3933.

Neuman, A. C., Waltzman, S. B., Shapiro, W. H., Neukam, J. D., Zeman, A. M., & Svirsky, M. A. (2017). Self-Reported Usage, Functional Benefit, and Audiologic Characteristics of Cochlear Implant Patients Who Use a Contralateral Hearing Aid. *Trends in Hearing*, *21*. https://doi.org/10.1177/2331216517699530

Ochoa, J., & Torebjörk, E. (1983). Sensations evoked by intraneural microstimulation of single mechanoreceptor units innervating the human hand. *The Journal of Physiology*, *342*, 633.

Olausson, H., Wessberg, J., & Kakuda, N. (2000). Tactile directional sensibility: Peripheral neural mechanisms in man. *Brain Research*, *866*(1–2), 178–187. https://doi.org/10.1016/S0006-8993(00)02278-2

Oxenham, A. J., & Kreft, H. A. (2014). Speech Perception in Tones and Noise via Cochlear Implants Reveals Influence of Spectral Resolution on Temporal Processing. *Trends in Hearing*, *18*, 233121651455378. https://doi.org/10.1177/2331216514553783

Paré, M., Behets, C., & Cornu, O. (2003). Paucity of presumptive ruffini corpuscles in the index finger pad of humans. *Journal of Comparative Neurology*, *456*(3), 260–266.

Paré, M., Smith, A. M., & Rice, F. L. (2002). Distribution and terminal arborizations of cutaneous mechanoreceptors in the glabrous finger pads of the monkey. *Journal of Comparative Neurology*, *445*(4), 347–359.

Peters, B. R., Wyss, J., & Manrique, M. (2010). Worldwide trends in bilateral cochlear implantation. *The Laryngoscope*, *120*(S2), S17–S44. https://doi.org/10.1002/lary.20859

Phillips, J. R., Johnson, K. O., & Hsiao, S. S. (1988). Spatial pattern representation and transformation in monkey somatosensory cortex. *Proceedings of the National Academy of Sciences*, *85*(4), 1317–1321.

Poulton, E. C., & Poulton, S. (1989). Bias in quantifying judgements. Taylor & Francis.

Qin, M. K., & Oxenham, A. J. (2006). Effects of introducing unprocessed low-frequency information on the reception of envelope-vocoder processed speech. *The Journal of the Acoustical Society of America*, *119*(4), 2417–2426.

Rabinowitz, W. M., Houtsma, A. J. M., Durlach, N. I., & Delhorne, L. A. (1987). Multidimensional tactile displays: Identification of vibratory intensity, frequency, and contactor area. *The Journal of the Acoustical Society of America*, *82*(4), 1243–1252.

Rakerd, B., & Hartmann, W. M. (1986). Localization of sound in rooms, III: Onset and duration effects. *The Journal of the Acoustical Society of America*, *80*(6), 1695–1706. https://doi.org/10.1121/1.394282

Richardson, B. L., & Frost, B. J. (1979). Tactile localization of the direction and distance of sounds. *Perception & Psychophysics*, *25*(4), 336–344. https://doi.org/10.3758/BF03198813

Richardson, B. L., Wuillemin, D. B., & Saunders, F. J. (1978). Tactile discrimination of competing sounds. *Perception & Psychophysics*, *24*(6), 546–550. https://doi.org/10.3758/BF03198782

Rothenberg, M., Verrillo, R. T., Zahorian, S. A., Brachman, M. L., & Bolanowski, S. J. (1977). Vibrotactile frequency for encoding a speech parameter. *The Journal of the Acoustical Society of America*, *62*(4), 1003–1012.

Rouger, J., Lagleyre, S., Fraysse, B., Deneve, S., Deguine, O., & Barone, P. (2007). Evidence that cochlear-implanted deaf patients are better multisensory integrators. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(17), 7295–300. https://doi.org/10.1073/pnas.0609419104

Roy, E. A., & Hollins, M. (1998). A ratio code for vibrotactile pitch. *Somatosensory & Motor Research*, *15*(2), 134–145. https://doi.org/10.1080/08990229870862

Saal, H. P., & Bensmaia, S. J. (2014a). Touch is a team effort: Interplay of submodalities in cutaneous sensibility. *Trends in Neurosciences*, *37*(12), 689–697. https://doi.org/10.1016/J.TINS.2014.08.012

Saal, H. P., & Bensmaia, S. J. (2014b). Touch is a team effort: Interplay of submodalities in cutaneous sensibility. *Trends in Neurosciences*, *37*(12), 689–697. https://doi.org/10.1016/j.tins.2014.08.012

Salimi, I., Brochier, T., & Smith, A. M. (1999). Neuronal activity in somatosensory cortex of monkeys using a precision grip. I. Receptive fields and discharge patterns. *Journal of Neurophysiology*, *81*(2), 825–834. Retrieved from Scopus.

Salinas, E., Hernández, A., Zainos, A., & Romo, R. (2000). Periodicity and Firing Rate As Candidate Neural Codes for the Frequency of Vibrotactile Stimuli. *The Journal of Neuroscience*, *20*(14), 5503–5515.

Saunders, F., Hill, W., & Simpson, C. (1976). Speech perception via the tactile mode: Progress report. *ICASSP'76. IEEE International Conference on Acoustics, Speech, and Signal Processing*, *1*, 594–597. IEEE.

Schorr, E. A., Fox, N. A., van Wassenhove, V., & Knudsen, E. I. (2005). Auditory-visual fusion in speech perception in children with cochlear implants. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(51), 18748–50. https://doi.org/10.1073/pnas.0508862102

Shannon, R. V., Zeng, F.-G., Kamath, V., Wygonski, J., & Ekelid, M. (1995). Speech recognition with primarily temporal cues. *Science*, *270*(5234), 303–304.

Sherrick, C. E. (1984). Basic and applied research on tactile aids for deaf people: Progress and prospects. *The Journal of the Acoustical Society of America*, *75*(5), 1325–1342.

Shore, S. E., El Kashlan, H., & Lu, J. (2003). Effects of trigeminal ganglion stimulation on unit activity of ventral cochlear nucleus neurons. *Neuroscience*, *119*(4), 1085–1101.

Shore, Susan E., Vass, Z., Wys, N. L., & Altschuler, R. A. (2000). Trigeminal ganglion innervates the auditory brainstem. *Journal of Comparative Neurology*, *419*(3), 271–285.

Skedung, L., Arvidsson, M., Chung, J. Y., Stafford, C. M., Berglund, B., & Rutland, M. W. (2013). Feeling small: Exploring the tactile perception limits. *Scientific Reports*, *3*, 2617. https://doi.org/10.1038/srep02617

Sparks, D. W., Kuhl, P. K., Edmonds, A. E., & Gray, G. P. (1978). Investigating the MESA (Multipoint Electrotactile Speech Aid): The transmission of segmental features of speech. *The Journal of the Acoustical Society of America*, *63*(1), 246–257.

Spriet, A., Van Deun, L., Eftaxiadis, K., Laneau, J., Moonen, M., van Dijk, B., … Wouters, J. (2007). Speech Understanding in Background Noise with the Two-Microphone Adaptive Beamformer BEAM in the Nucleus Freedom Cochlear Implant System. *Ear and Hearing*, *28*(1), 62–72. https://doi.org/10.1097/01.aud.0000252470.54246.54

Srinivasan, M. A., & LaMotte, R. H. (1991). Encoding of Shape in the Responses of Cutaneous Mechanoreceptors. In O. Franzén & J. Westman (Eds.), *Information Processing in the Somatosensory System* (pp. 59–69). https://doi.org/10.1007/978-1-349-11597-6_5

Stickney, G. S., Zeng, F.-G., Litovsky, R., & Assmann, P. (2004). Cochlear implant speech recognition with speech maskers. *The Journal of the Acoustical Society of America*, *116*(2), 1081–1091.

Strauss, A., & Corbin, J. M. (1990). *Basics of qualitative research: Grounded theory procedures and techniques.* Sage Publications, Inc.
Su, Z., Fishel, J. A., Yamamoto, T., & Loeb, G. E. (2014). Use of tactile feedback to control exploratory movements to characterize object compliance. *Active Touch Sensing*, 51.
Sumby, W. H., & Pollack, I. (1954). Visual contribution to speech intelligibility in noise. *The Journal of the Acoustical Society of America*, *26*(2), 212–215.
Summers, I. R., Cooper, P. G., Wright, P., Gratton, D. A., Milnes, P., & Brown, B. H. (1997). Information from time-varying vibrotactile stimuli. *The Journal of the Acoustical Society of America*, *102*(6), 3686–3696.
Summers, I. R., Whybrow, J. J., Gratton, D. A., Milnes, P., Brown, B. H., & Stevens, J. C. (2005). Tactile information transfer: A comparison of two stimulation sites. *The Journal of the Acoustical Society of America*, *118*(4), 2527–2534. https://doi.org/10.1121/1.2031979
Thornton, A. R. D., & Phillips, A. J. (1992). A comparative trial of four vibrotactile aids. *Tactile Aids for the Hearing Impaired Ed. IR Summers (London: Whurr) Pp*, 231–251.
Tommerdahl, M., Hester, K. D., Felix, E. R., Hollins, M., Favorov, O. V., Quibrera, P. M., & Whitsel, B. L. (2005). Human vibrotactile frequency discriminative capacity after adaptation to 25 Hz or 200 Hz stimulation. *Brain Research*, *1057*(1), 1–9.
Treisman, M. (1964). The effect of one stimulus on the threshold for another: an application of signal detectability theory. *British Journal of Statistical Psychology*, *17*(1), 15–35.
Trotter, P. D., McGlone, F., Reniers, R. L. E. P., & Deakin, J. F. W. (2018). Construction and Validation of the Touch Experiences and Attitudes Questionnaire (TEAQ): A Self-report Measure to Determine Attitudes Toward and Experiences of Positive Touch. *Journal of Nonverbal Behavior*, *42*(4), 379–416. https://doi.org/10.1007/s10919-018-0281-8
Vallbo, A. B., Johansson, R. S., & others. (1984). Properties of cutaneous mechanoreceptors in the human hand related to touch sensation. *Hum Neurobiol*, *3*(1), 3–14.
Vallbo, A., & Johansson, R. (1978). The tactile sensory innervation of the glabrous skin of the human hand. In *Active Touch, the Mechanism of Recognition of Objects by Manipulation*. Oxford: Pergamom Press.
Van Doren, C. L. (1985). Temporal summation by Pacinian corpuscles precludes entrainment at the detection threshold. *The Journal of the Acoustical Society of America*, *77*(6), 2188–2189.
Vega-Bermudez, F., & Johnson, K. O. (1999). Surround Suppression in the Responses of Primate SA1 and RA Mechanoreceptive Afferents Mapped with a Probe Array. *Journal of Neurophysiology*, *81*(6), 2711–2719.
Verrillo, R. T. (1965). Temporal summation in vibrotactile sensitivity. *The Journal of the Acoustical Society of America*, *37*(5), 843–846.
Verrillo, R. T. (1966). Effect of spatial parameters on the vibrotactile threshold. *Journal of Experimental Psychology*, *71*(4), 570.
Verrillo, R. T. (1985). Psychophysics of vibrotactile stimulation. *The Journal of the Acoustical Society of America*, *77*(1), 225–232.
Verrillo, R. T., & Bolanowski, S. J. (1986). The effects of skin temperature on the psychophysical responses to vibration on glabrous and hairy skin. *The Journal of the Acoustical Society of America*, *80*(2), 528–532.
Verrillo, R. T., Fraioli, A. J., & Smith, R. L. (1969). Sensation magnitude of vibrotactile stimuli. *Perception & Psychophysics*, *6*(6), 366–372.
Verrillo, R. T., & Gescheider, G. A. (1975). Enhancement and summation in the perception of two successive vibrotactile stimuli. *Perception & Psychophysics*, *18*(2), 128–136. https://doi.org/10.3758/BF03204100
Verrillo, R. T., & Gescheider, G. A. (1977). Effect of prior stimulation on vibrotactile thresholds. *Sensory Processes*, *1*(4), 292–300.
Verrillo, R. (1963a). Effect of contactor area on the vibrotactile threshold. *The Journal of the Acoustical Society of America*, *35*(12), 1962–1966.

Verrillo, R. (1963b). Effect of contactor area on the vibrotactile threshold. *The Journal of the Acoustical Society of America*, *35*(12), 1962–1966.
Verrillo, R. (1968). A duplex mechanism of mechanoreception. *The Skin Senses*, 139–159.
Verrillo, R. (1982). Effects of aging on the suprathreshold responses to vibration. *Perception & Psychophysics*, *32*(1), 61–68. https://doi.org/10.3758/BF03204869
Verrillo, R., Bolanowski, S. J., & Gescheider, G. A. (2002). Effect of aging on the subjective magnitude of vibration. *Somatosensory & Motor Research*, *19*(3), 238–244. https://doi.org/10.1080/0899022021000009161
Verschuur, C. A., Lutman, M. E., Ramsden, R., Greenham, P., & O'Driscoll, M. (2005). Auditory Localization Abilities in Bilateral Cochlear Implant Recipients. *Otology & Neurotology*, *26*(5), 965. https://doi.org/10.1097/01.mao.0000185073.81070.07
Verschuur, C., Hellier, W., & Teo, C. (2016). An evaluation of hearing preservation outcomes in routine cochlear implant care: Implications for candidacy. *Cochlear Implants International*, *17*(sup1), 62–65. https://doi.org/10.1080/14670100.2016.1152007
von Békésy, G. (1939). *Über die Vibrationsempfindung*. S. Hirzel.
von Békésy, G. (1955). Human skin perception of traveling waves similar to those on the cochlea. *The Journal of the Acoustical Society of America*, *27*(5), 830–841.
Wagenmakers, E.-J., Marsman, M., Jamil, T., Ly, A., Verhagen, J., Love, J., … Epskamp, S. (2018). Bayesian inference for psychology. Part I: Theoretical advantages and practical ramifications. *Psychonomic Bulletin & Review*, *25*(1), 35–57.
Waldstein, R. S., & Boothroyd, A. (1995). Comparison of two multichannel tactile devices as supplements to speechreading in a postlingually deafened adult. *Ear and Hearing*, *16*(2), 198–208.
Wanna, G. B., O'Connell, B. P., Francis, D. O., Gifford, R. H., Hunter, J. B., Holder, J., … Haynes, D. S. (2018). Predictive factors for short- and long term hearing preservation in cochlear implantation with conventional length electrodes. *The Laryngoscope*, *128*(2), 482–489. https://doi.org/10.1002/lary.26714
Weber, A. I., Saal, H. P., Lieber, J. D., Cheng, J.-W., Manfredi, L. R., Dammann, J. F., & Bensmaia, S. J. (2013). Spatial and temporal codes mediate the tactile perception of natural textures. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(42), 17107–17112. https://doi.org/10.1073/pnas.1305509110
Weisenberger, J. M. (1986). Sensitivity to amplitude-modulated vibrotactile signals. *The Journal of the Acoustical Society of America*, *80*(6), 1707–1715. https://doi.org/10.1121/1.394283
Weisenberger, J. M., Broadstone, S. M., & Saunders, F. A. (1989). Evaluation of two multichannel tactile aids for the hearing impaired. *The Journal of the Acoustical Society of America*, *86*(5), 1764–1775. https://doi.org/10.1121/1.398608
Westling, G., & Johansson, R. S. (1987). Responses in glabrous skin mechanoreceptors during precision grip in humans. *Experimental Brain Research*, *66*(1), 128–140. https://doi.org/10.1007/BF00236209
Whitehouse, D. J., & Griffin, M. J. (2002). A comparison of vibrotactile thresholds obtained using different diagnostic equipment: The effect of contact conditions. *International Archives of Occupational and Environmental Health*, *75*(1–2), 85–89.
Wilson, B. S. (2015). Getting a decent (but sparse) signal to the brain for users of cochlear implants. *Hearing Research*, *322*, 24–38.
Witney, A. G., Wing, A., Thonnard, J.-L., & Smith, A. M. (2004). The cutaneous contribution to adaptive precision grip. *Trends in Neurosciences*, *27*(10), 637–643. https://doi.org/10.1016/j.tins.2004.08.006
Wouters, J., & Vanden Berghe, J. (2001). Speech recognition in noise for cochlear implantees with a two-microphone monaural adaptive noise reduction system. *Ear and Hearing*, *22*(5), 420–30.
Wright, B. A., & Fitzgerald, M. B. (2001). Different patterns of human discrimination learning for two interaural cues to sound-source location. *Proceedings of the National Academy of Sciences*, *98*(21), 12307–12312. https://doi.org/10.1073/pnas.211220498

Yamaguchi, C. T., & Goffi-Gomez, M. V. S. (2013). Prevalence of Contralateral Hearing Aid Use in Adults with Cochlear Implants. *International Archives of Otorhinolaryngology*, *17*(4), 370–374. https://doi.org/10.1055/s-0033-1352501

Yıldız, M. Z., Toker, İ., Özkan, F. B., & Güçlü, B. (2015). Effects of passive and active movement on vibrotactile detection thresholds of the Pacinian channel and forward masking. *Somatosensory & Motor Research*, *32*(4), 262–272.

Yost, W. A., Dye, R. H., & Sheft, S. (1996). A simulated “cocktail party” with up to three sound sources. *Perception & Psychophysics*, *58*(7), 1026–1036.

Zeng, F.-G., Rebscher, S., Harrison, W., Sun, X., & Feng, H. (2008). Cochlear implants: System design, integration, and evaluation. *IEEE Reviews in Biomedical Engineering*, *1*, 115–142.

Zwicker, E., & Scharf, B. (1965). A model of loudness summation. *Psychological Review*, *72*(1), 3–26. https://doi.org/10.1037/h0021703

Appendix A Health Questionnaire

UNIVERSITY OF Southampton

Pre-Experiment Questionnaire

Study Title: Effects of magnitude on vibration discrimination

Researcher: Sean R Mills

Ethics Reference number: 41875

Participant Number:

Please answer the questions below. The experimenter will help with your hand measurements. All information will be treated as CONFIDENTIAL.

Name: ___________________________________

Age: _____________ Gender: ________

Dominant hand (*please tick one*):

Left-Handed ☐ Right-Handed ☐

Hand length:_____________ Hand circumference:____________

Screening questions

These questions are to see if you are suitable for this experimental study of touch perception. Please read each question carefully and *tick one answer*. Ask the experimenter if you have any questions.

	Yes	No
Do you have any conditions that might affect your sense of touch? (e.g. Hand-Arm Vibration Syndrome, Diabetes, Autism Spectrum Disorder, Dyspraxia…)	☐	☐
Are you taking any medication that might affect your perception? (e.g. Opiates)	☐	☐
Have you had any injury or surgery on your hands?	☐	☐
Have you been exposed to severe or long periods of hand vibration? (e.g. Motorbike, power tools…)	☐	☐
Have you had any very recent exposure to hand vibration?	☐	☐

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Appendix B Individual data for Experiment 1

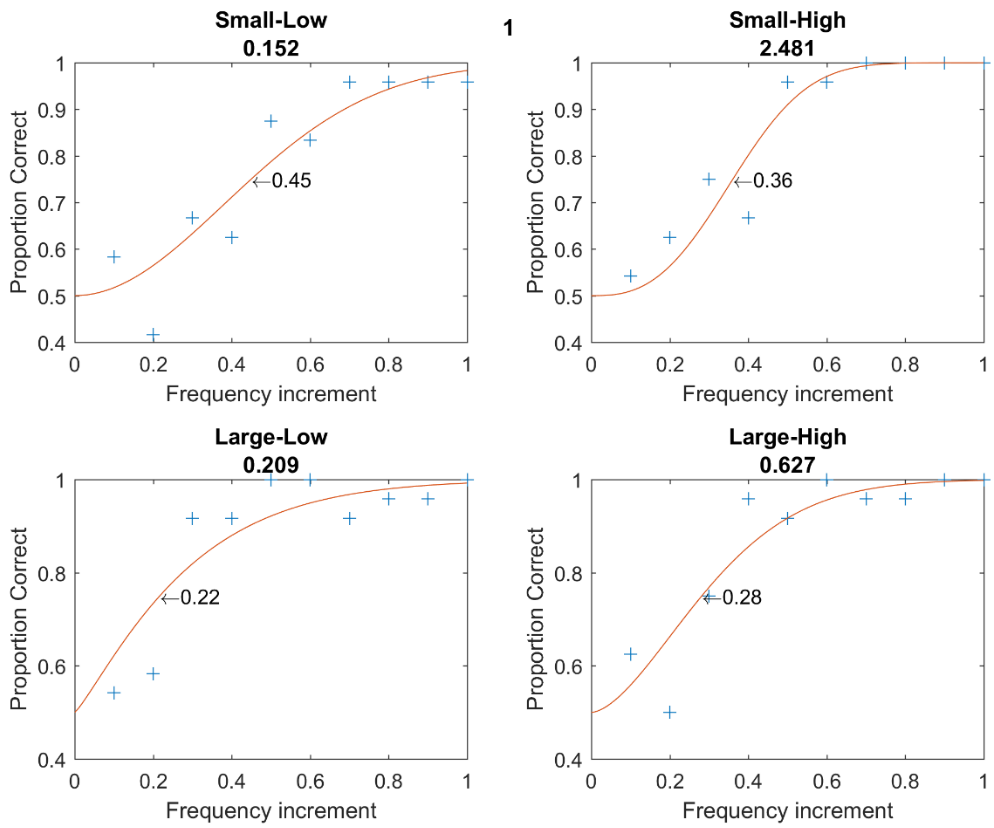


Figure 63. Psychometric functions in 4 conditions for P1. Points give measured performance in proportion correct, lines give maximum likelihood estimation psychometric functions. The labelled points are frequency increments corresponding to 75% correct (i.e. Weber fraction). Numbers below each graph title refer to the magnitude of the test stimuli in that condition (in ms^{-2} RMS).

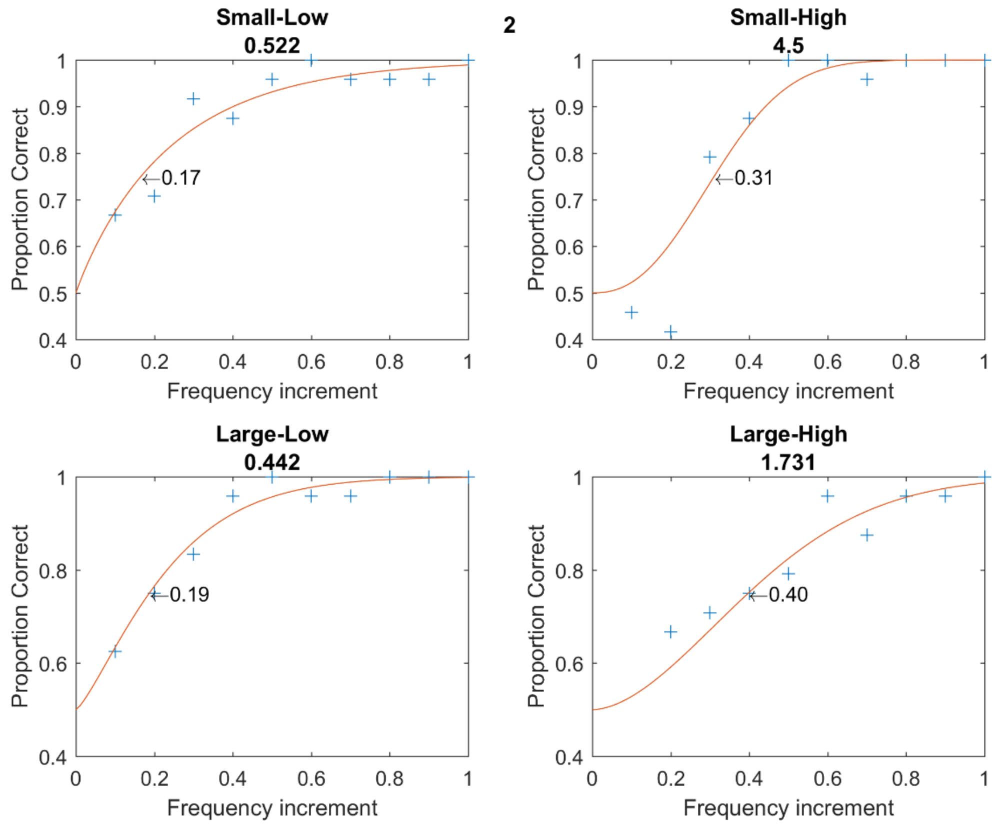


Figure 64. Psychometric functions in 4 conditions for P2.

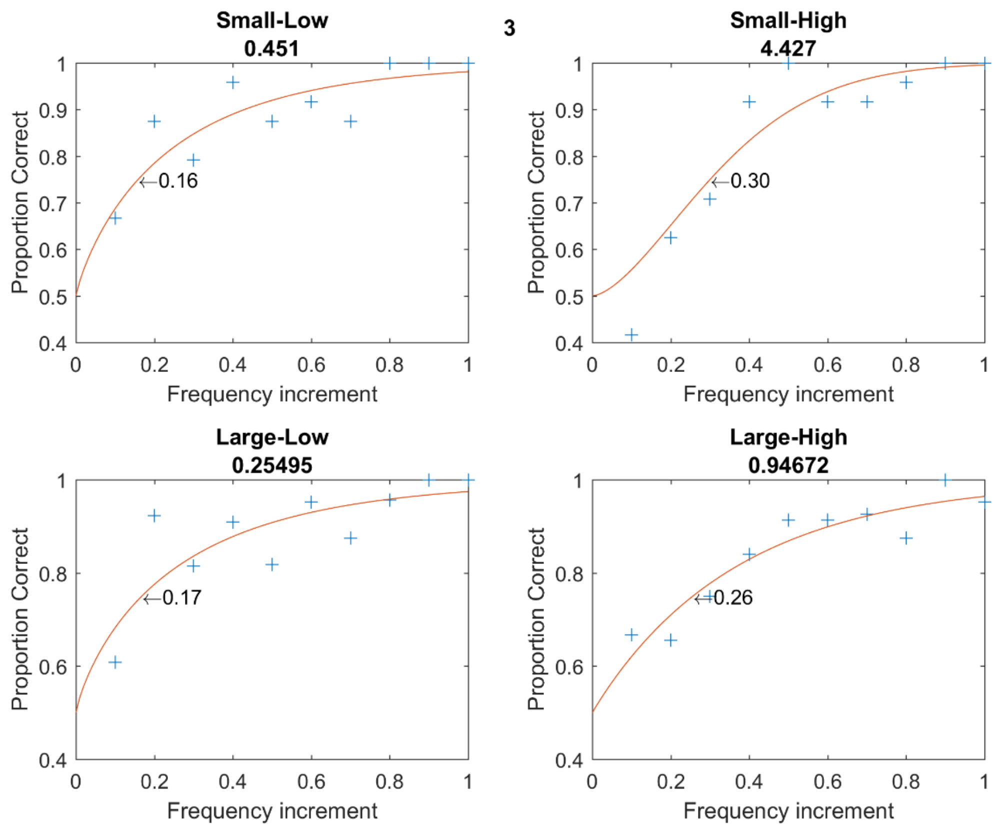


Figure 65. Psychometric functions in 4 conditions for P3.

