The Touch Perception Puzzle: A Basis for Choosing Stimlus Parameters in Vibrotactile Psychophysics

2 authors:

Sean R Mills
University of Southampton

Michael J. Griffin
University of Southampton

THE TOUCH PERCEPTION PUZZLE: A BASIS FOR CHOOSING STIMULUS PARAMETERS IN VIBROTACTILE PSYCHOPHYSICS

Sean R. Mills and Michael J. Griffin
Institute of Sound and Vibration Research
University of Southampton
Southampton, SO17 1BJ
United Kingdom

Abstract

A full understanding of the relationship between the physics of vibration and the perception of vibration, vibrotactile psychophysics, would be a powerful tool. However, vibration perception is complex: vibrations are perceived more easily at some frequencies than at others and the perception of vibration varies with contactor size, body location, temperature, duration, and various other parameters. Touch perception can be investigated by designing stimuli with different values of these parameters in order to selectively activate the four underlying information processing channels (PC, RA, SA1, and SA2). However, it remains unclear what combinations of stimulus parameters are optimum for selecting each channel. We collate the findings of psychophysical research to summarise the factors affecting perception of vibration and estimate the relative sensitivity of the channels to vibration of various frequencies. The findings imply that while the conditions suggested in ISO 13091-1:2001 for using vibrotactile thresholds to assess sensorineural dysfunction at the fingertips may identify the PC response, they will be less successful in identifying the RA response and fail to identify the SA1 response.

1. Introduction

Understanding of the perception of vibration can contribute to understanding of human touch perception. For vibration stimuli applied to the skin, observations of how accurately participants are able to detect stimuli, or discriminate between stimuli, with each of various physical parameters (the frequency of vibration, static force, duration, body location, etc.) allow the construction of a model of the underlying perceptual system. This approach is generally known as a 'psycho-physical method', and is also used to identify impairments in touch perception (Griffin, 1990; ISO 13091-1, 2001).

The psychophysics of vibration has generally been focussed on detection thresholds (also called absolute thresholds) – an estimate of the minimum vibration amplitude that can be perceived. How the thresholds vary as a function of stimulus parameters led to the identification of four 'information processing channels' that independently process the signal (Bolanowski *et al.*, 1988; Gescheider *et al.*, 2010; Mowbray and Gebhard, 1958; Verrillo, 1968). These channels have been associated with four distinct neurophysiological systems that respond selectively to different vibration stimuli (Bolanowski *et al.*, 1988). For clarity and consistency, the channels are referred to here by the labels given to their associated nerve fibres: Pacinian corpuscle (PC), rapid-adapting (RA), slow-adapting type 1 (SA1), and slow-adapting type 2 (SA2).

The use of psychophysical techniques for research or the diagnosis of disorders depends on being able to selectively activate a particular tactile channel. This study collates findings from psychophysical research to summarise the selectivity of the four-channel model of vibrotactile perception (Figure 1). The model is then applied to provide estimates of channel responses to vibrotactile stimuli, and provides a rationale for choosing particular vibration parameters to selectively activate each tactile channel.

Presented at the 52nd UK Human Response to Vibration Conference and Workshop www.hrv2017.co.uk, Sept 5-6, 2017, Shrivenham, Cranfield University, Cranfield Defence and Security, UK Defence Academy.