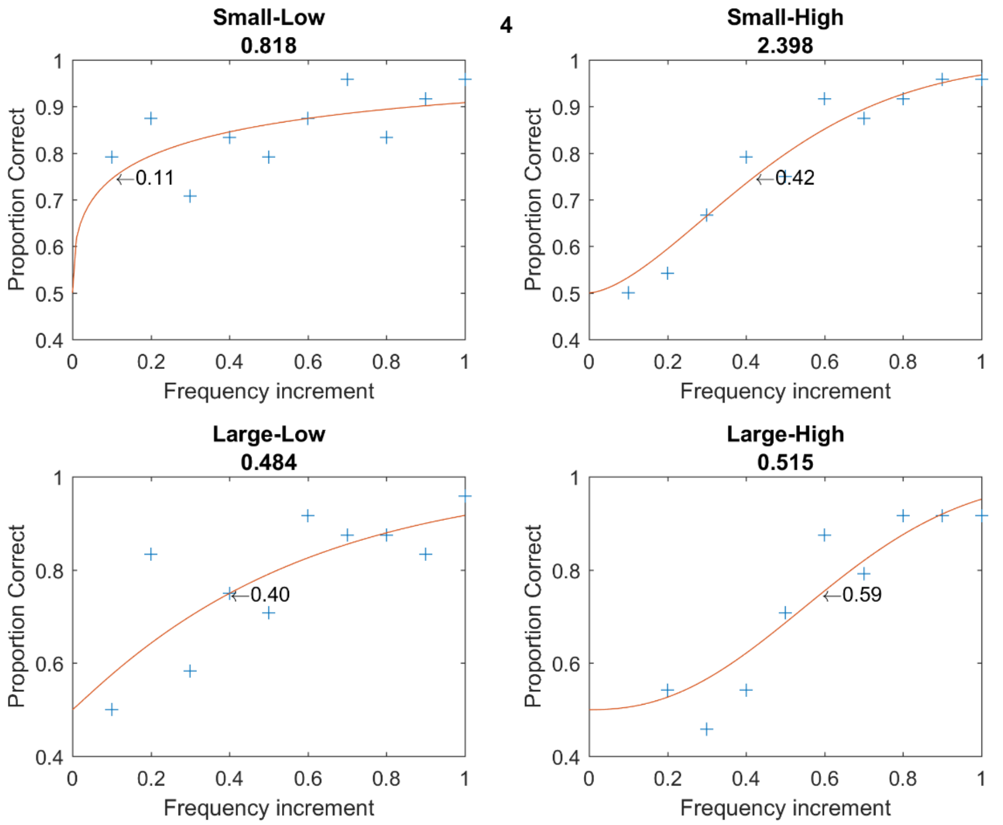


Figure 66. Psychometric functions in 4 conditions for P4.

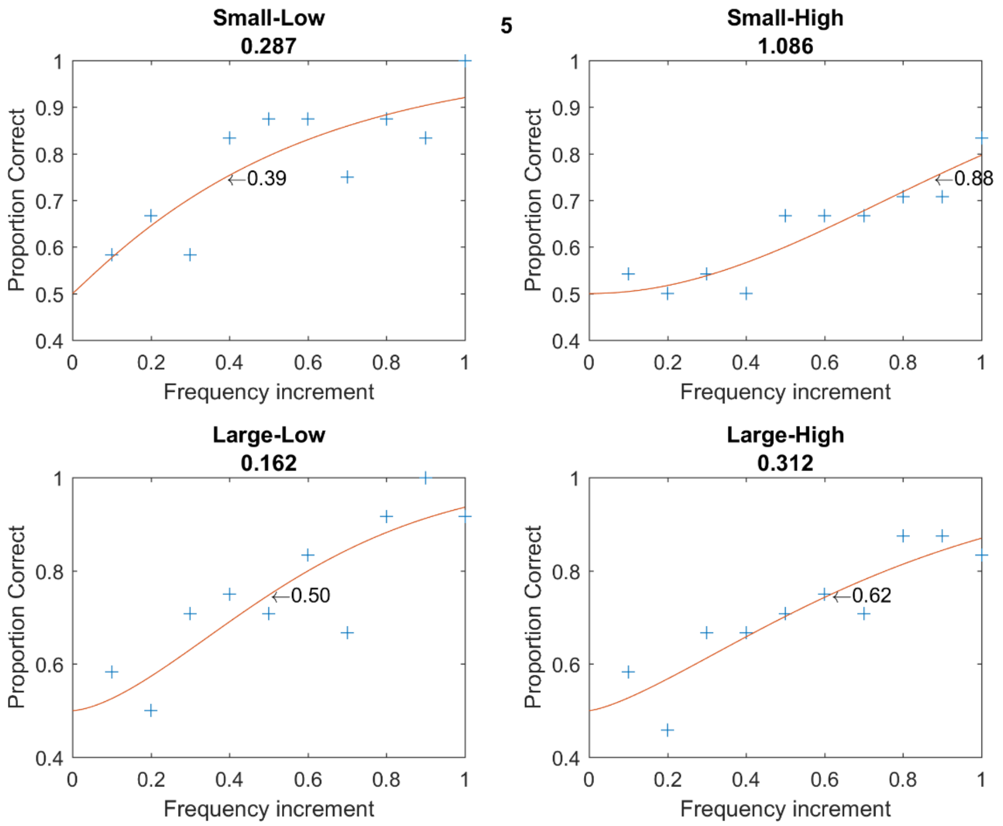


Figure 67. Psychometric functions in 4 conditions for P5.

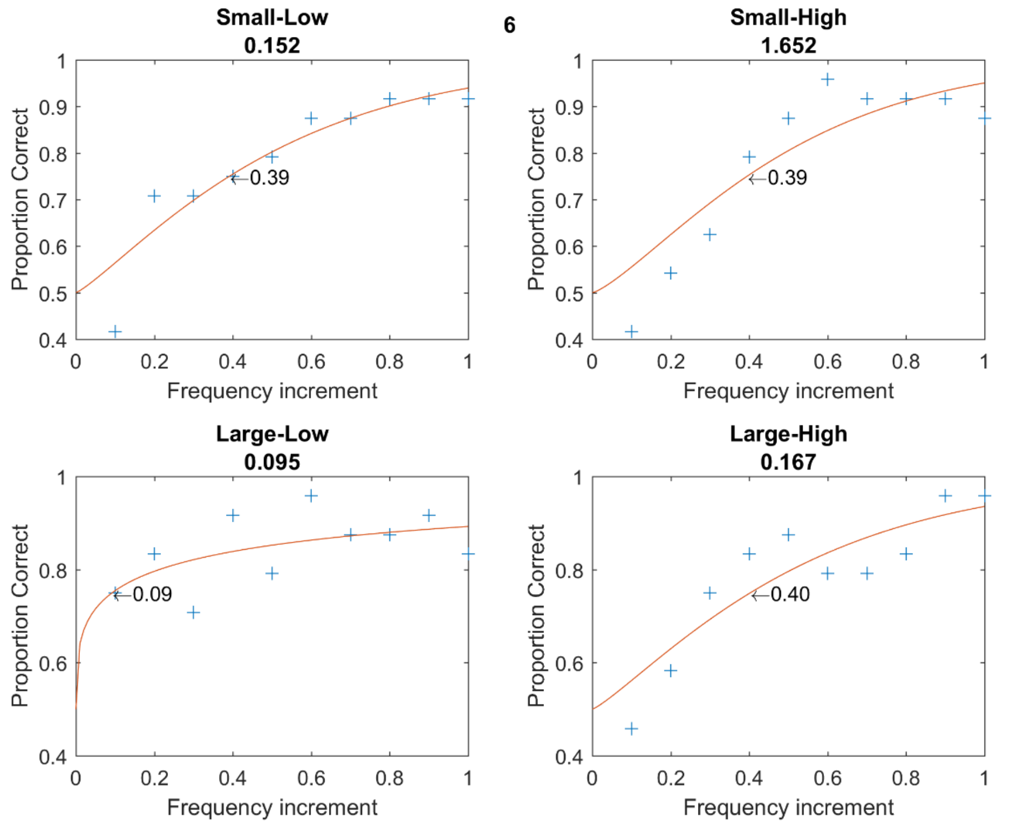


Figure 68. Psychometric functions in 4 conditions for P6.

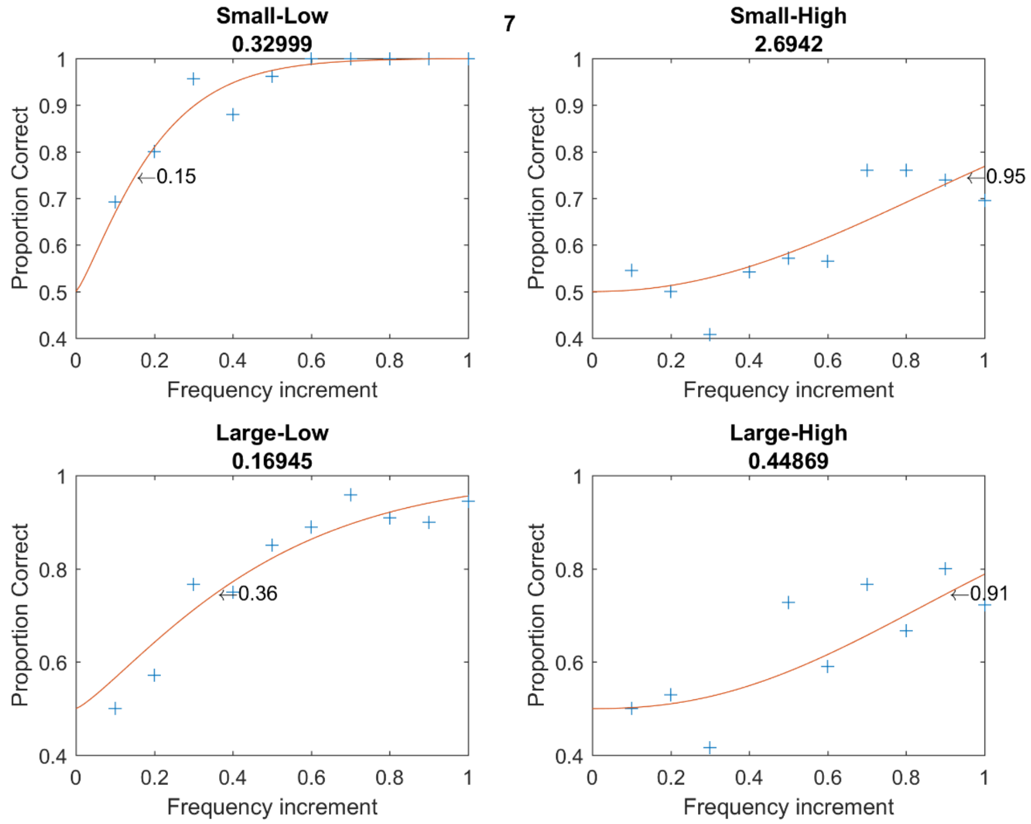


Figure 69. Psychometric functions in 4 conditions for P7.

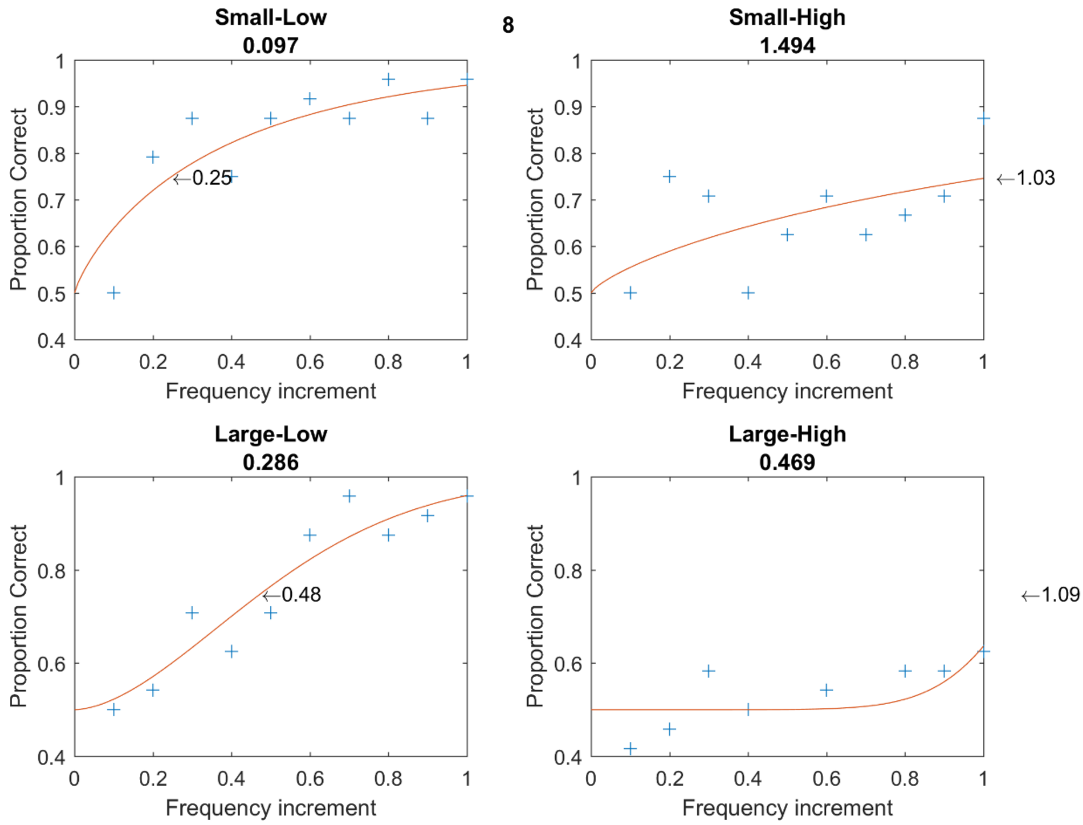


Figure 70. Psychometric functions in 4 conditions for P8.

B.1 Excluded Participants

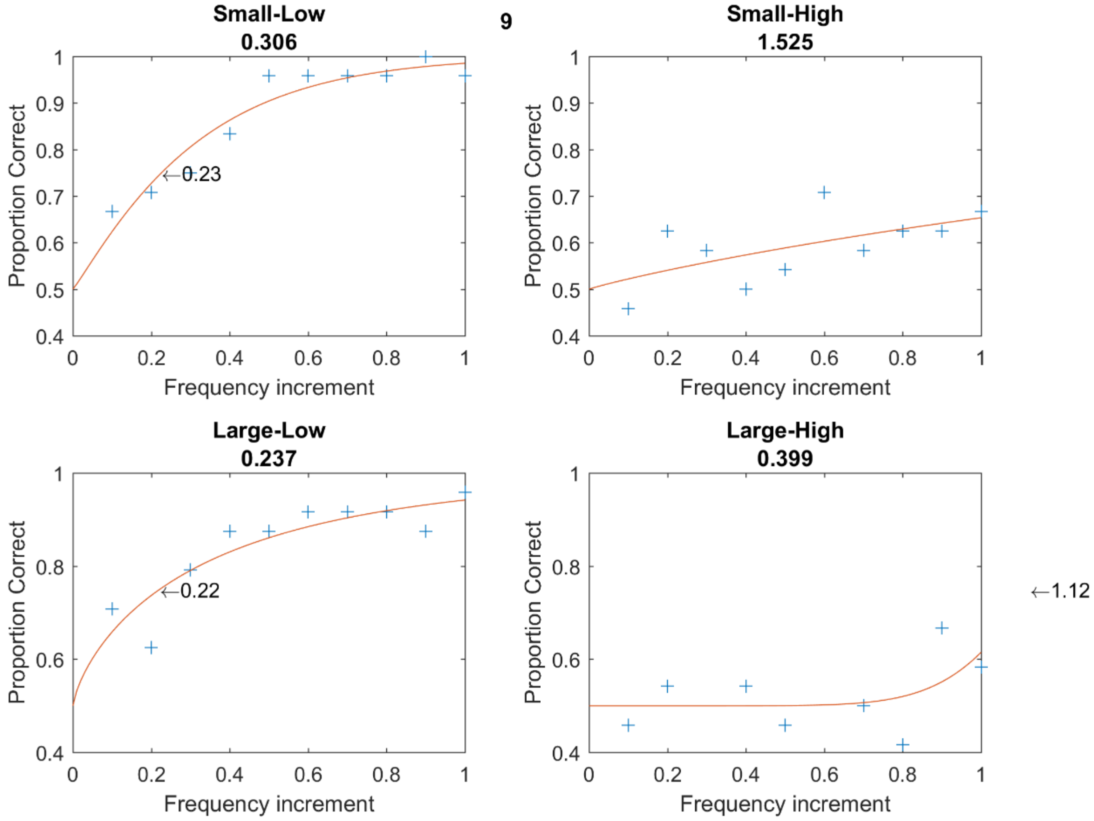


Figure 71. Psychometric functions in 4 conditions for P9. This participant was excluded from the analysis because they had a condition that may have affected their sense of touch (Autism Spectrum Disorder). Note that psychometric functions could not be adequately fit to the frequency discrimination performance in some conditions.

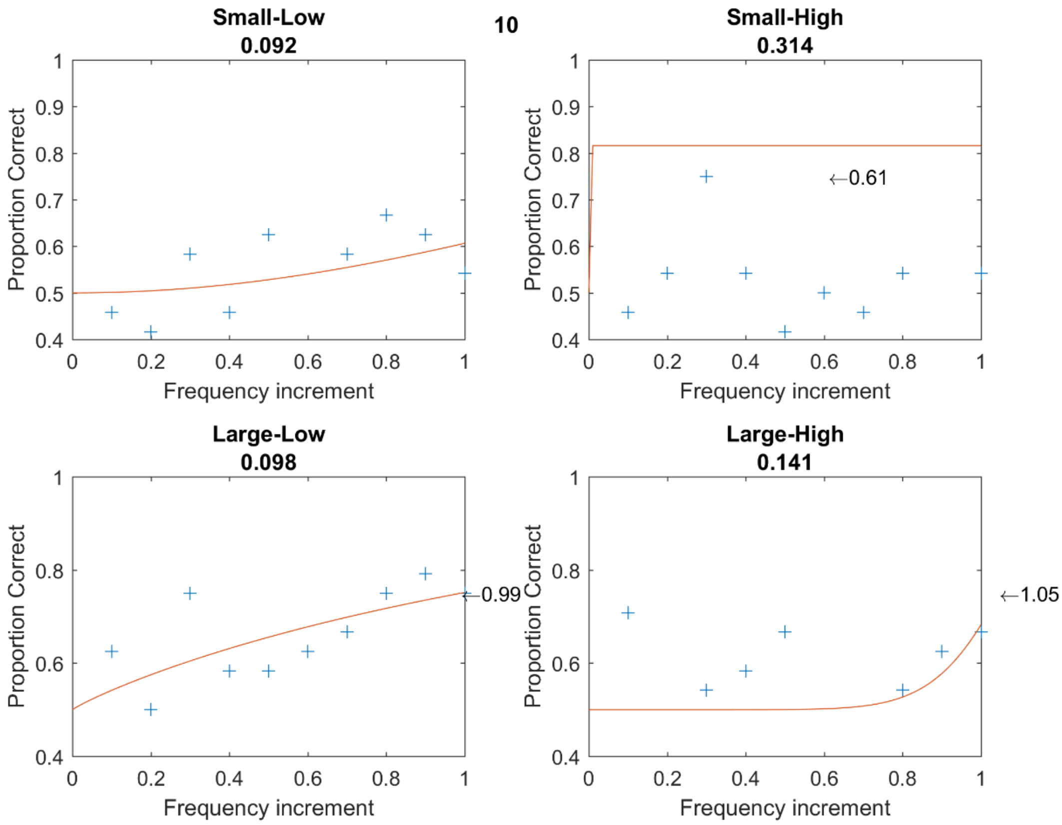


Figure 72. Psychometric functions in 4 conditions for P10. This participant was excluded from the analysis because they had a condition that may have affected their sense of touch (Autism Spectrum Disorder and Dyspraxia). Note that psychometric functions could not be adequately fit to the frequency discrimination performance in some conditions.

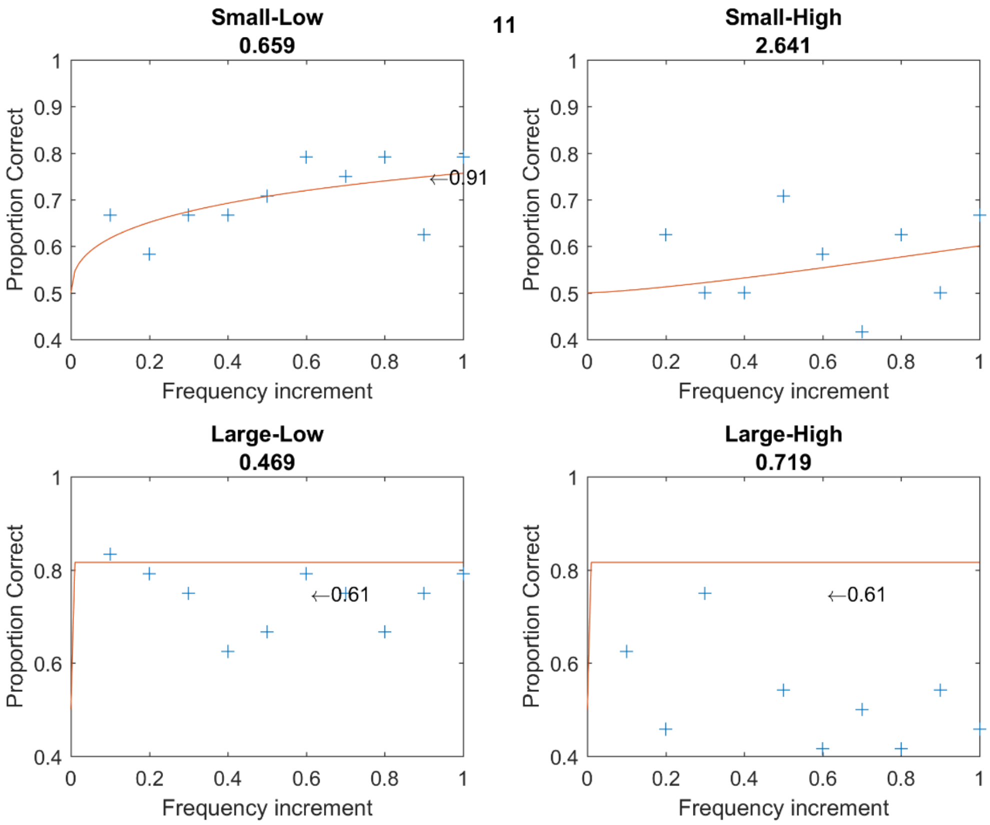


Figure 73. Psychometric functions in 4 conditions for P11. This participant was excluded from the analysis because they had a condition that may have affected their sense of touch (Dyspraxia). Note that psychometric functions could not be adequately fit to the frequency discrimination performance in some conditions.

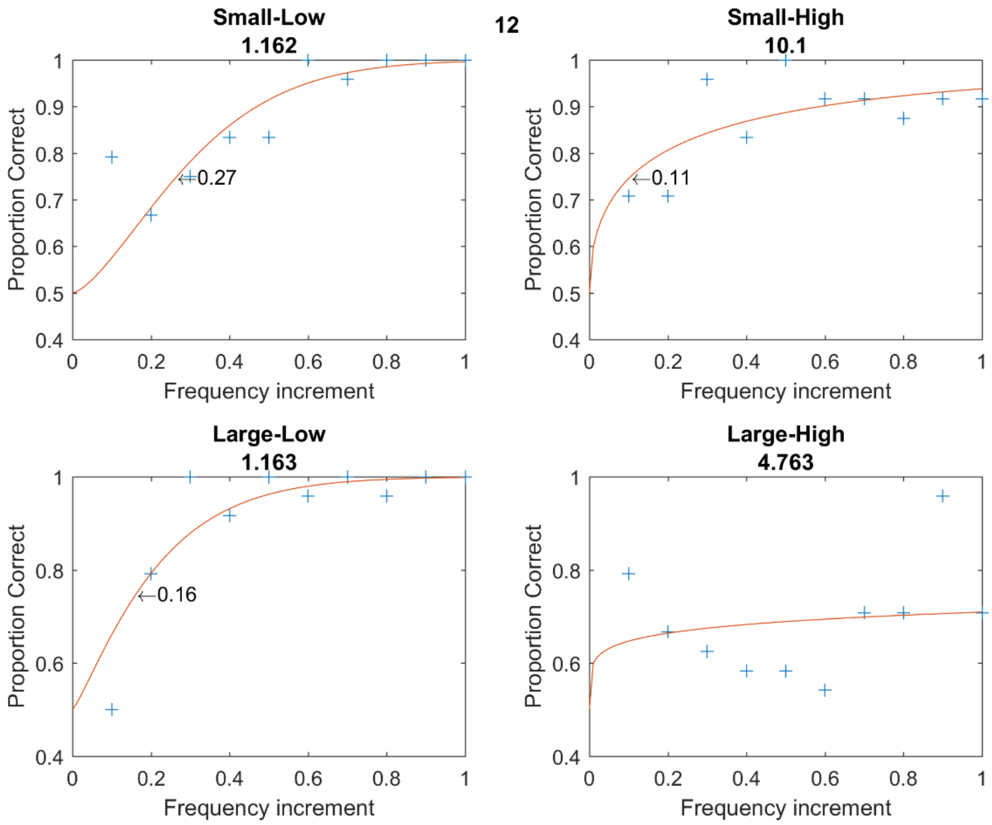


Figure 74. Psychometric functions in 4 conditions for P9. This participant was excluded from the analysis because they had a condition that may have affected their sense of touch (Autism Spectrum Disorder and Dyspraxia). Note that: 1) psychometric functions could not be adequately fit to the frequency discrimination performance in some conditions 2) the participant presented with extremely high detection thresholds, resulting in high test amplitudes for experimental stimuli (> $4ms^{-2}$ RMS).

Appendix C Individual data for Experiment 2

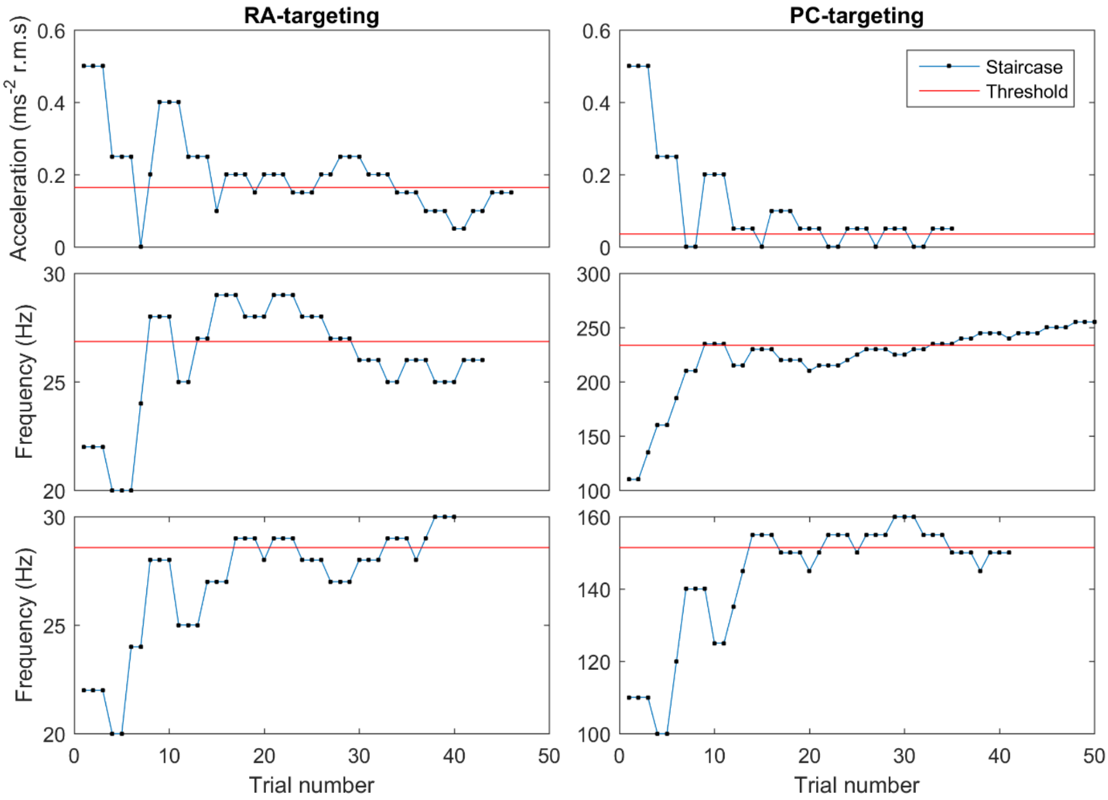


Figure 75. Completed staircase procedures in all 6 conditions for participant 1. The top two panels illustrate trials in the detection threshold task. The remaining panels illustrate performance in the frequency discrimination task. For all panels the target value intersects with the x-axis, and test values vary depending on past performance.

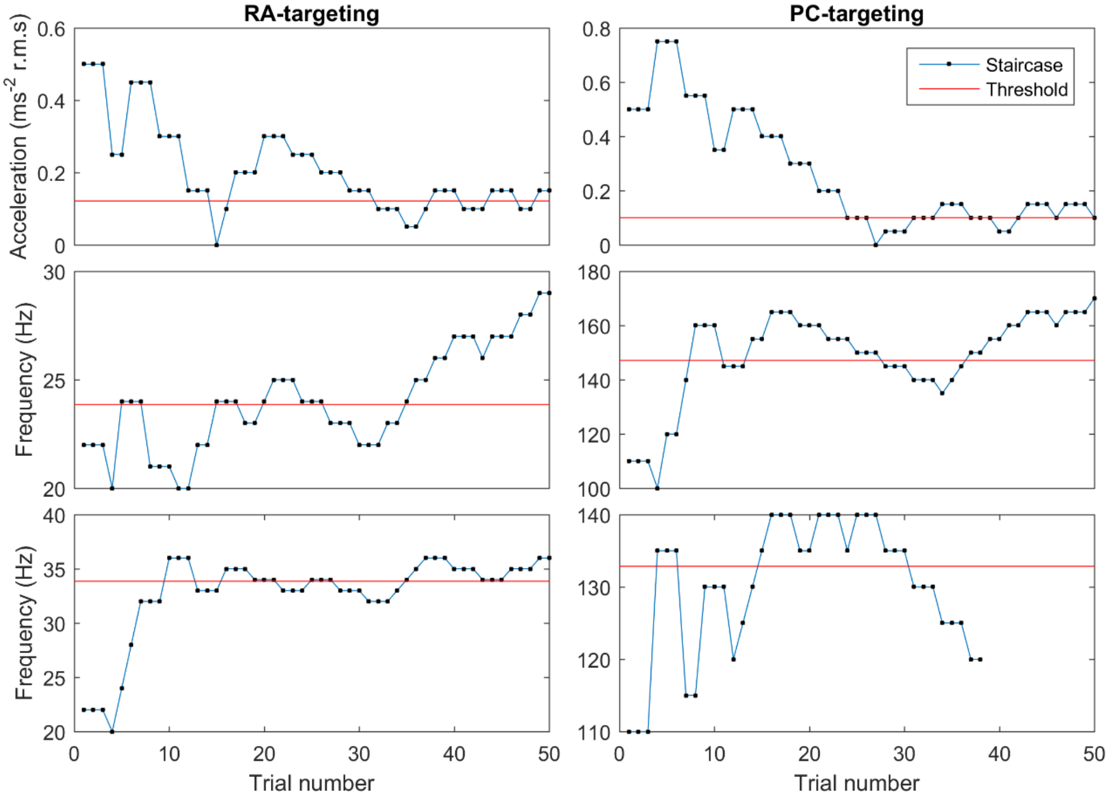


Figure 76. Completed staircase procedures in all 6 conditions for participant 2.

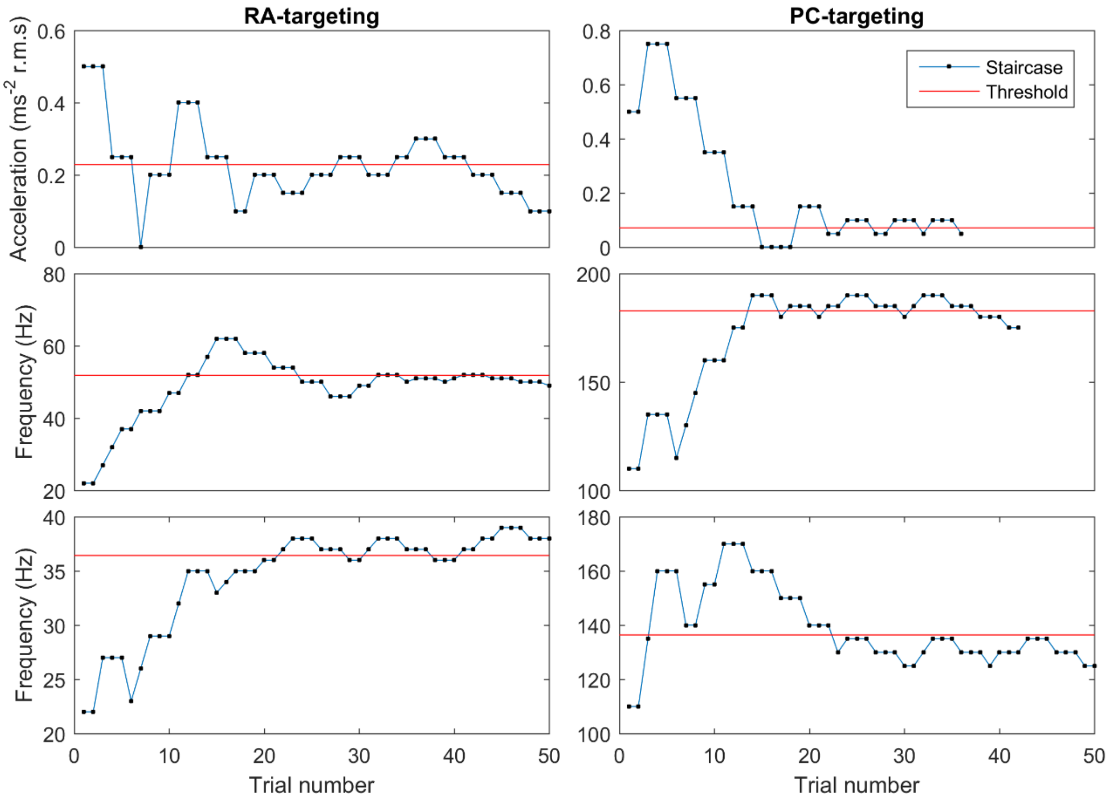


Figure 77. Completed staircase procedures in all 6 conditions for participant 3.

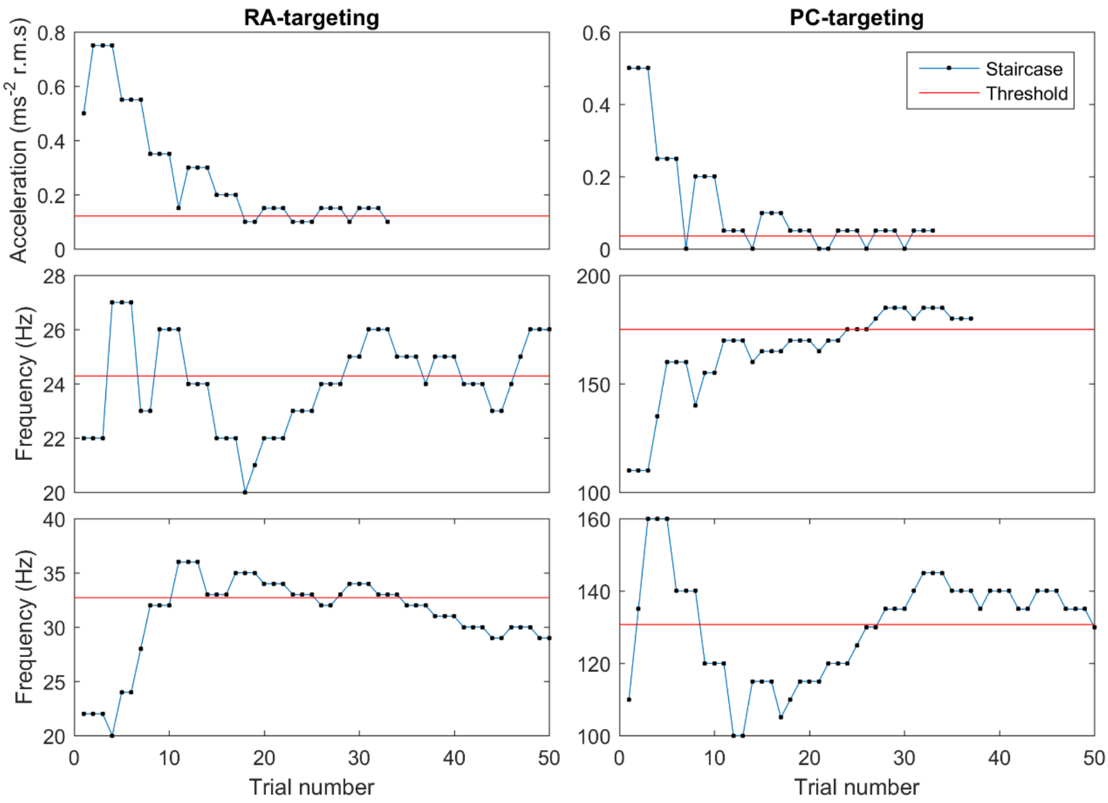


Figure 78. Completed staircase procedures in all 6 conditions for participant 4.

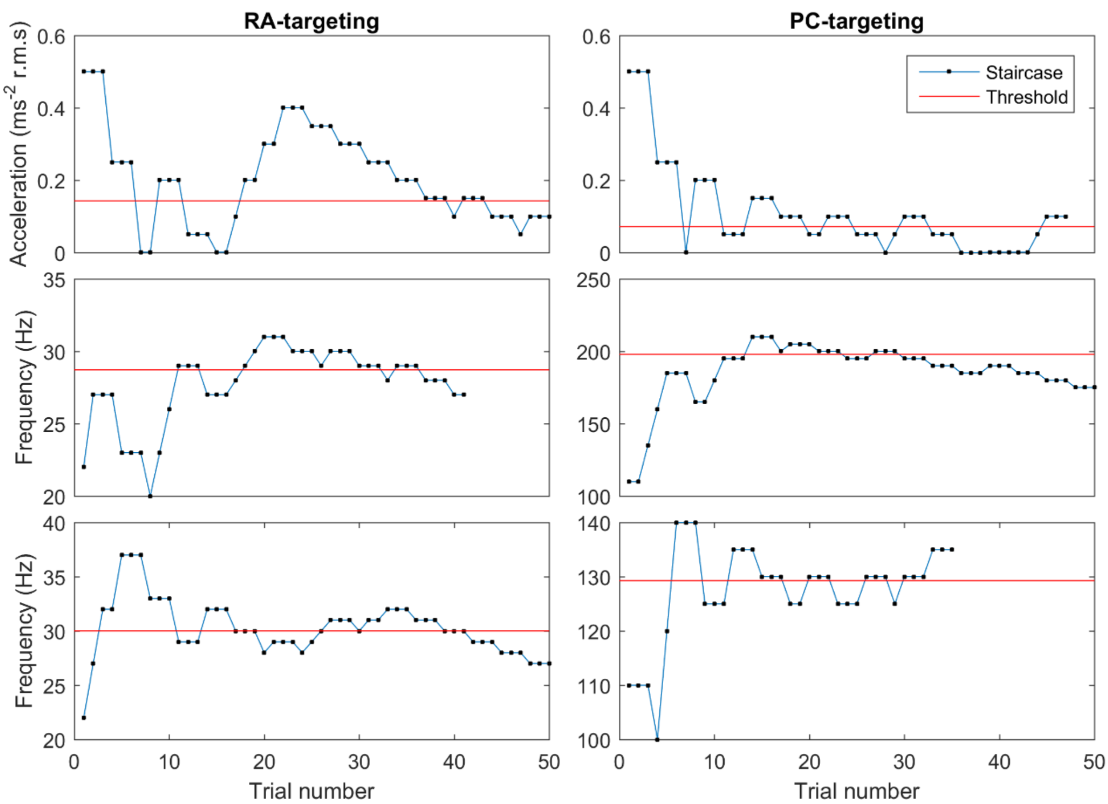


Figure 79. Completed staircase procedures in all 6 conditions for participant 5.

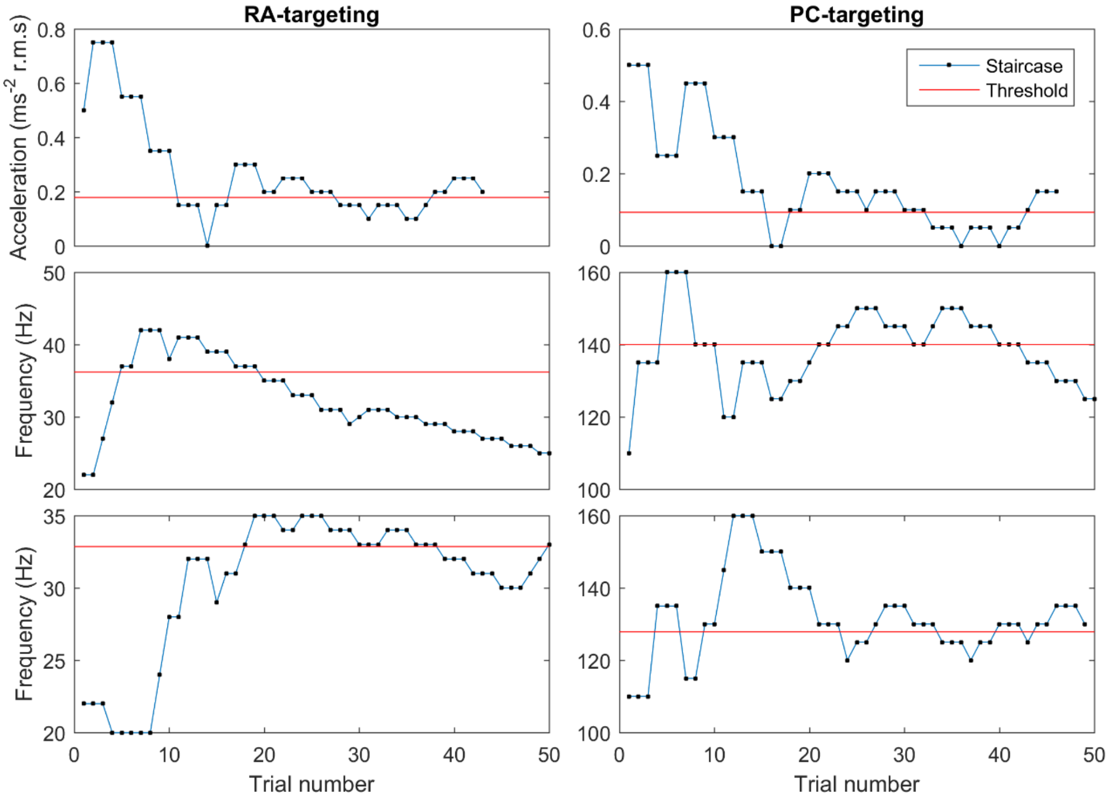


Figure 80. Completed staircase procedures in all 6 conditions for participant 6.

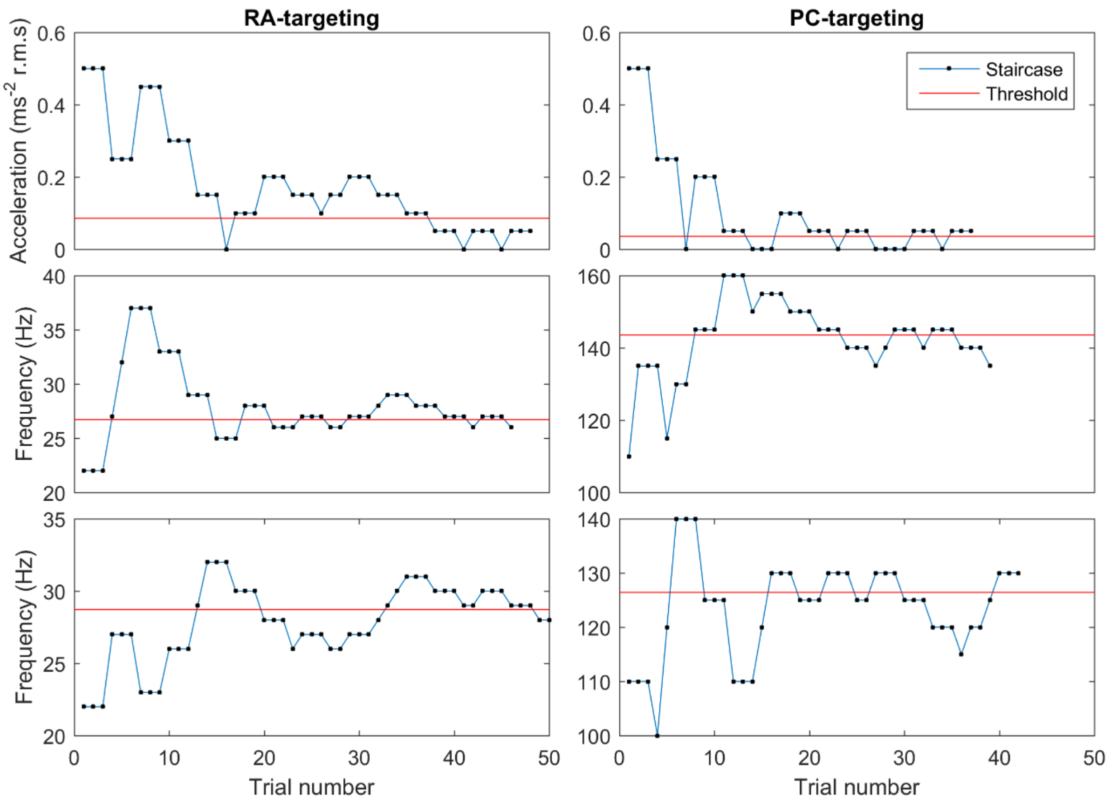


Figure 81. Completed staircase procedures in all 6 conditions for participant 7.

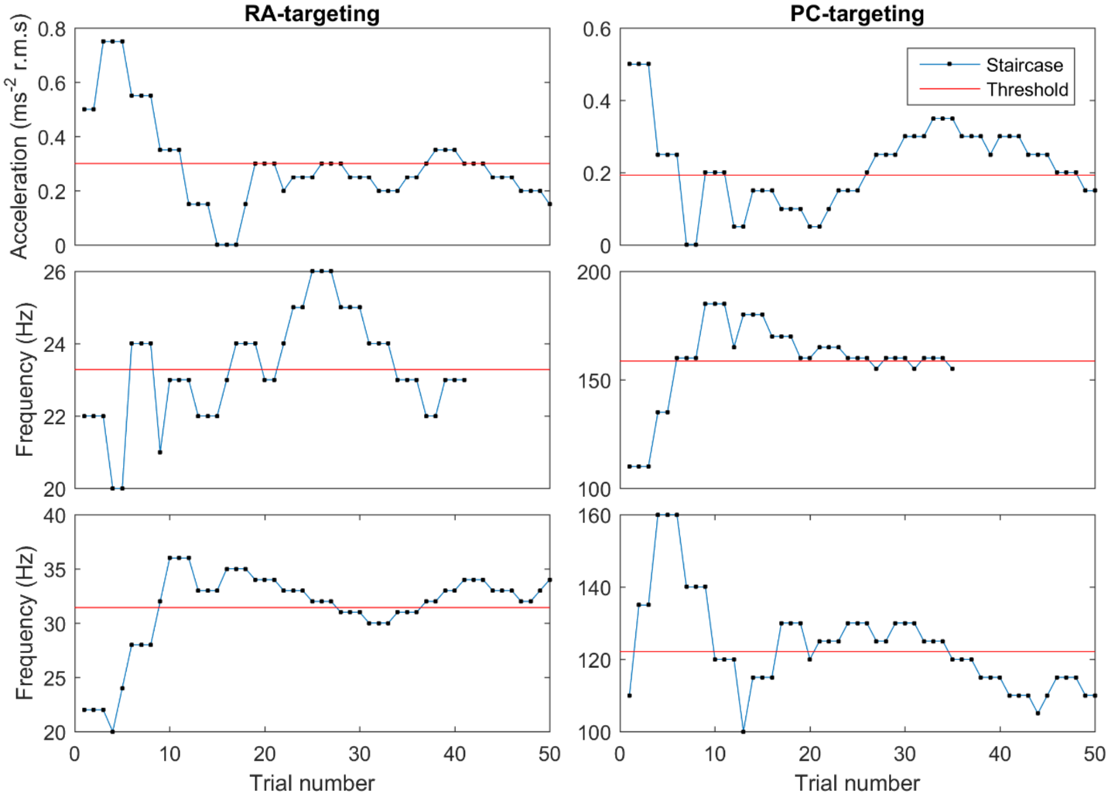


Figure 82. Completed staircase procedures in all 6 conditions for participant 8.

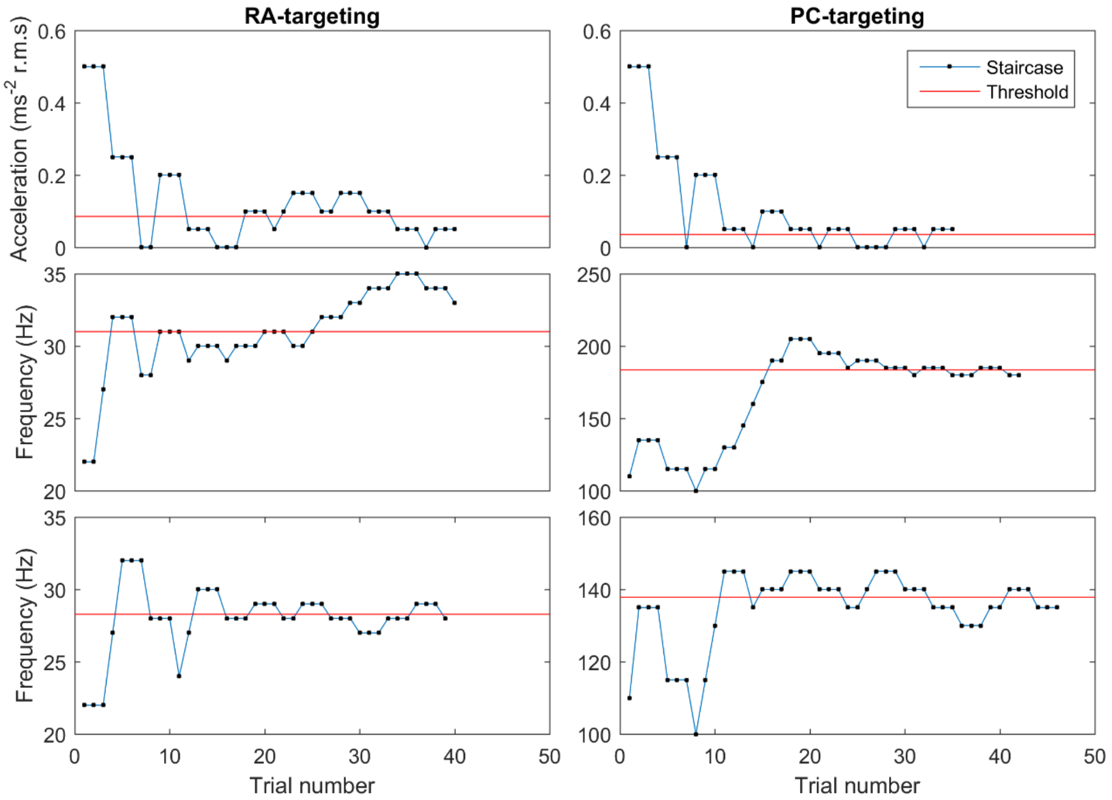


Figure 83. Completed staircase procedures in all 6 conditions for participant 9.

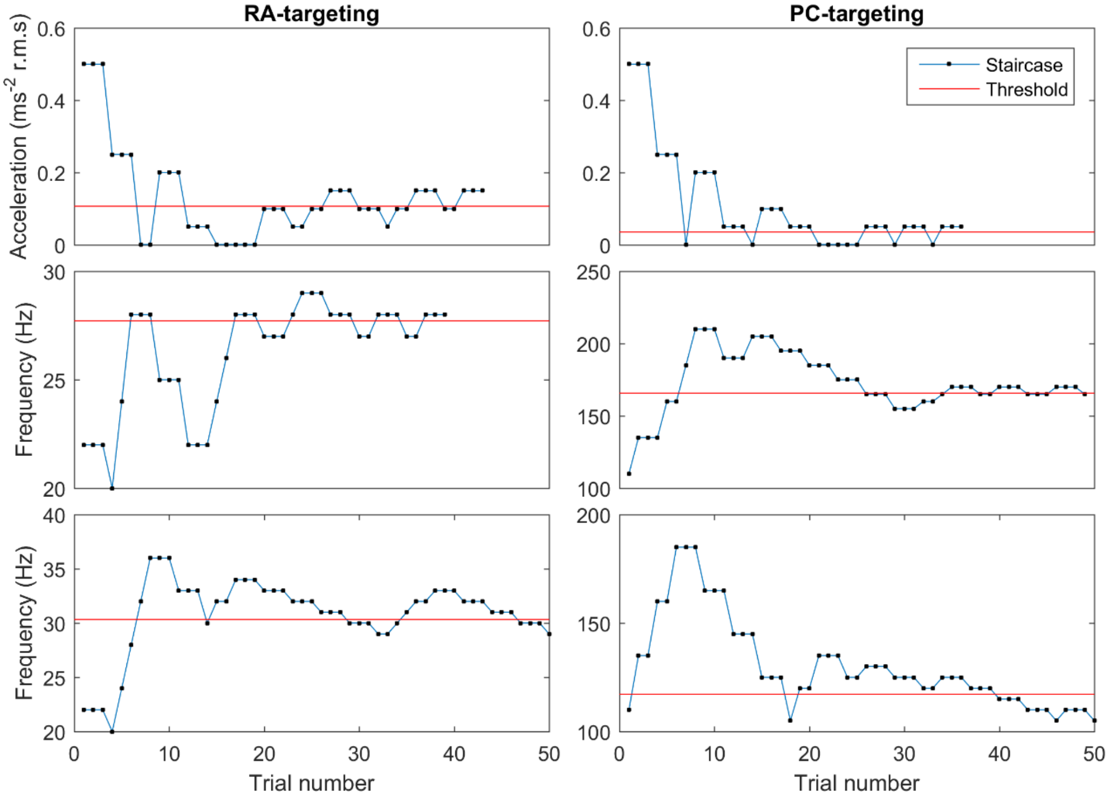


Figure 84. Completed staircase procedures in all 6 conditions for participant 10.

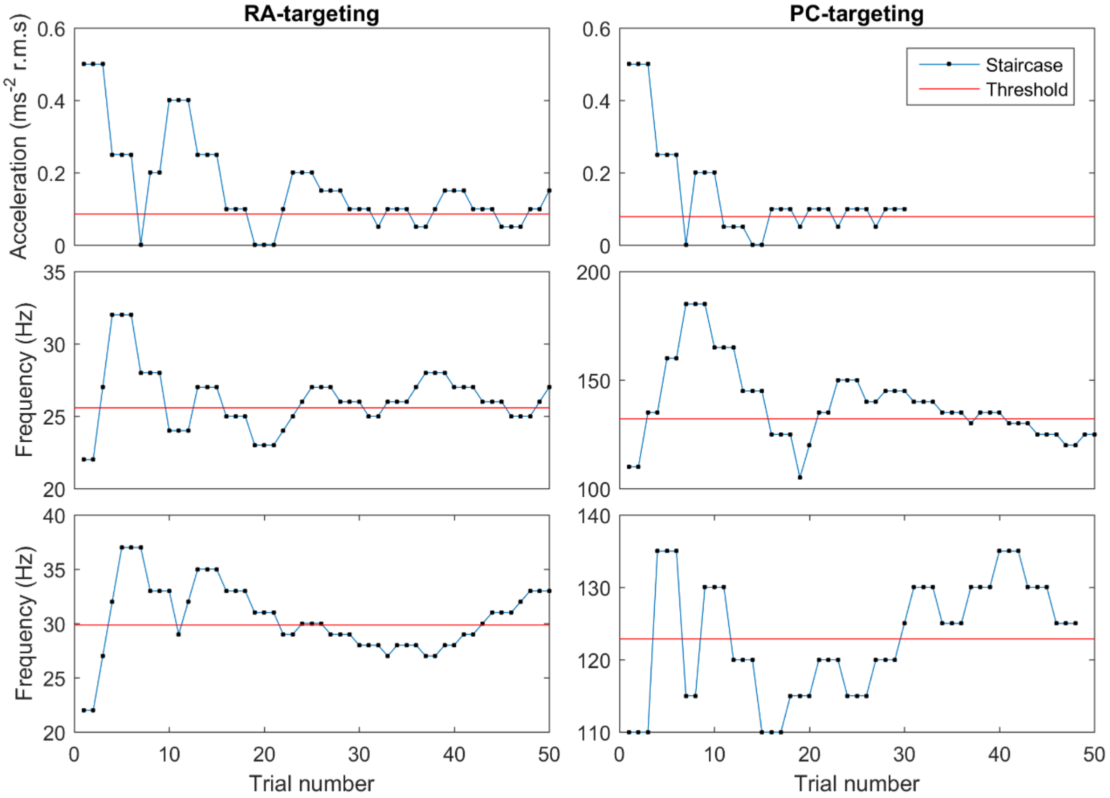


Figure 85. Completed staircase procedures in all 6 conditions for participant 11.

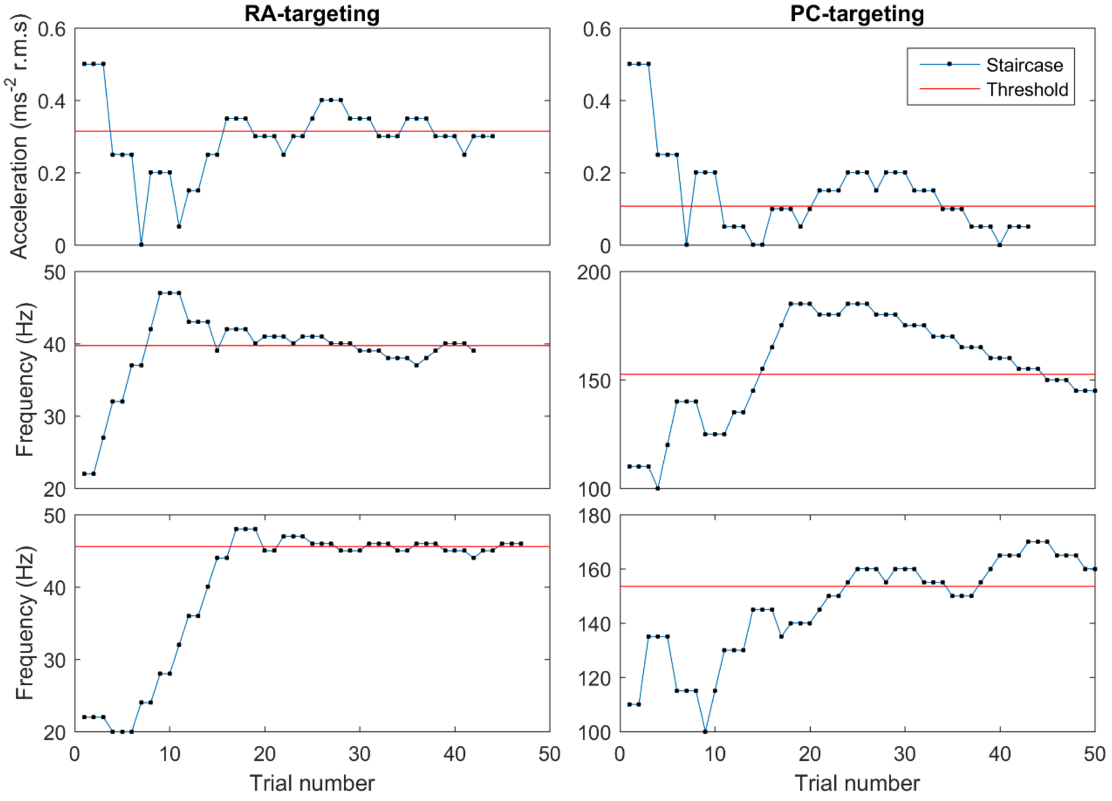


Figure 86. Completed staircase procedures in all 6 conditions for participant 12.

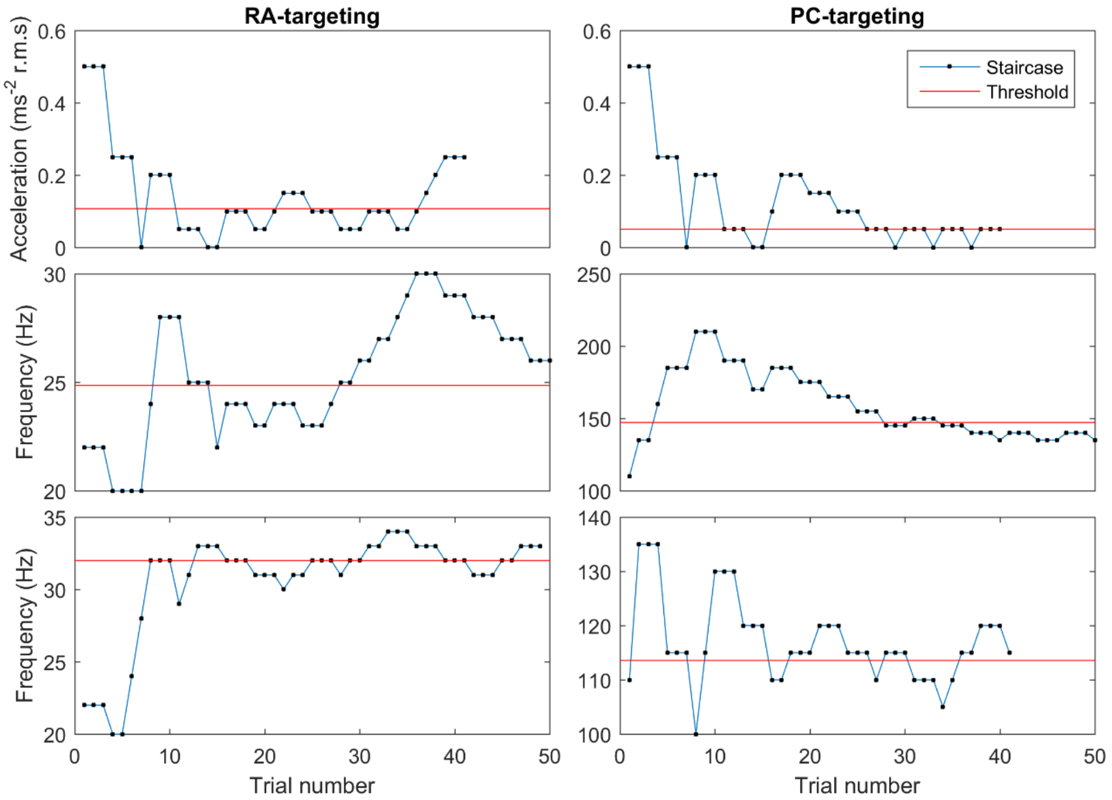


Figure 87. Completed staircase procedures in all 6 conditions for participant 13.

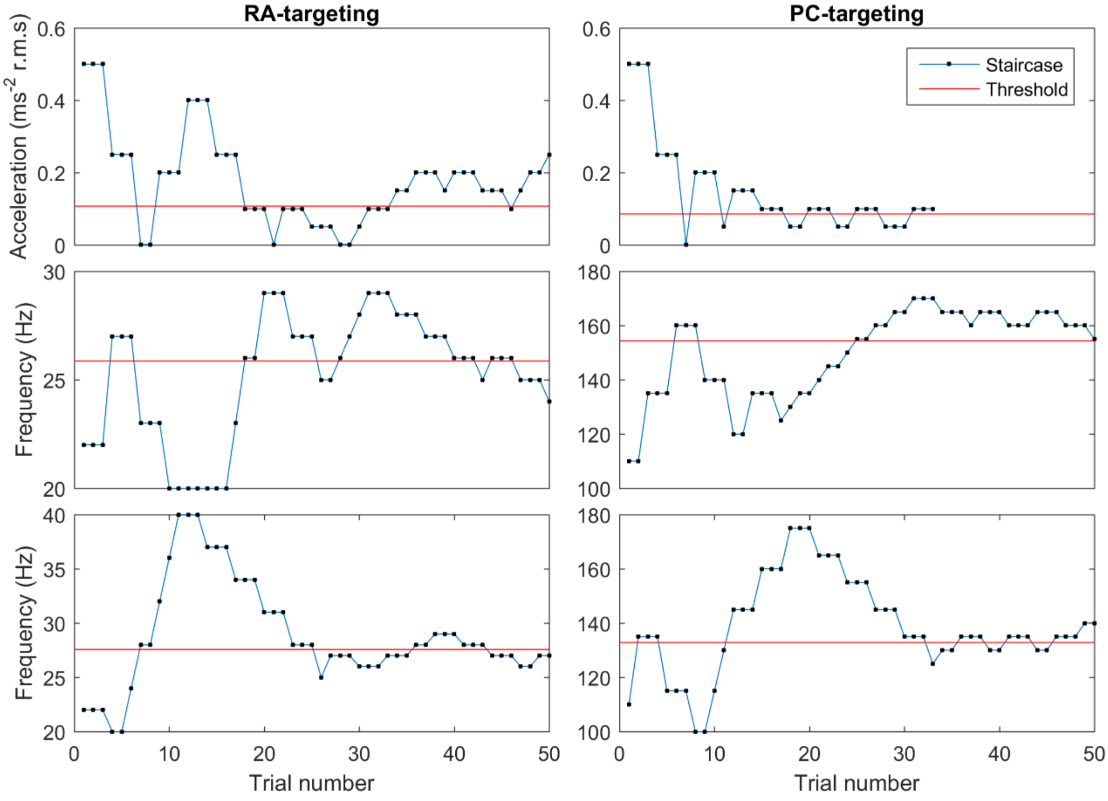


Figure 88. Completed staircase procedures in all 6 conditions for participant 14.

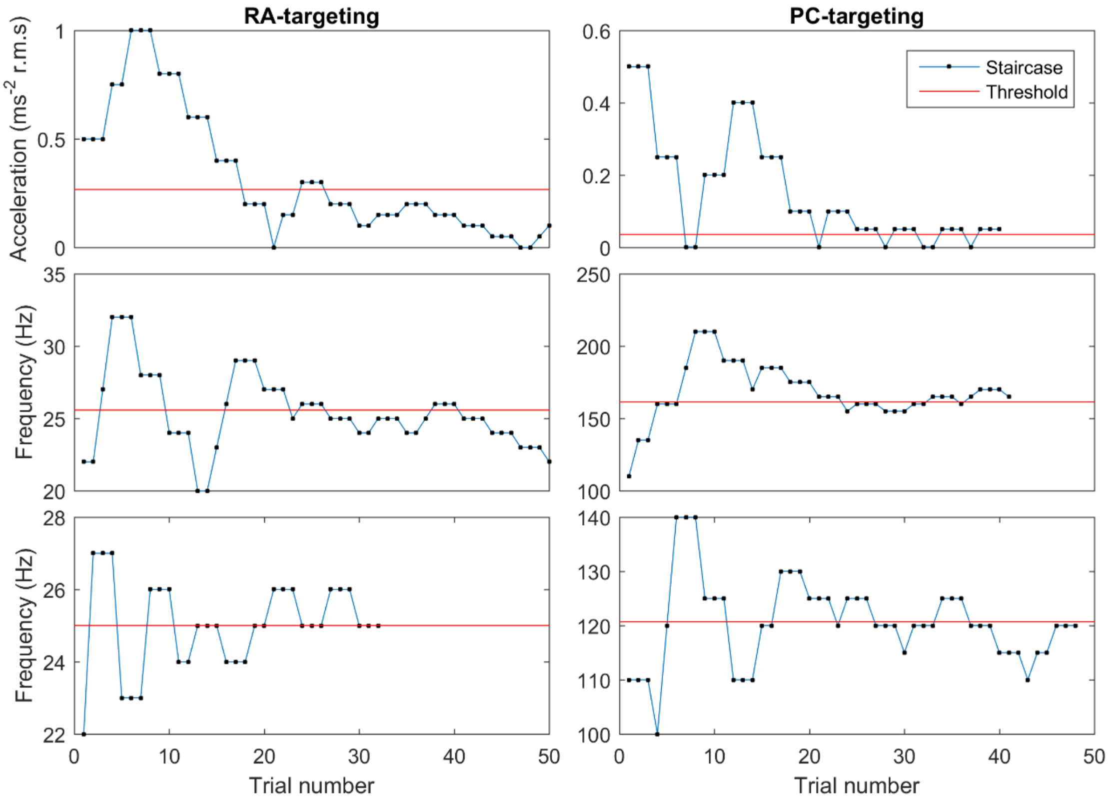


Figure 89. Completed staircase procedures in all 6 conditions for participant 15.

Appendix D Individual data for Experiment 3

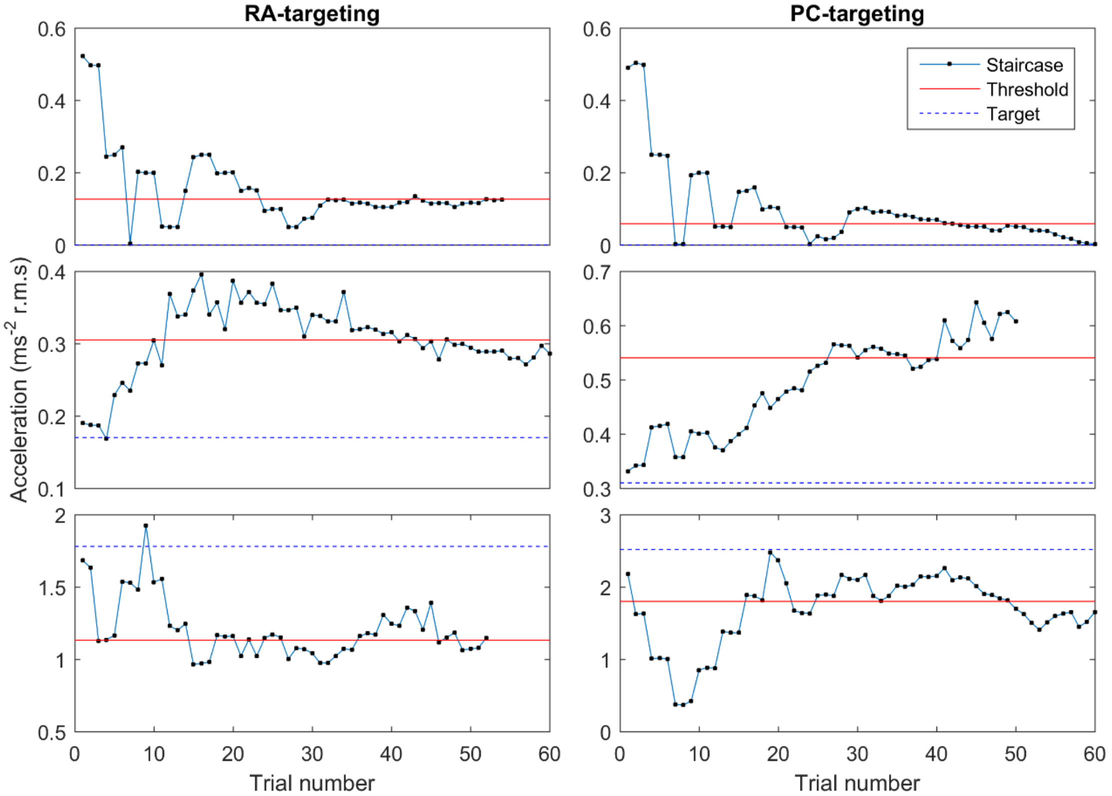


Figure 90. Completed staircase procedures in all 6 conditions for participant 1. The top two panels illustrate trials in the detection threshold task. The remaining panels illustrate performance in the acceleration magnitude discrimination task. For all panels the target value intersects with the x-axis, and test values vary depending on past performance following a 3-down 1-up procedure.

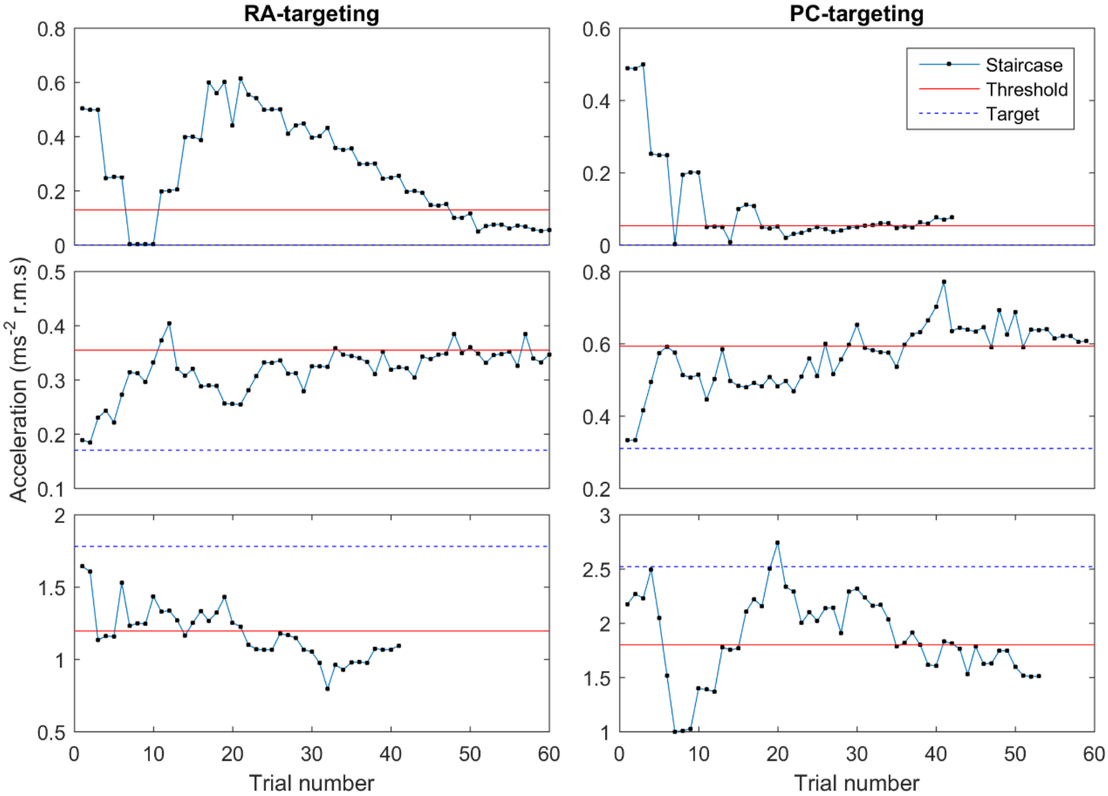


Figure 91. Completed staircase procedures in all 6 conditions for participant 2.

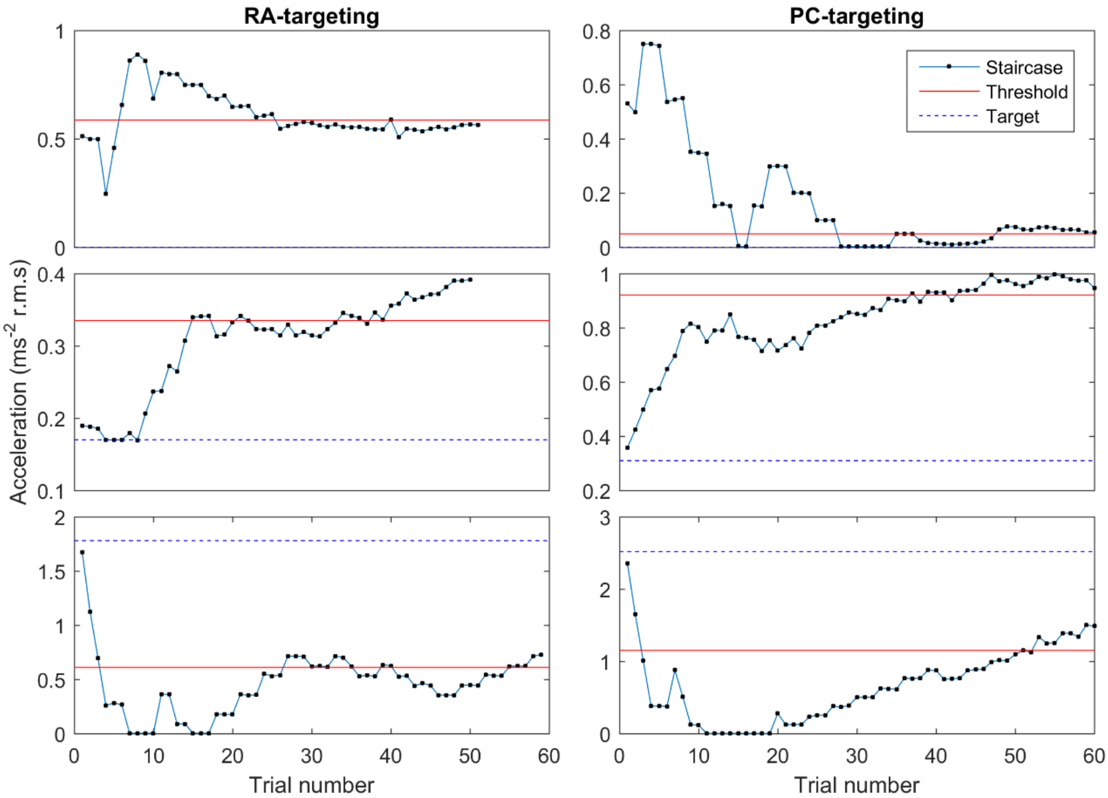


Figure 92. Completed staircase procedures in all 6 conditions for participant 3.

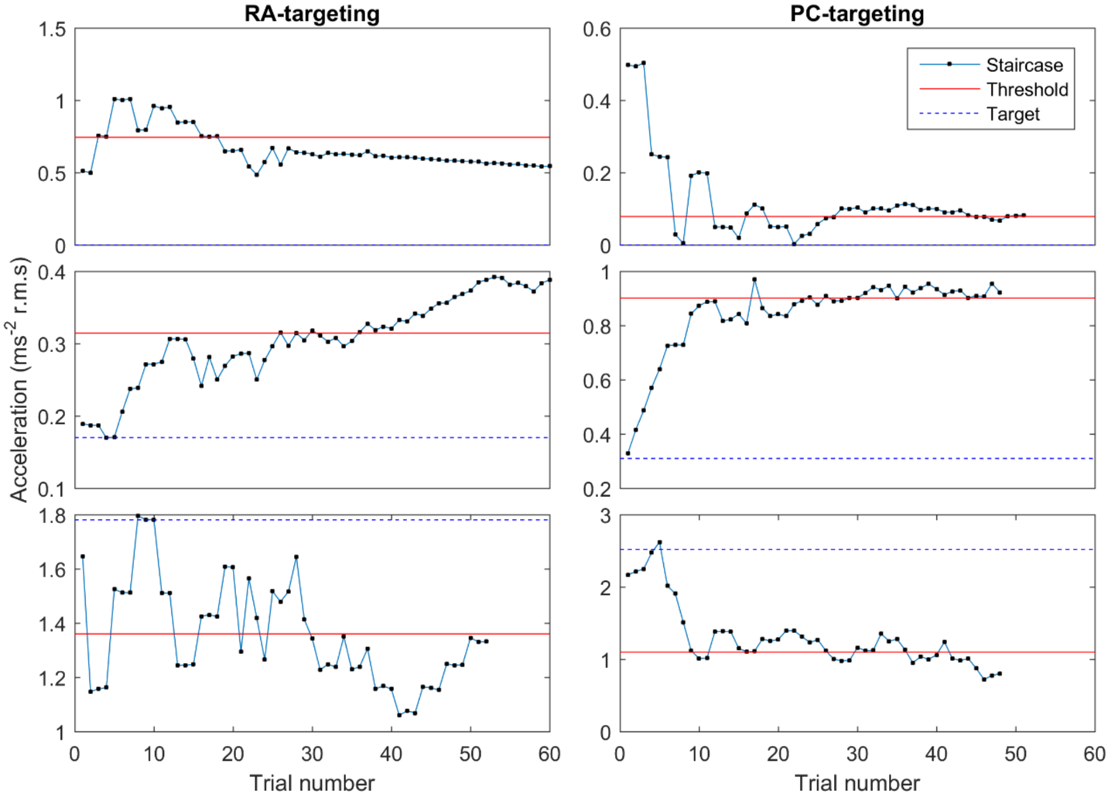


Figure 93. Completed staircase procedures in all 6 conditions for participant 4.

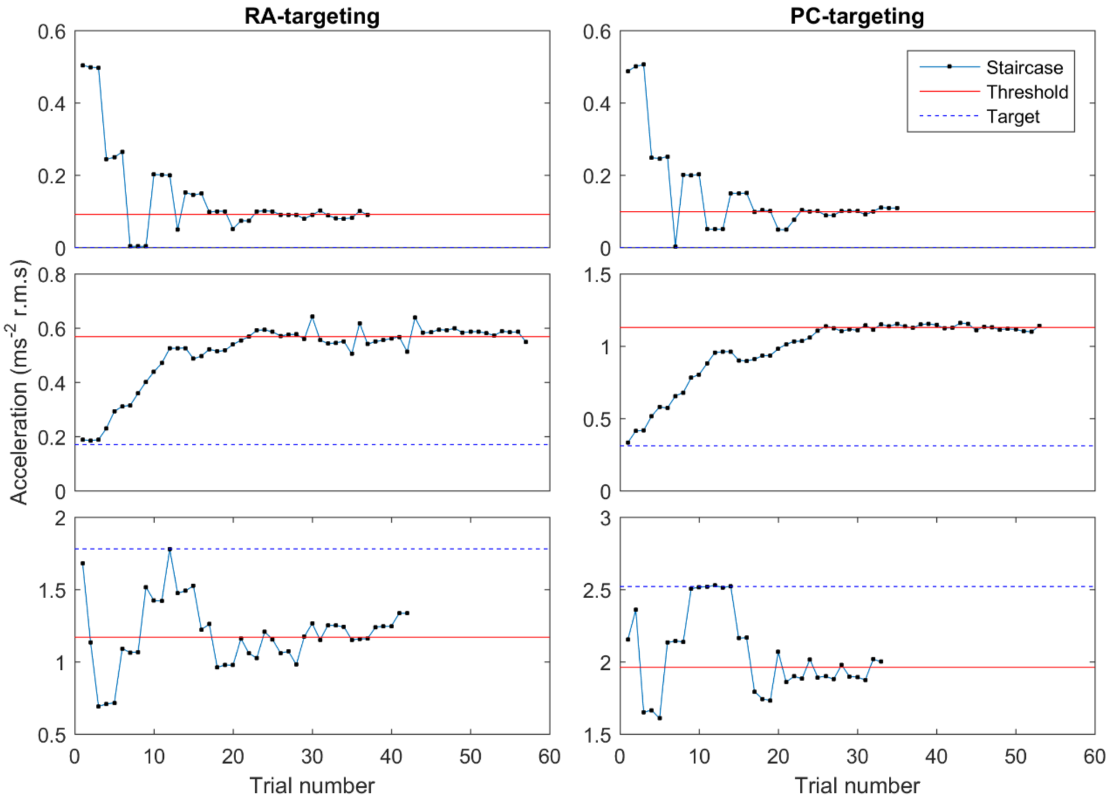


Figure 94. Completed staircase procedures in all 6 conditions for participant 5.

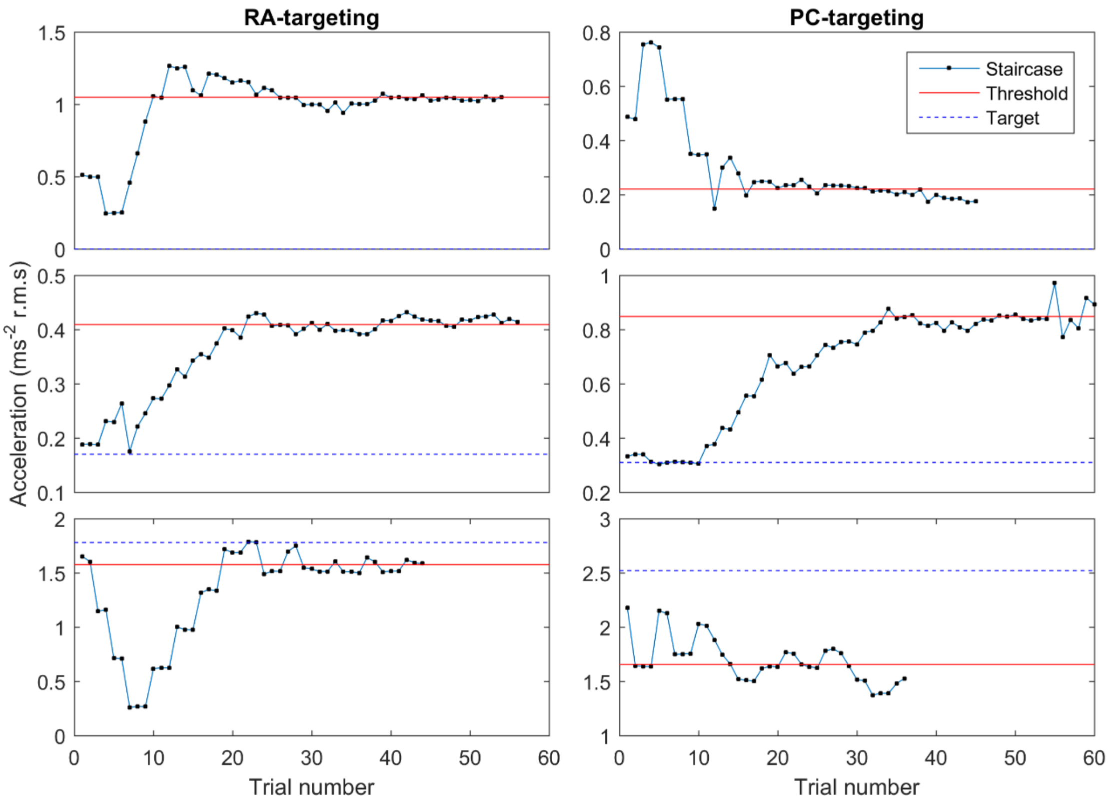


Figure 95. Completed staircase procedures in all 6 conditions for participant 6.

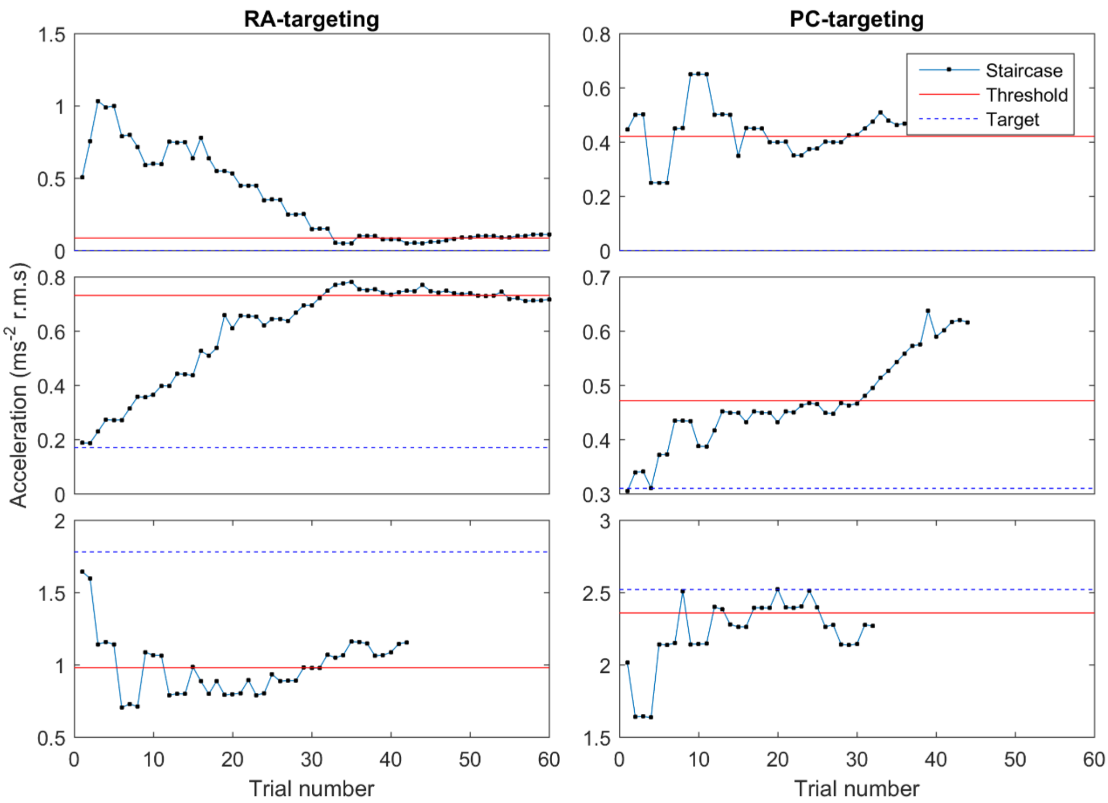


Figure 96. Completed staircase procedures in all 6 conditions for participant 7.

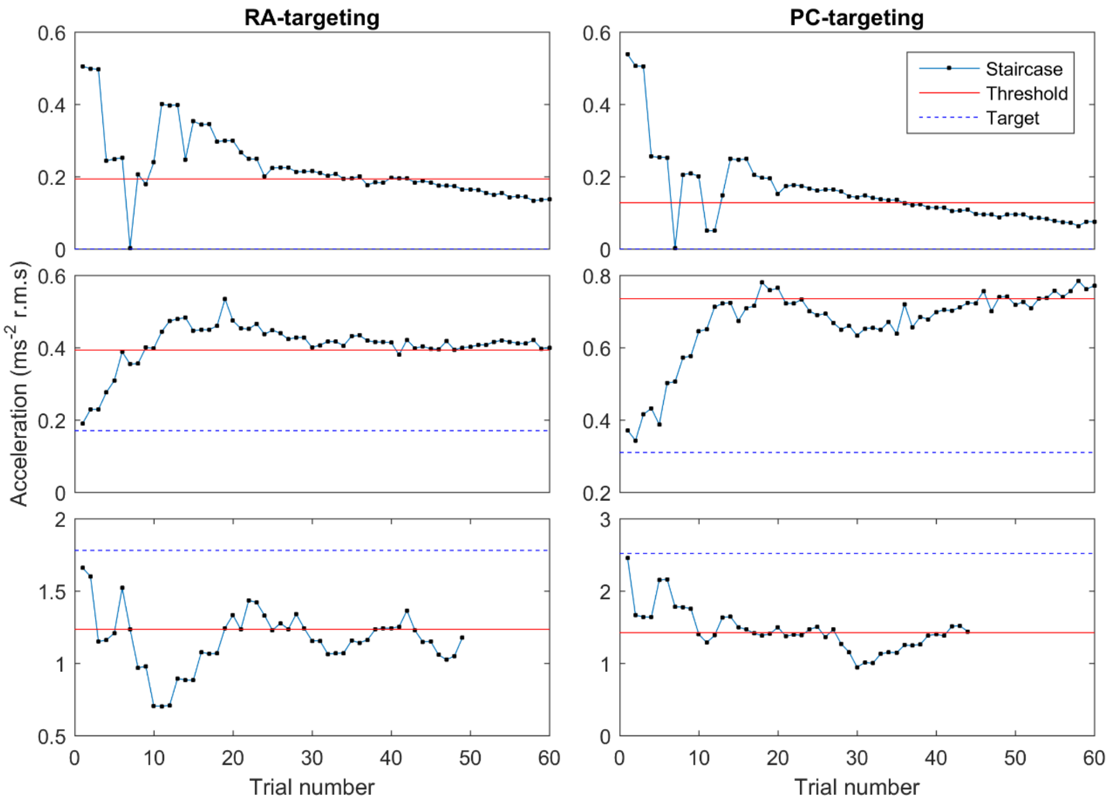


Figure 97. Completed staircase procedures in all 6 conditions for participant 8.

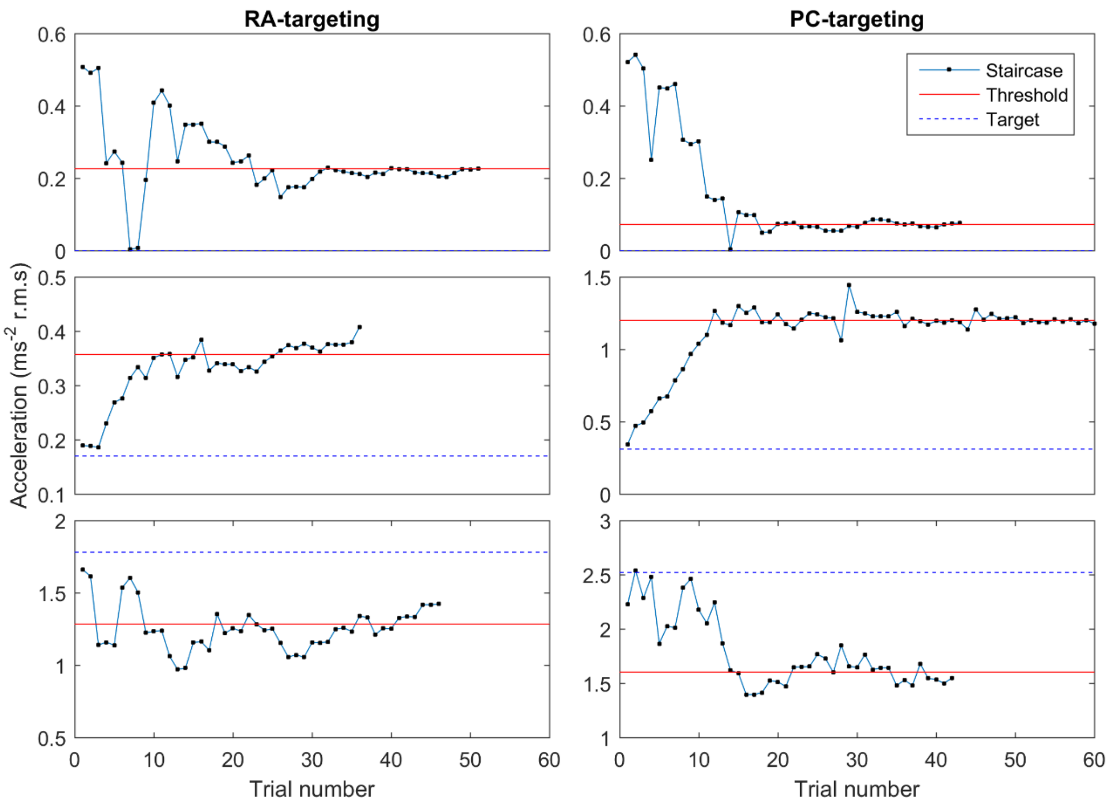


Figure 98. Completed staircase procedures in all 6 conditions for participant 9.

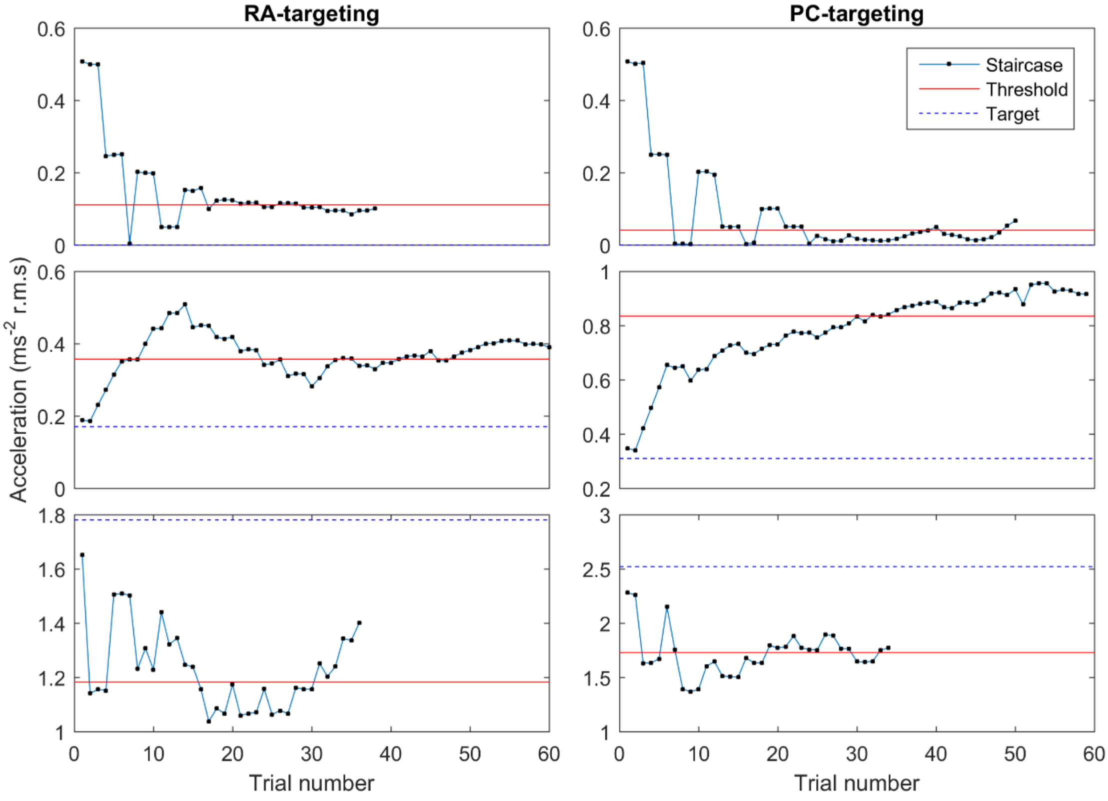


Figure 99. Completed staircase procedures in all 6 conditions for participant 10.

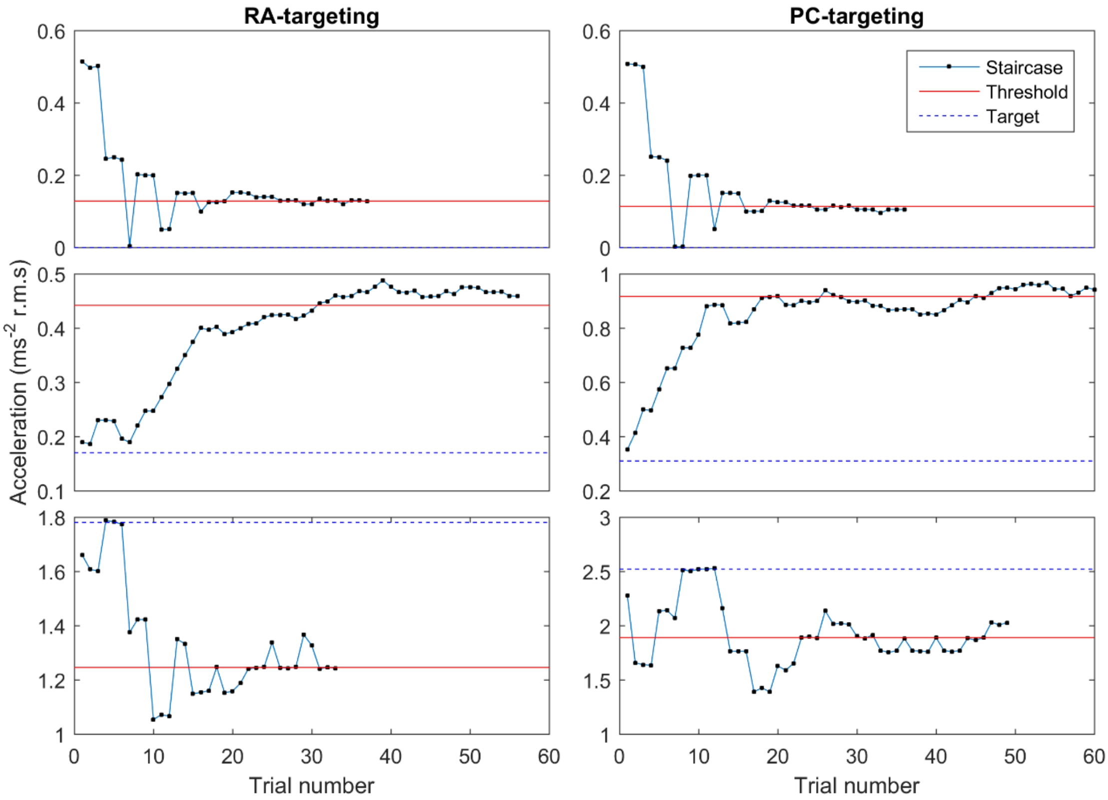


Figure 100. Completed staircase procedures in all 6 conditions for participant 11.

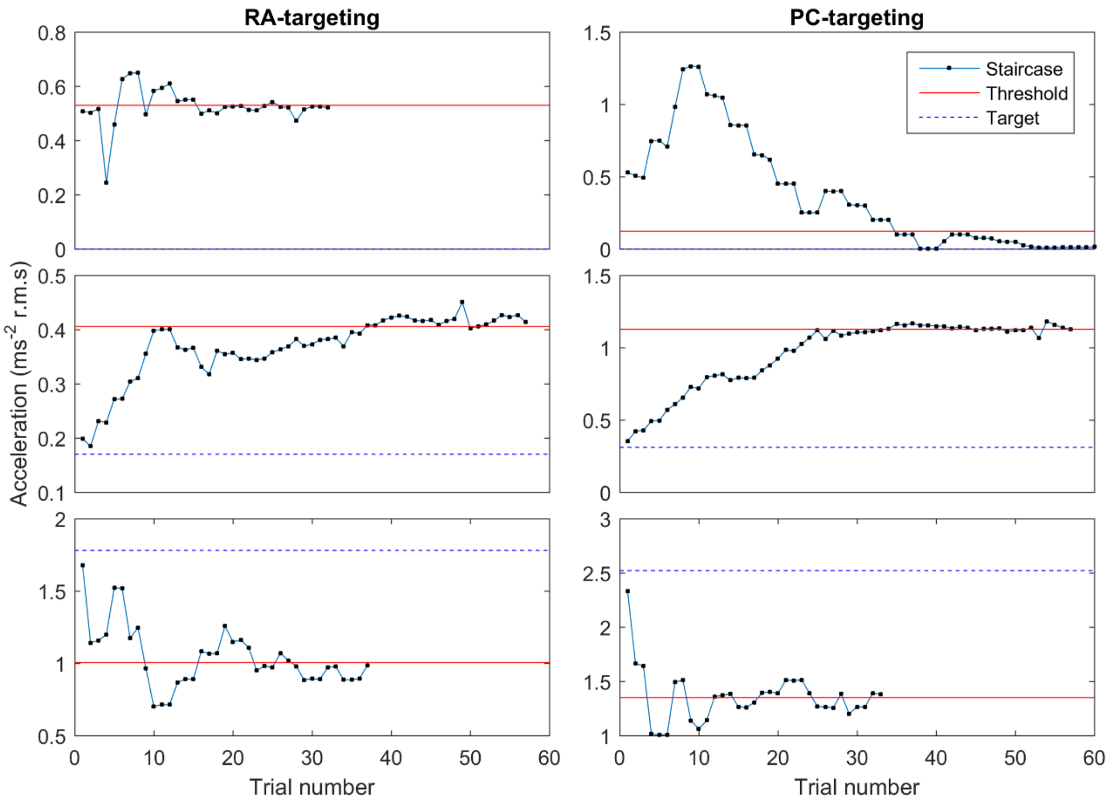


Figure 101. Completed staircase procedures in all 6 conditions for participant 12.

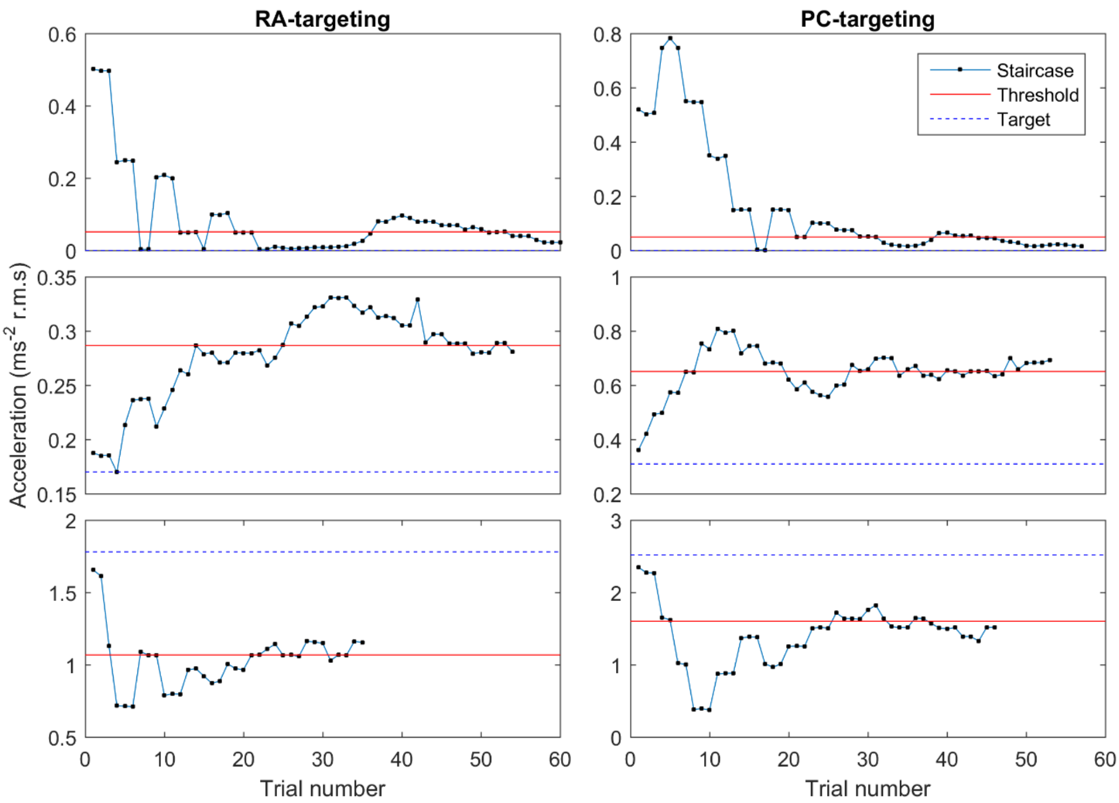


Figure 102. Completed staircase procedures in all 6 conditions for participant 13.

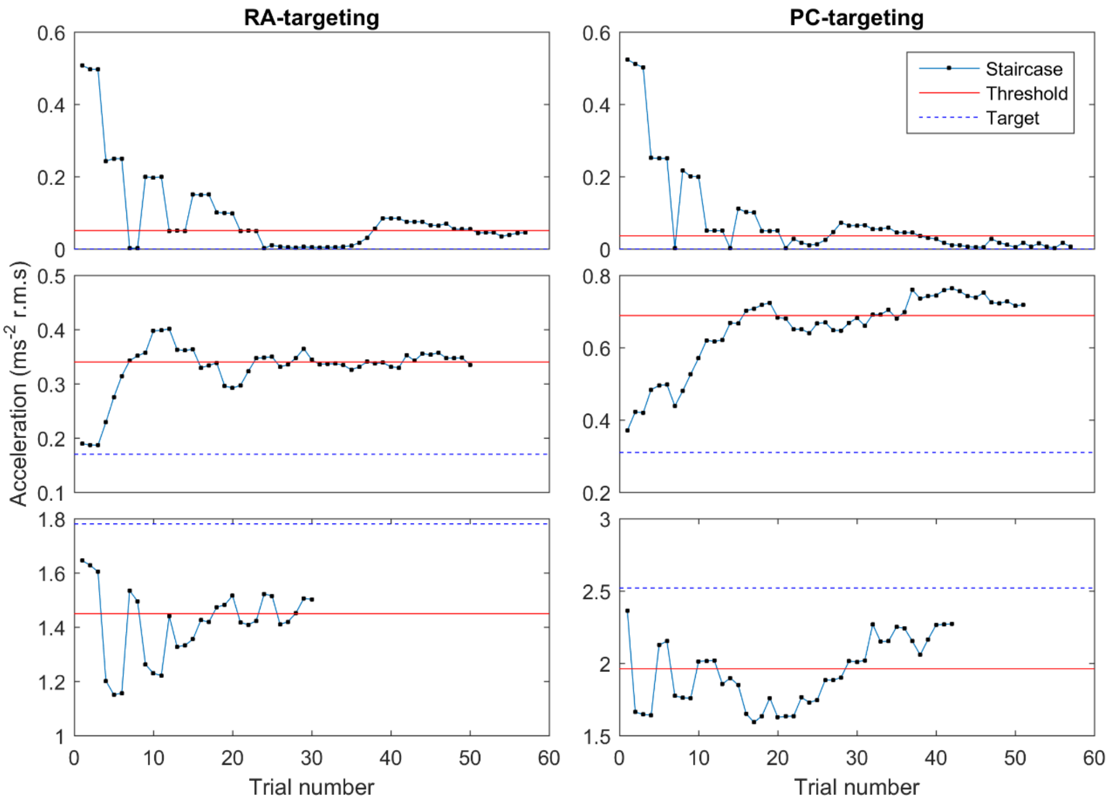


Figure 103. Completed staircase procedures in all 6 conditions for participant 14.

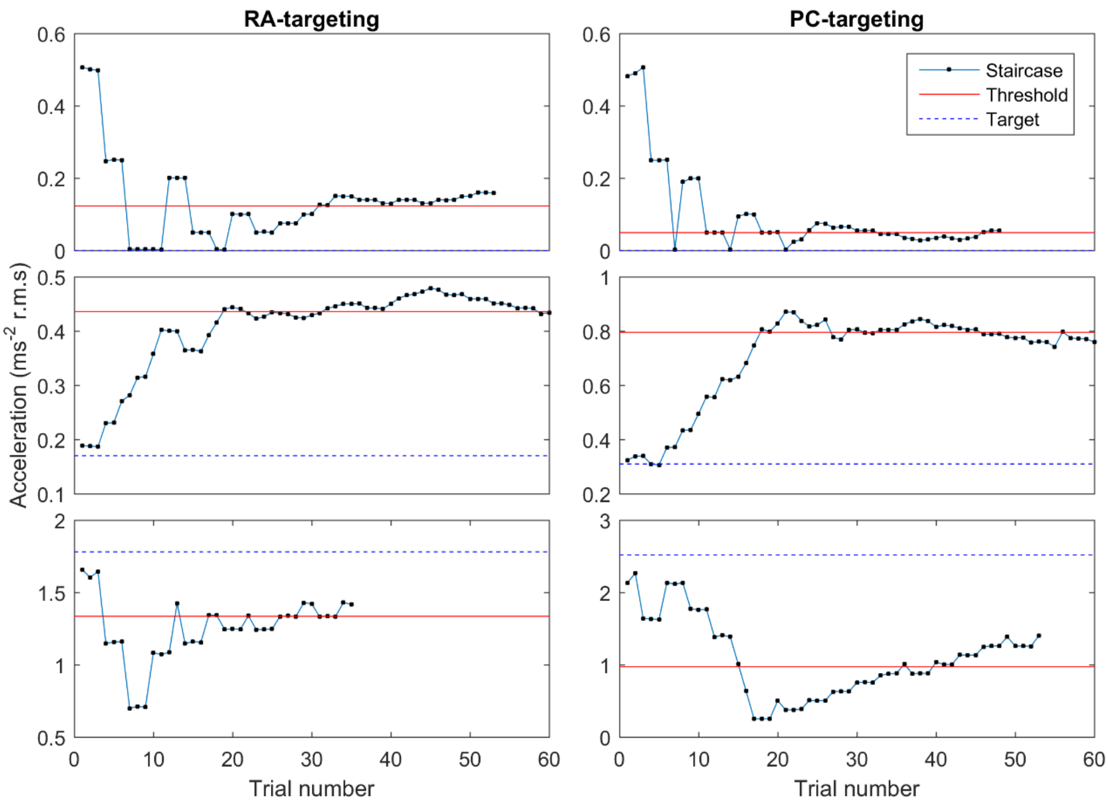


Figure 104. Completed staircase procedures in all 6 conditions for participant 15.

Appendix E Individual data for Experiment 4

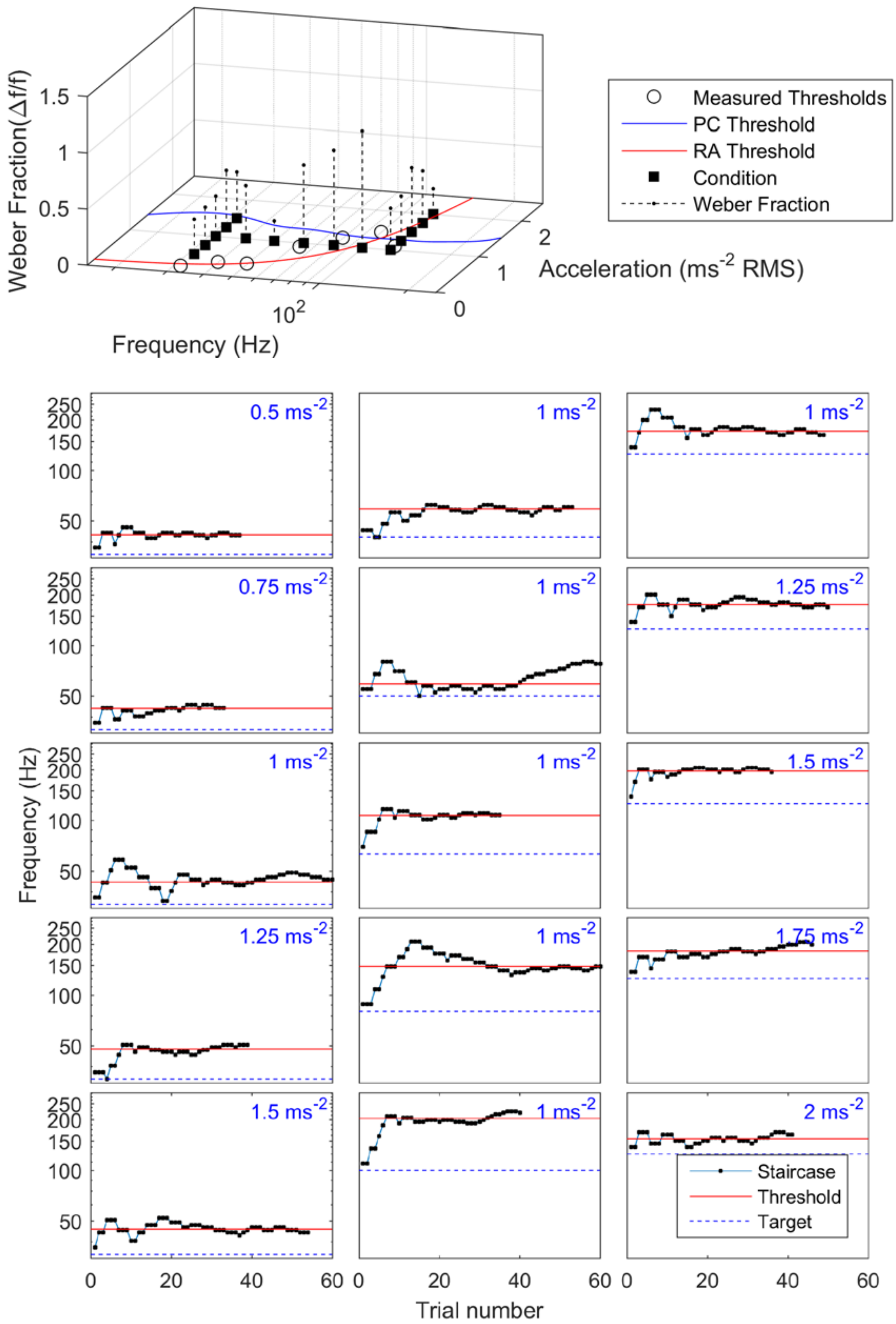


Figure 105. Individual data for P1. The top panel shows estimated PC and RA tuning curves and weber fractions. The bottom channel shows individual staircases.

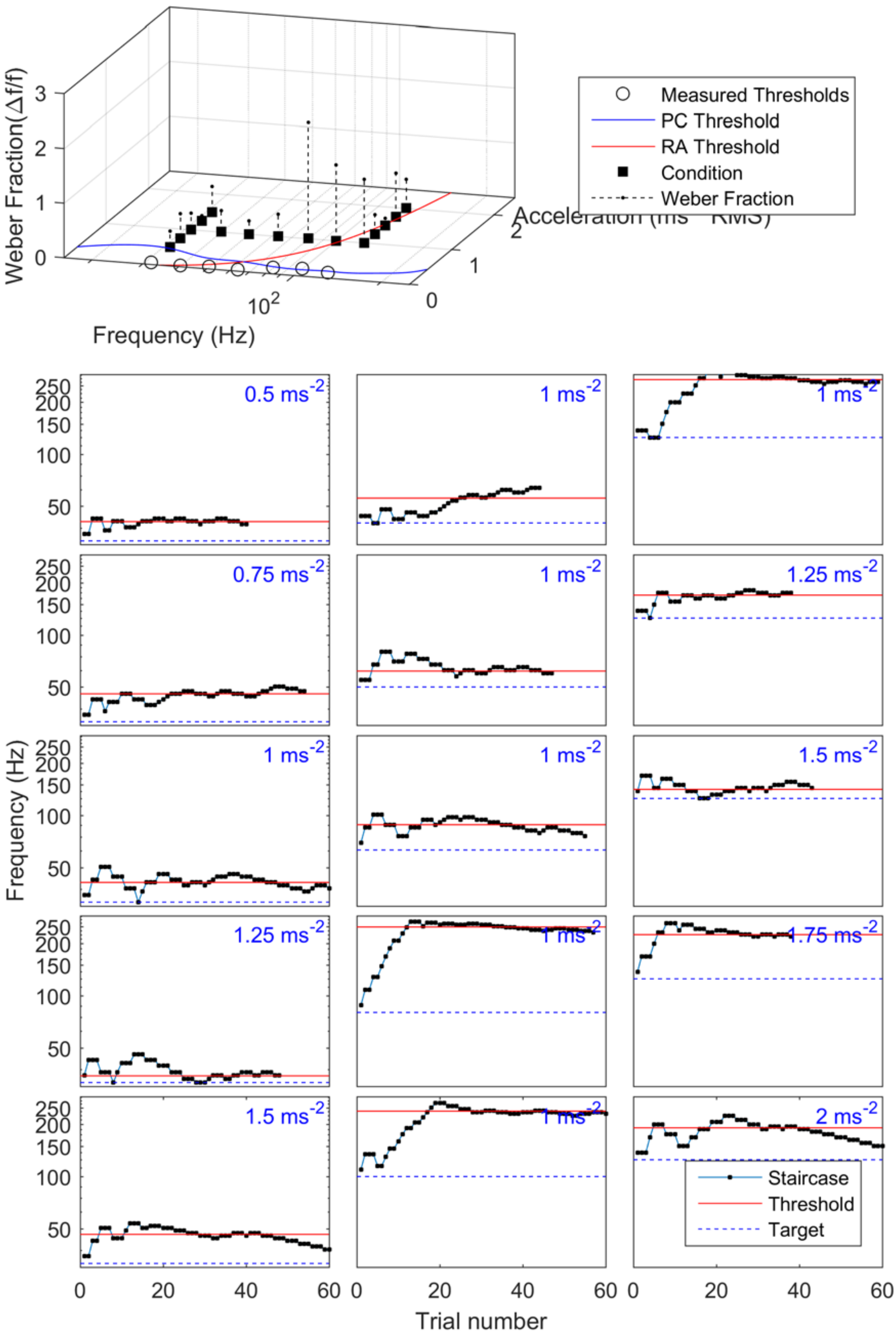


Figure 106. Individual data for P2. The top panel shows estimated PC and RA tuning curves and weber fractions. The bottom channel shows individual staircases.

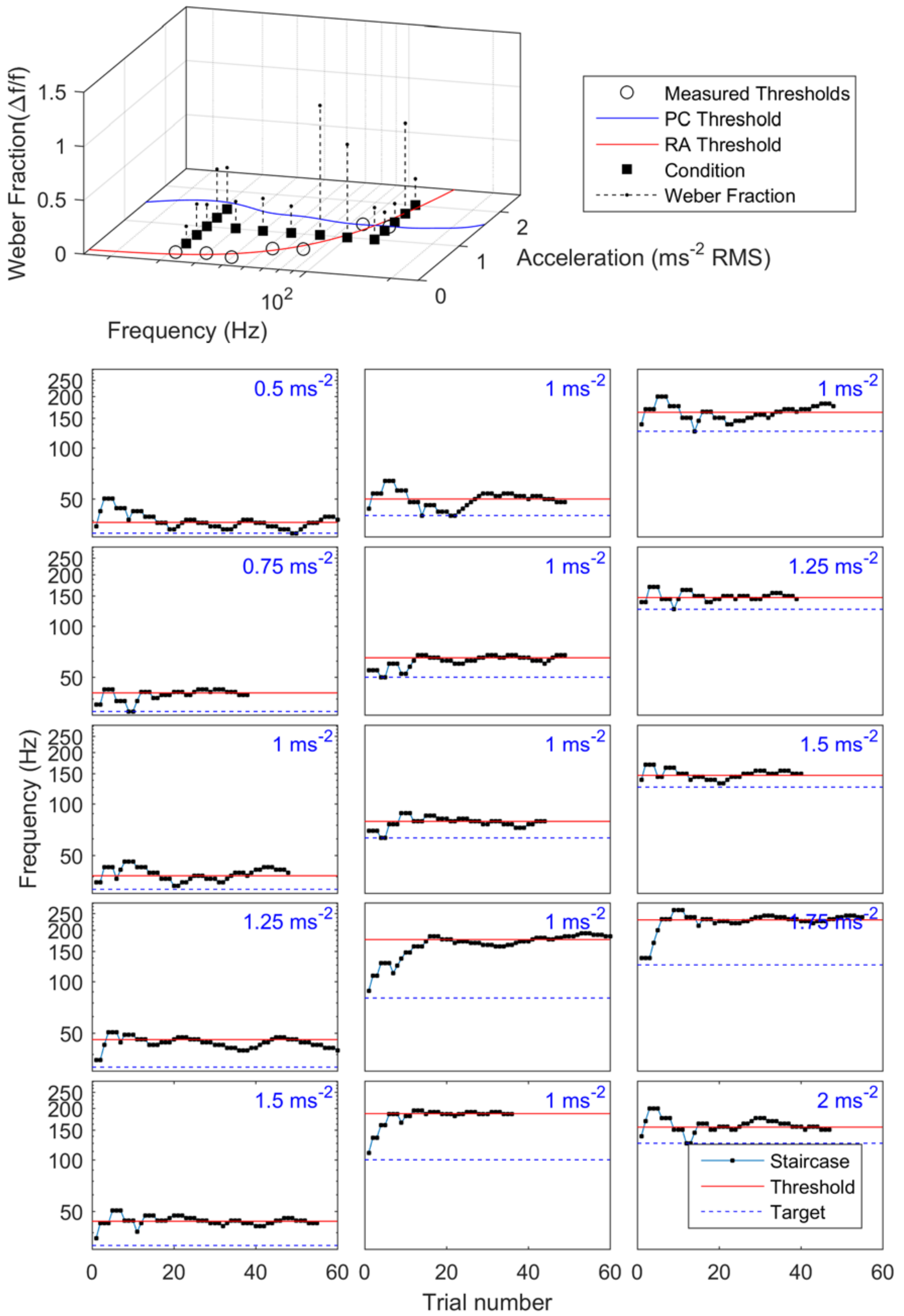


Figure 107. Individual data for P3. The top panel shows estimated PC and RA tuning curves and weber fractions. The bottom channel shows individual staircases.

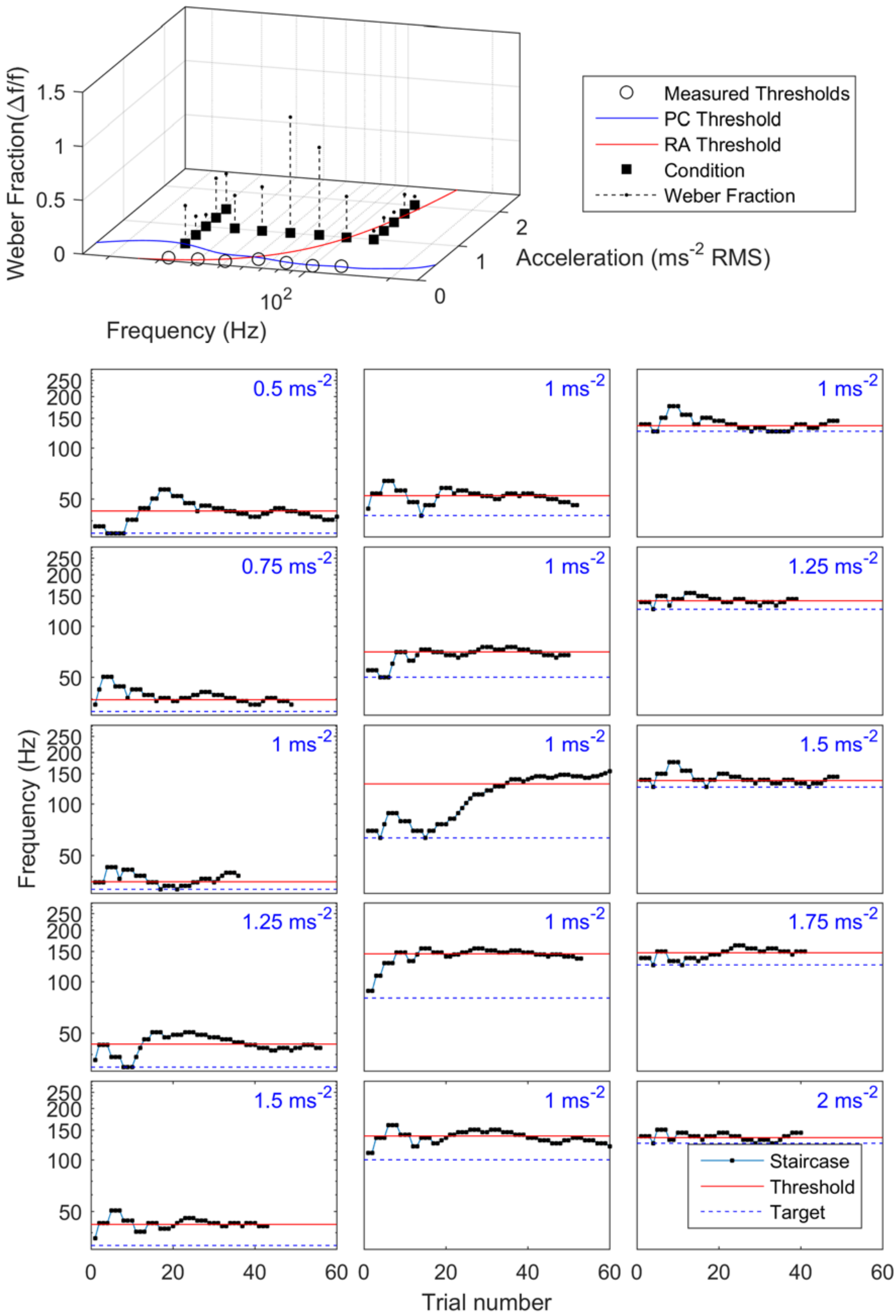


Figure 108. Individual data for P4. The top panel shows estimated PC and RA tuning curves and weber fractions. The bottom channel shows individual staircases.

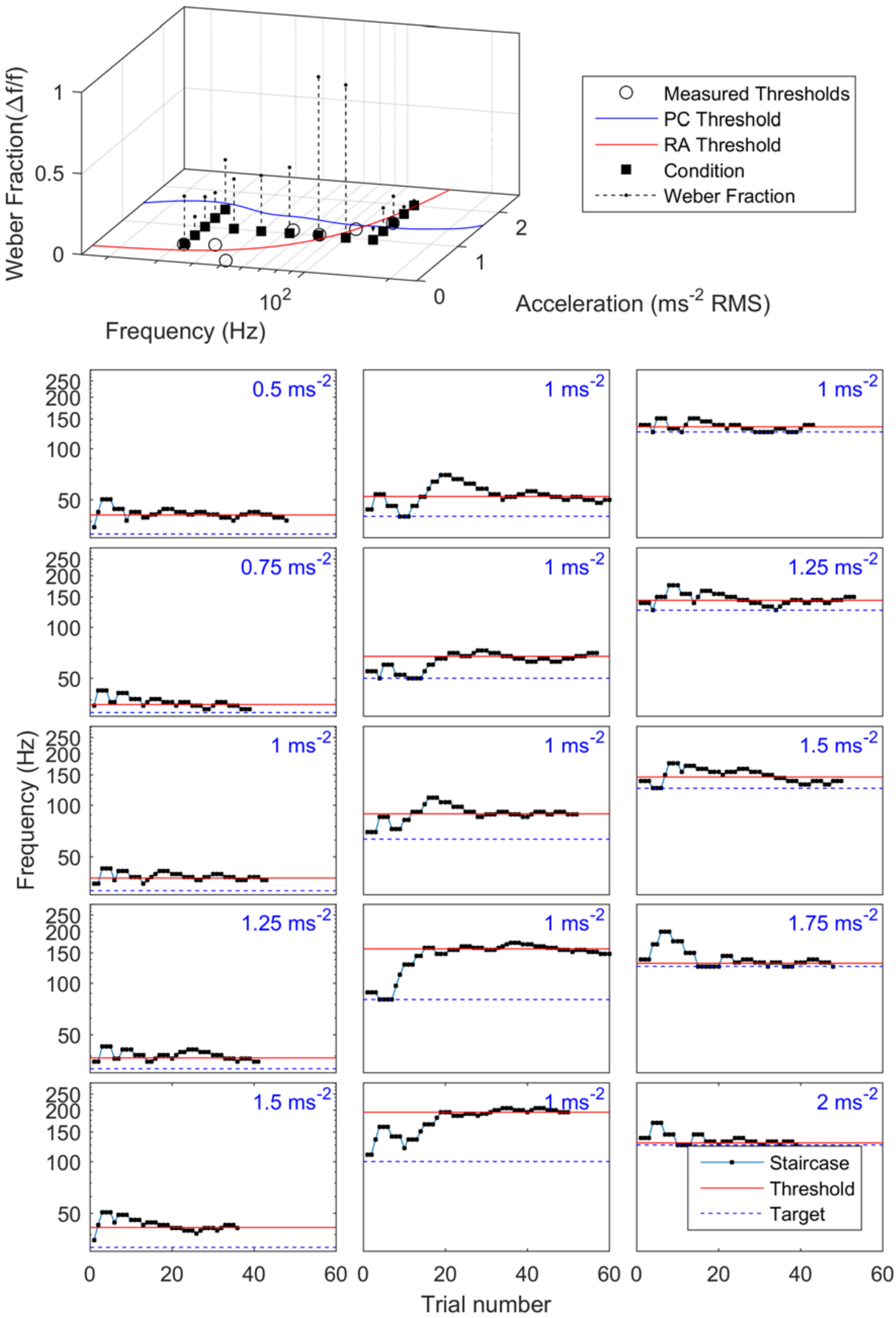


Figure 109. Individual data for P5. The top panel shows estimated PC and RA tuning curves and weber fractions. The bottom channel shows individual staircases.

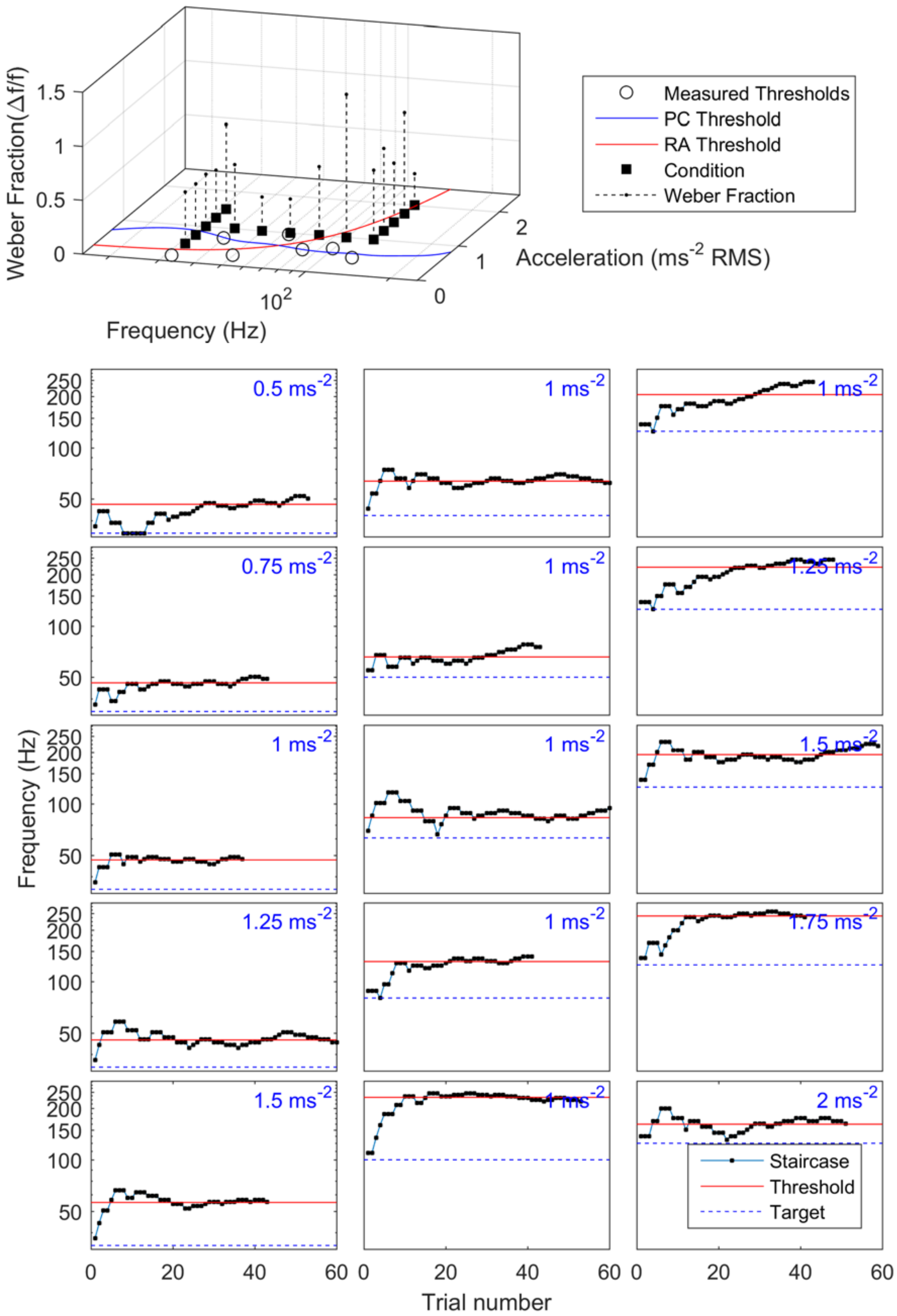


Figure 110. Individual data for P6. The top panel shows estimated PC and RA tuning curves and weber fractions. The bottom channel shows individual staircases.

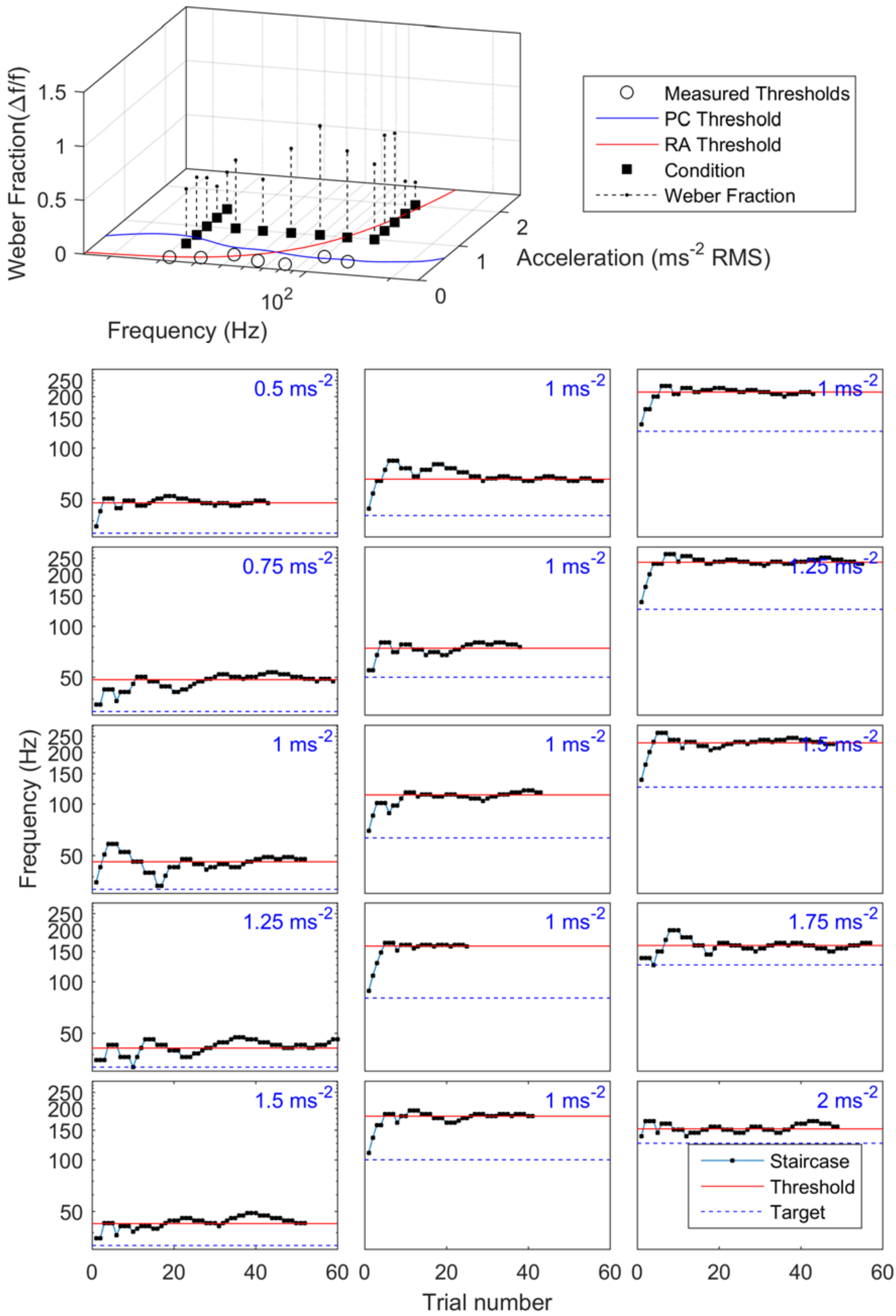


Figure 111. Individual data for P7. The top panel shows estimated PC and RA tuning curves and weber fractions. The bottom channel shows individual staircases.

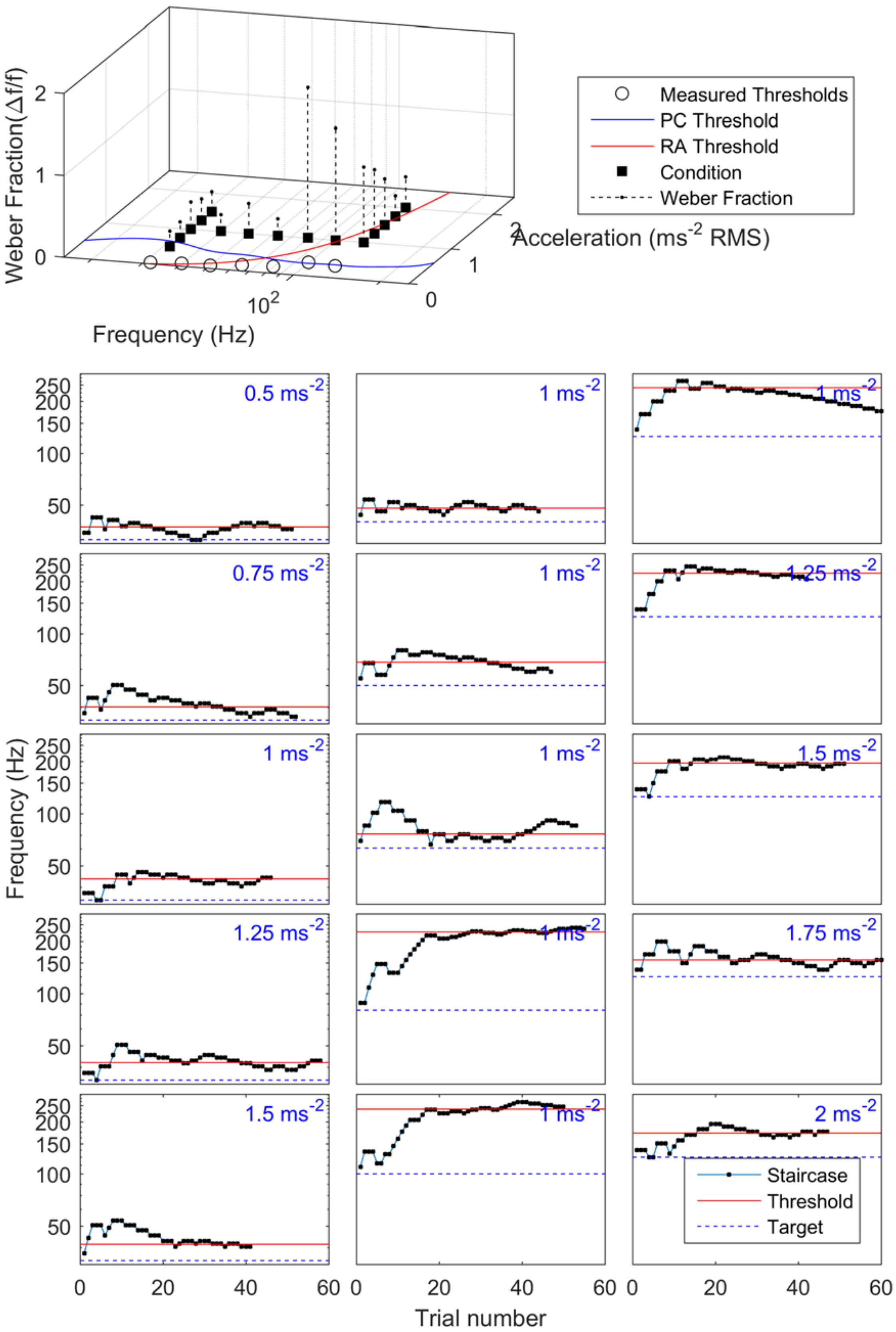


Figure 112. Individual data for P8. The top panel shows estimated PC and RA tuning curves and weber fractions. The bottom channel shows individual staircases.

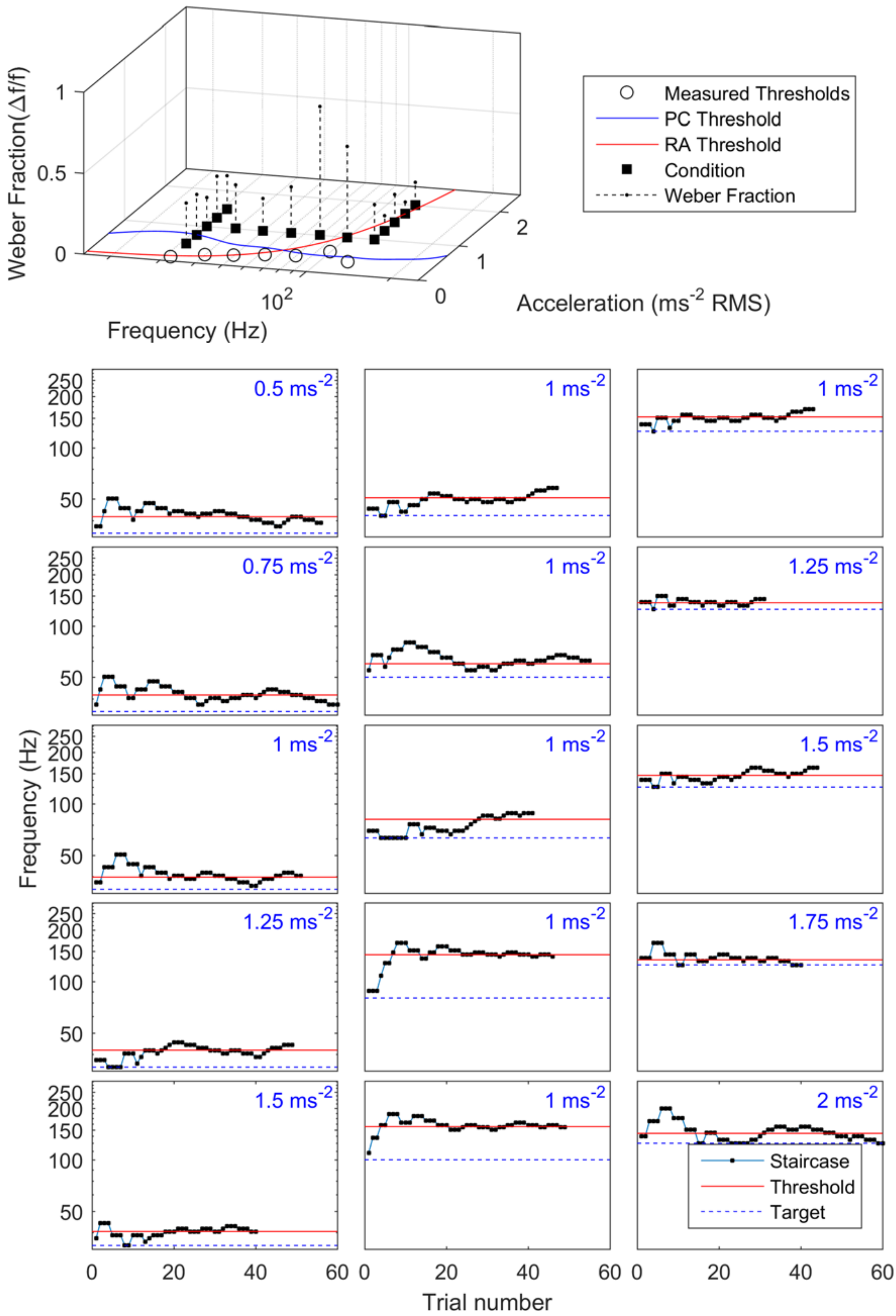


Figure 113. Individual data for P9. The top panel shows estimated PC and RA tuning curves and weber fractions. The bottom channel shows individual staircases.

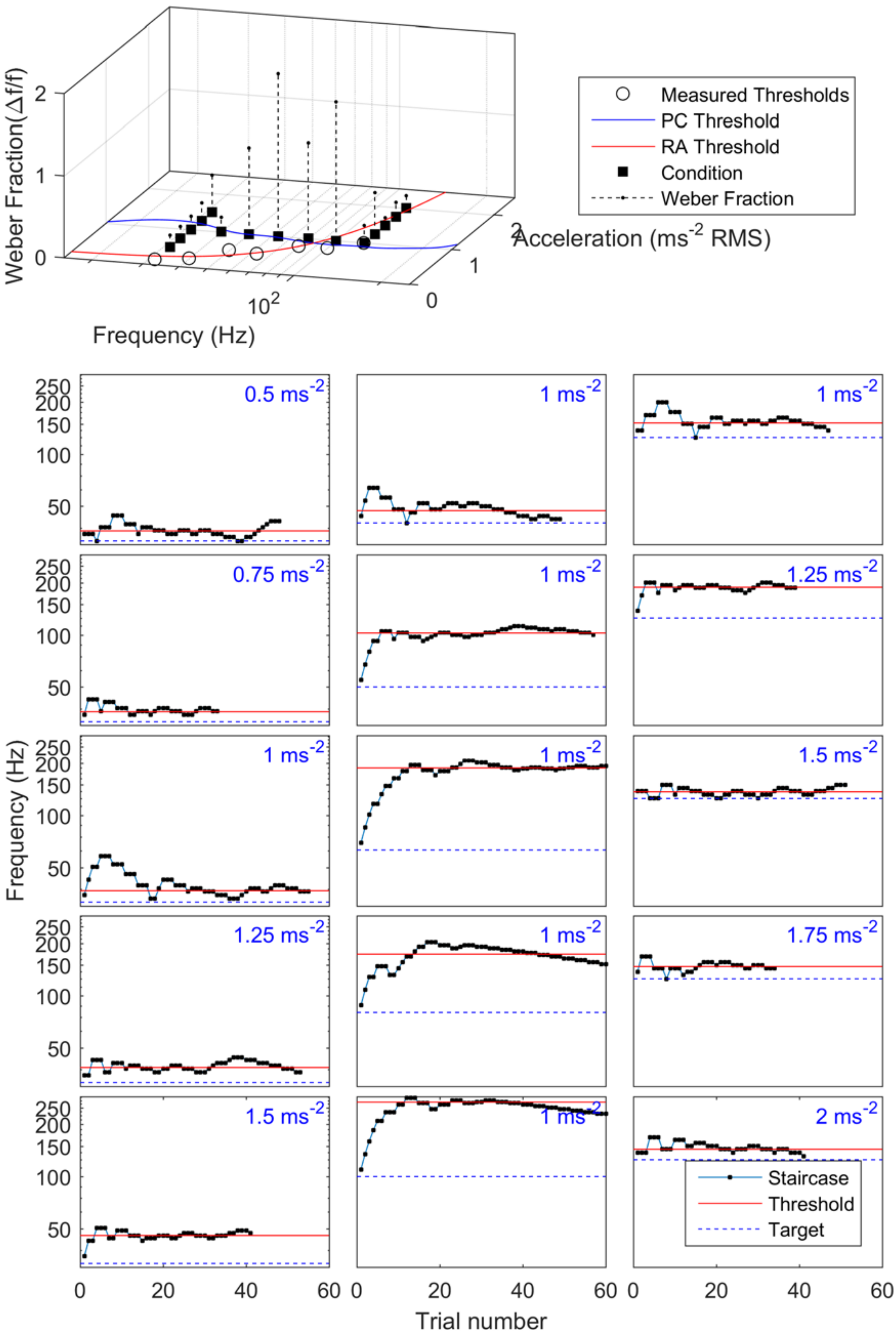


Figure 114. Individual data for 10. The top panel shows estimated PC and RA tuning curves and weber fractions. The bottom channel shows individual staircases.

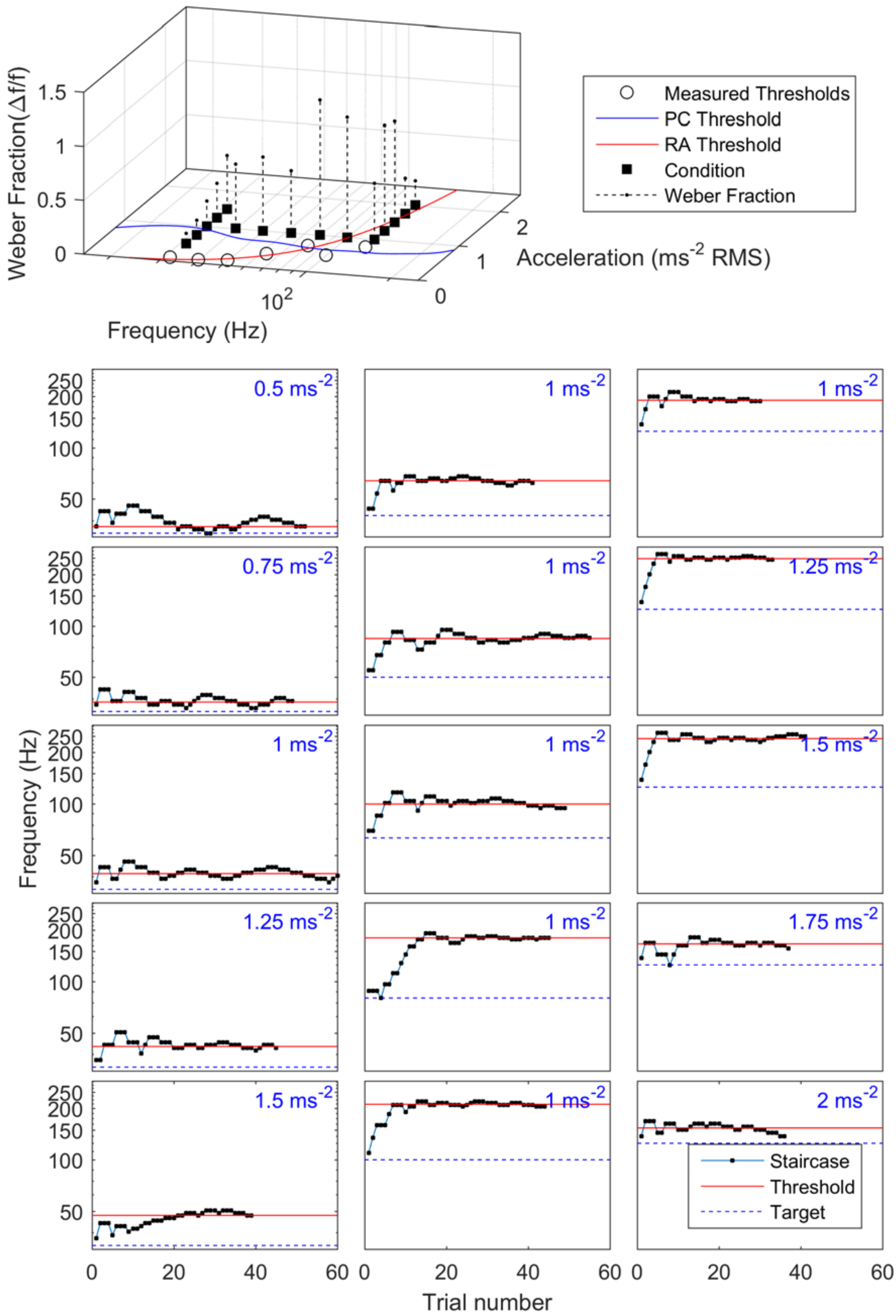
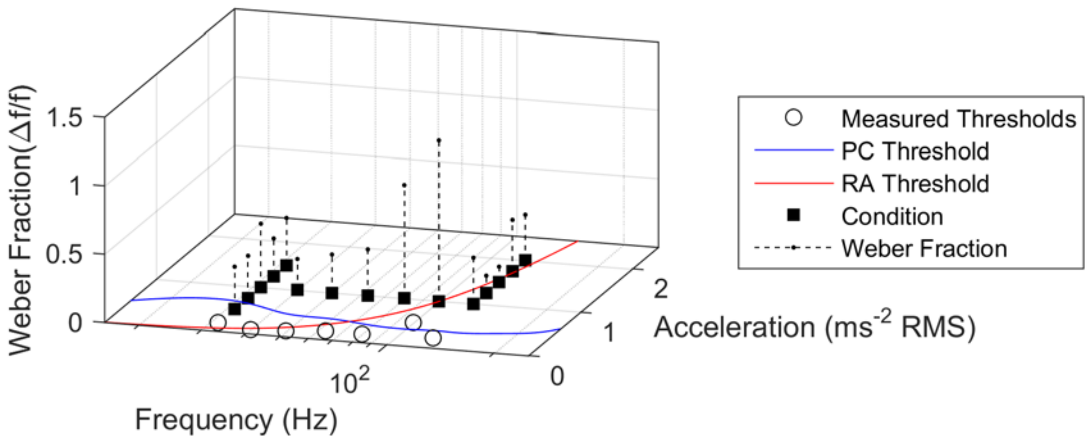


Figure 115. Individual data for P11. The top panel shows estimated PC and RA tuning curves and weber fractions. The bottom channel shows individual staircases.



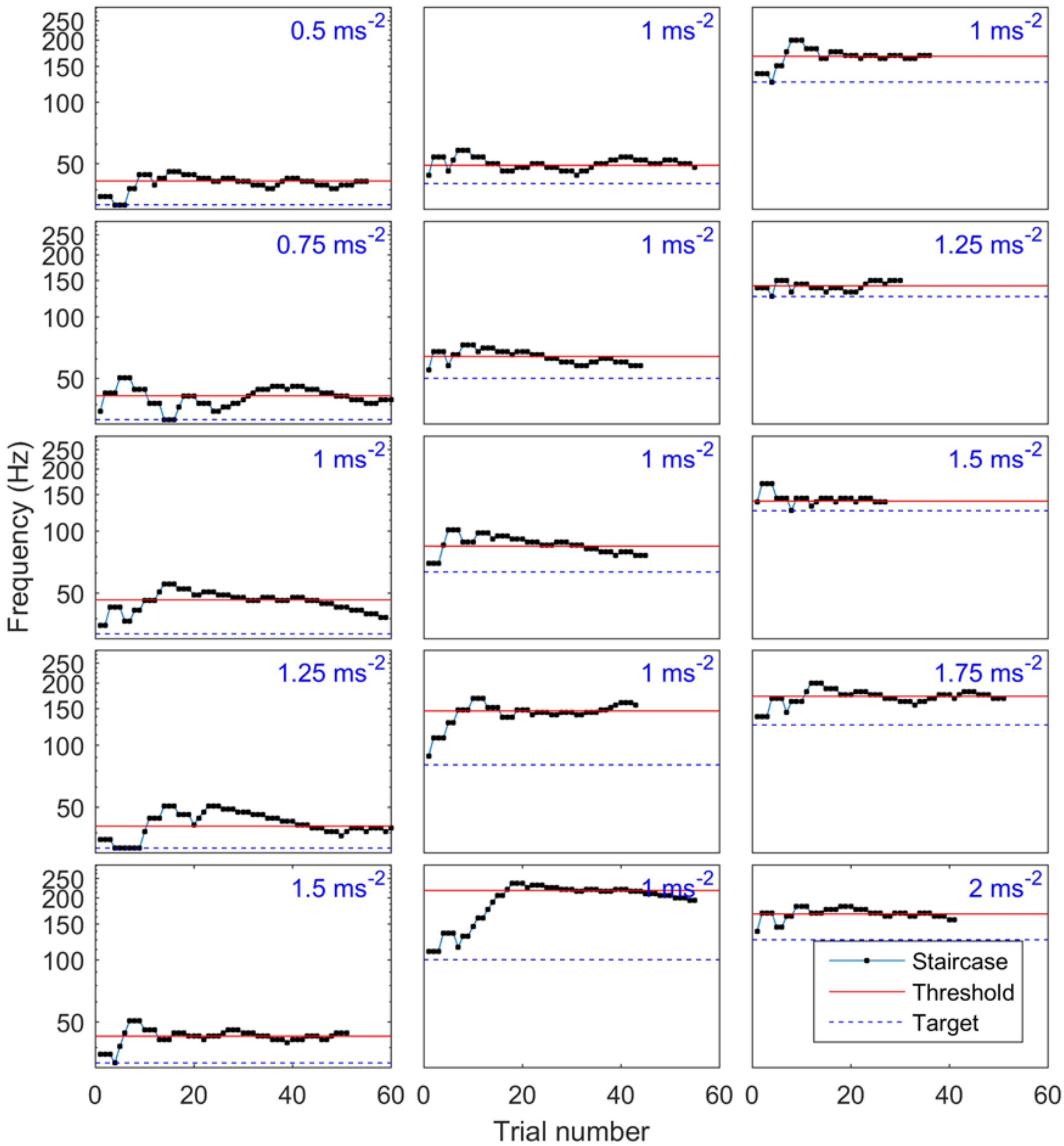
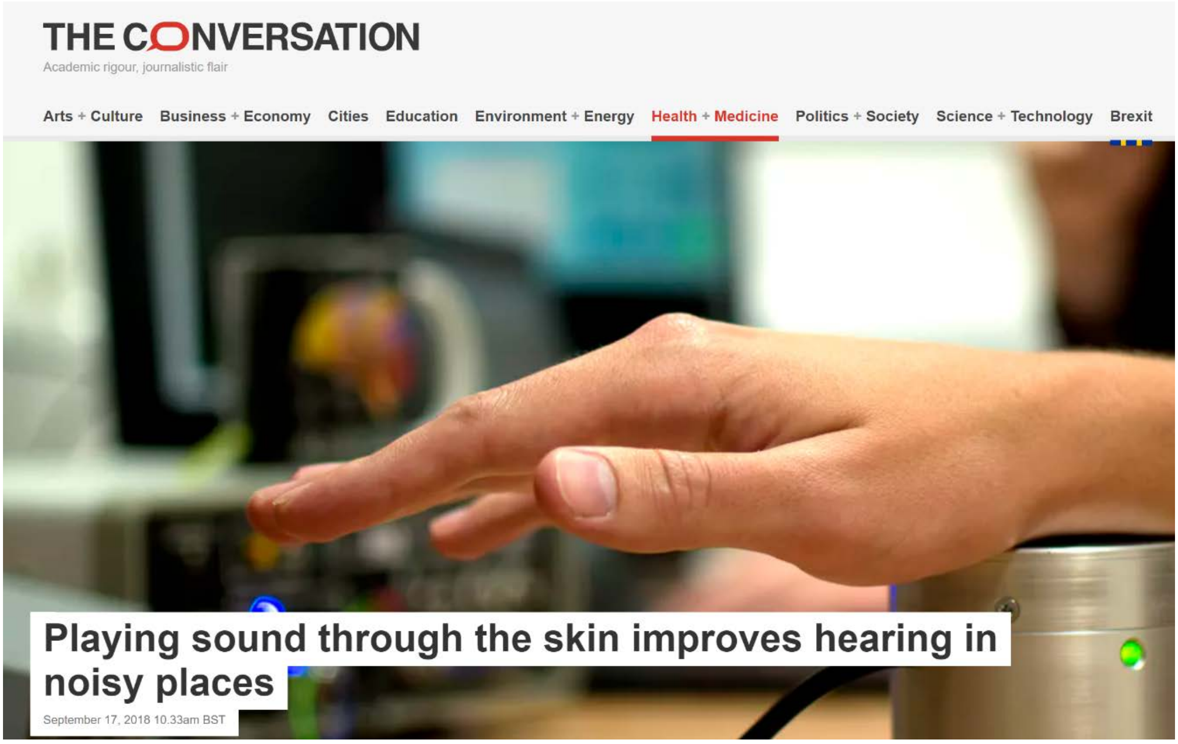


Figure 116. Individual data for P12. The top panel shows estimated PC and RA tuning curves and weber fractions. The bottom channel shows individual staircases.

Appendix F Playing sound through the skin improves hearing in noisy places



Sean R Mills & Mark Fletcher, in *The Conversation*, September 17, 2018 10.33am BS

Available at: https://theconversation.com/playing-sound-through-the-skin-improves-hearing-in-noisy-places-97033

Hundreds of thousands of people with severe hearing loss depend on surgically implanted electronic devices to recover some of their hearing. These devices, known as auditory or cochlear implants, aren't perfect. In particular, implant users find it difficult to understand speech when there is background noise. We have a new approach to solve this problem that involves playing sound through the skin.

People with auditory implants hear the world in a very different way to people with healthy hearing (the video below simulates what it's like to hear through an auditory implant). In an implant user, the sound that is usually transmitted to the brain by tens of thousands of extraordinarily sensitive cells in the ear is instead transmitted by just 22 tiny electrodes. This means that the information transmitted to the brain is severely limited.

This is a big problem in complex sound environments, with a conversation in the corner, music blaring, the bang of a door and the clatter of cutlery. The implant user is unable to join a conversation in a busy office or hear a teacher in a chaotic classroom. We need a new way to get crucial sound information to the brain and bypass the information bottleneck at the implant.

(video available at: https://www.youtube.com/watch?v=n9fvlG7LfSc) 'I beg your pardon?' Auditory implant users struggle to understand speech in noisy places.

F.1 Fusing the senses

The brain is continuously combining information from all our senses to build a picture of the world. When a sense is impaired, as in a deaf or blind person, the brain can compensate by using information from another sense.

In the late 1960s, Paul Bach-y-Rita showed that blind people are able to "see" what is happening in a film when visual information is presented through vibration on the lower back. Since then, researchers have shown that people are able to "see" using sound, and that people who have lost their sense of balance are able to balance again when the missing information is presented through touch.

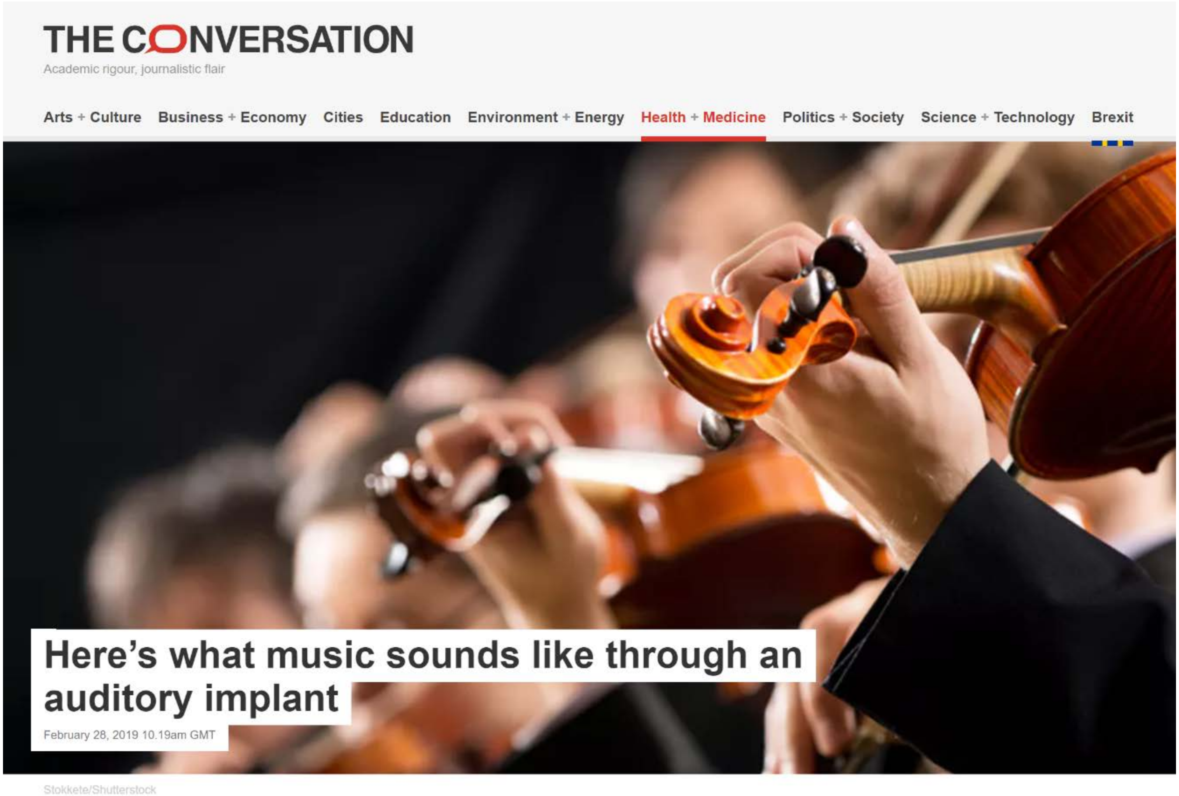
As auditory implant users only get limited sound information through their implant, we wondered whether providing extra sound information through touch could improve their hearing.

To do this, we developed a simple, adaptable system that takes speech in a noisy environment and extracts the broad sound-level fluctuations, known as the "speech envelope". This speech envelope information is not conveyed effectively by the implant and is known to be important for understanding speech in noise. The speech envelope information is then converted into small vibrations on the skin. The brain can then combine these signals with the implant signal to improve understanding of speech.

In our latest study, published in Trends in Hearing, we presented speech in noise with and without vibration from our system and measured how many words participants were able to identify. We found that the device improved word identification for seven of our eight participants. Training was important. Participants were able to identify an average of 5% more words in noise with the device when first using it, and an average of 11% more words, after just 30 minutes of practice. It is possible that, with everyday use, we may find even larger benefits.

Our goal is to develop a compact, inexpensive, wrist-worn device that can be used in the real world within two years. We hope that this device will help implant users hear in noisy places and expand their access to education, work and leisure.

Appendix G Here's what music sounds like through an auditory implant



Sean R Mills & Mark Fletcher, in *The Conversation,* February 28, 2019 10.19am GMT.

Available at https://theconversation.com/heres-what-music-sounds-like-through-an-auditory-implant-112457

For some people with severe hearing loss, it is possible to restore their hearing with an auditory implant (also known as cochlear implants). These electronic devices are surgically implanted into the inner ear, converting the sound from the world into electrical signals that are sent through the auditory nerve to the brain. The damaged parts of the ear are bypassed and people are – almost miraculously – able to hear again. With practice, auditory implant users emerge from a world of silence able to hear the doorbell, to use the phone, to talk and laugh with their friends. Unfortunately, though, music can be hard to enjoy. Smooth melodies become harsh buzzes, beeps and squawks.

People with auditory implants find that much of what they used to love about music is now absent. The implant is poor at conveying the pitch of voices and instruments, as well as the quality (timbre) of the music. This can make it hard to follow the melody, understand the lyrics, or separate one instrument from another. As you can hear in our simulation (below), almost all of the raw, untrammelled emotion that Ed Sheeran brings to his performance of Thinking Out Loud is lost, leaving the music abrasive and flat.

(video available at: https://www.youtube.com/watch?v=57WXFrnjzcU) Simulation of what music sounds like through a cochlear implant.

This poor transmission of music through the implant can have an enormous impact on people's quality of life. Music is all around us, not just at home or in concerts but also in the background in cafes, pubs, shops, TV shows and films. For people with auditory implants, this can make it hard to enjoy things they previously loved to do. People tell us that music is one of the main things they would like to be improved in their implant. This presents a challenge for engineers and scientists.

G.1 The trouble with music

In healthy hearing, the sound of music is captured by the activity of thousands of highly sensitive "hair cells" – sensory receptors that respond to minute changes in pressure in the ear, translating sound into electrical activity that can be interpreted by the brain. This extraordinary sensory system is able to code the tiny fluctuations in sound that we interpret as notes, instruments, timbre and emotional resonance. It is this complex coding that allows us to enjoy the melodic voice of Mr Sheeran. In an auditory implant, that system is replaced by a tiny number of micro-electrodes – usually between eight and 22. These electrodes are only able to transmit very crude pitch information, missing the more detailed sound information.

Over time, some people with auditory implants are able to adjust to their new hearing, finding ways to enjoy and love music again. They often find that they must actively learn to enjoy music again to adjust to their new experience. Others have decided to engage with it differently, reading the lyrics while they listen to improve their understanding. Because the implant is able to transmit rhythm much more effectively than pitch, some users find that they can only enjoy certain, more rhythmic genres of music (such as the Michael Jackson song in our simulation). Some, amazingly, have even learned to play instruments when using an implant.

G.2 Novel approaches

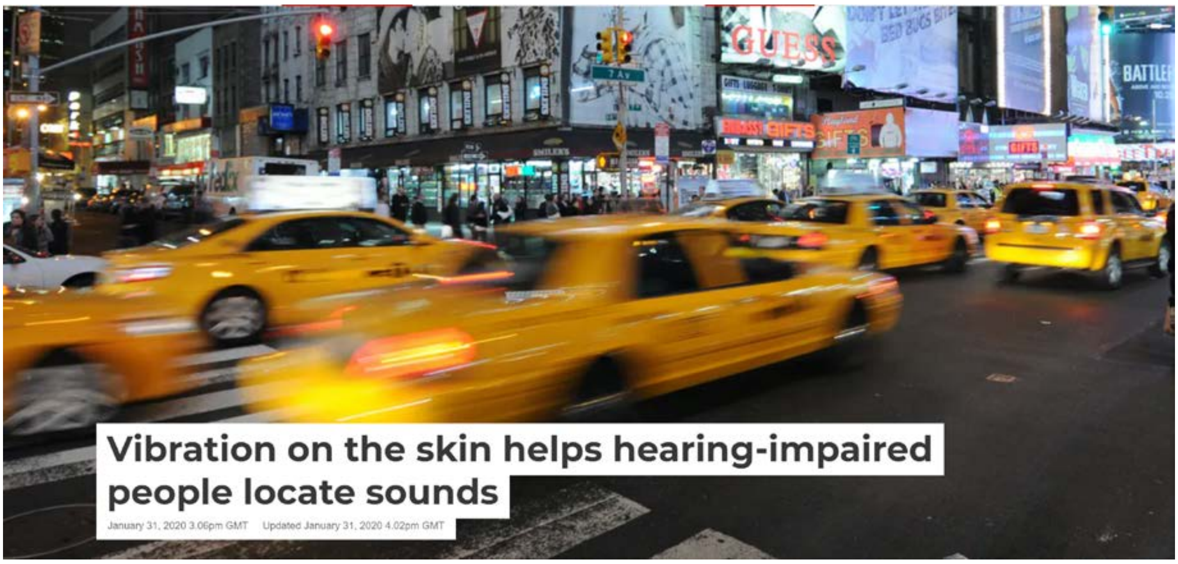
New approaches may hold the key to helping people with implants enjoy music again. One possibility is modifying musical tracks or even writing entirely new music specifically for implants, with qualities that can be more easily transferred by existing technology. For example, researchers have found that increasing the volume of the vocals and removing harmonic instruments improves the experience of listening to pop music.

Another option is changing the way that sounds are processed by the implant before sending the signals to the auditory nerve. Several implant makers now advertise their cutting-edge processing as best for listening to music. However, most implant users are still unable to enjoy music.

It may be necessary to take a radically new approach. We think that the information bottleneck at the implant could be bypassed by providing sound information through the sense of touch. We have recently used this approach to improve implant users' ability to understand speech in complex sound environments – perhaps we can improve their experience of music too.

Please note that the video in this article shows only a simulation of cochlear implant listening. The experience of implant users differs hugely across people, and this demonstration should not be used as a reference point for those considering getting an implant. Cochlear implants are an incredible technology that have transformed the lives of many people.

Appendix H Vibration on the skin helps hearing-impaired people locate sounds



Sean R Mills & Mark Fletcher, in *The Conversation*, January 31, 2020 3.06pm GMT.

Available at https://theconversation.com/vibration-on-the-skin-helps-hearing-impaired-people-locate-sounds-130105

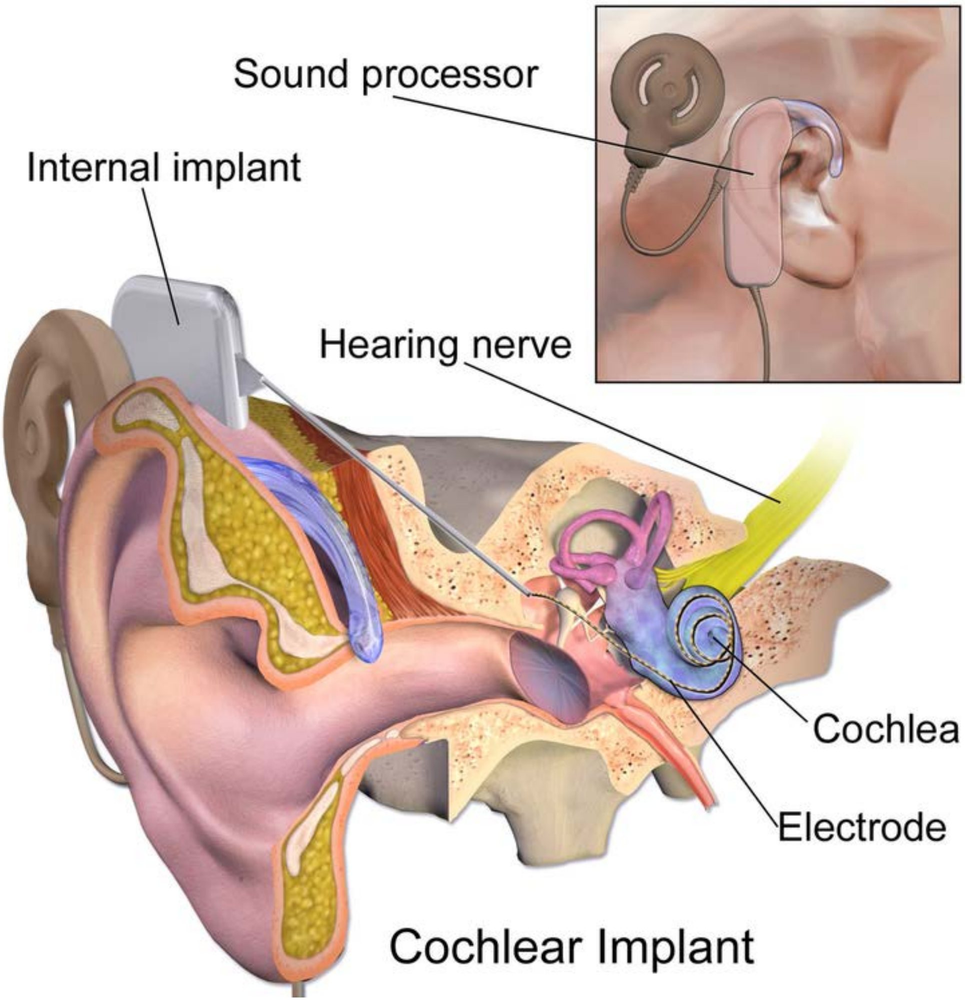
When we hear a car hurtling towards us, we usually immediately know where it is coming from so we can get out of the way. Our brains have an amazing ability to rapidly separate the sound of the car from background sounds and track its location in the world – an ability called spatial hearing.

To do this, our brains exploit the differences in the sounds arriving at our two ears. For example, if a sound comes from our left side, it is louder in our left ear and, because sound takes time to travel through the air, it arrives at our left ear first. Using these cues, our brain builds a continuously evolving picture of where sound-emitting things in the world are, which it uses to locate sound sources and avoid threats, such as that out-of-control car.

Unfortunately, for many people with hearing impairments, spatial hearing is often severely limited. This is particularly true for people who use a cochlear implant, who often find locating and separating different sounds very difficult.

We are trying a different approach. We take the information usually given by the difference in sound between the ears and present it through the sense of touch instead. The idea is that by providing the missing sound information through vibrations on the skin, the brain will be able to merge the two senses to improve perception.

Cochlear implants work by bypassing the damaged parts of the outer and middle ear and directly stimulating the auditory nerve. For thousands of people with severe hearing impairments, this technology has had an incredible impact on their lives, restoring some of their hearing and allowing them to follow conversations in quiet places similarly to people with normal hearing.



Cochlear implants are usually just put in one of the user's ears. BruceBlaus/Wikimedia Commons, CC BY

Unfortunately, most users only have an implant in one ear, usually because of the additional expense and risk of a second implantation surgery. Having only one implant means that those tiny differences in loudness and timing of sounds between the ears cannot be used for spatial hearing.

Although one implant works very well in a quiet place, this can make it difficult to cope in busy sound environments. Imagine trying to listen to your friend talk to you in a crowded restaurant - with clattering crockery and loud conversations - when you can't tell which direction the different sounds are coming from.

H.1 Once more, with feeling

Researchers have previously tried several approaches to improve spatial hearing in cochlear implant users by improving implant technology, but with limited success. In a new study, published in Scientific Reports, we tested whether providing spatial hearing cues to the wrists as vibrations would help cochlear implant users locate sounds.

To conduct our experiment, we set up a ring of loudspeakers. The participants were asked to identify which loudspeaker played the sound of a voice saying: "Where am I speaking from?" As expected, many implant users struggled when they only had the audio. But we found that when they had haptic stimuli (vibrations) alongside the audio, they could identify the location of the sound far more accurately.

After around 15 minutes of training with audio and haptic cues together, participants were able to effectively combine the two signals. We found that they were performing better with combined audio and haptic stimulation than with either sense by itself. This suggests that their brains were able to rapidly merge the information arriving through the two senses to improve spatial hearing.

These results highlight the huge potential of using haptics to aid hearing. In other work, we have already shown that haptics can improve speech perception in noisy environments in cochlear implant users.

In future work, we want to use haptics to help hearing-impaired listeners identify multiple sounds coming from different locations. For example, you might want to hear your friend's voice to one side, music from the radio from another side, and the patter of rain against the windowpane. This could help us find new ways to help hearing-impaired people build a rich and more accurate picture of their world through hearing.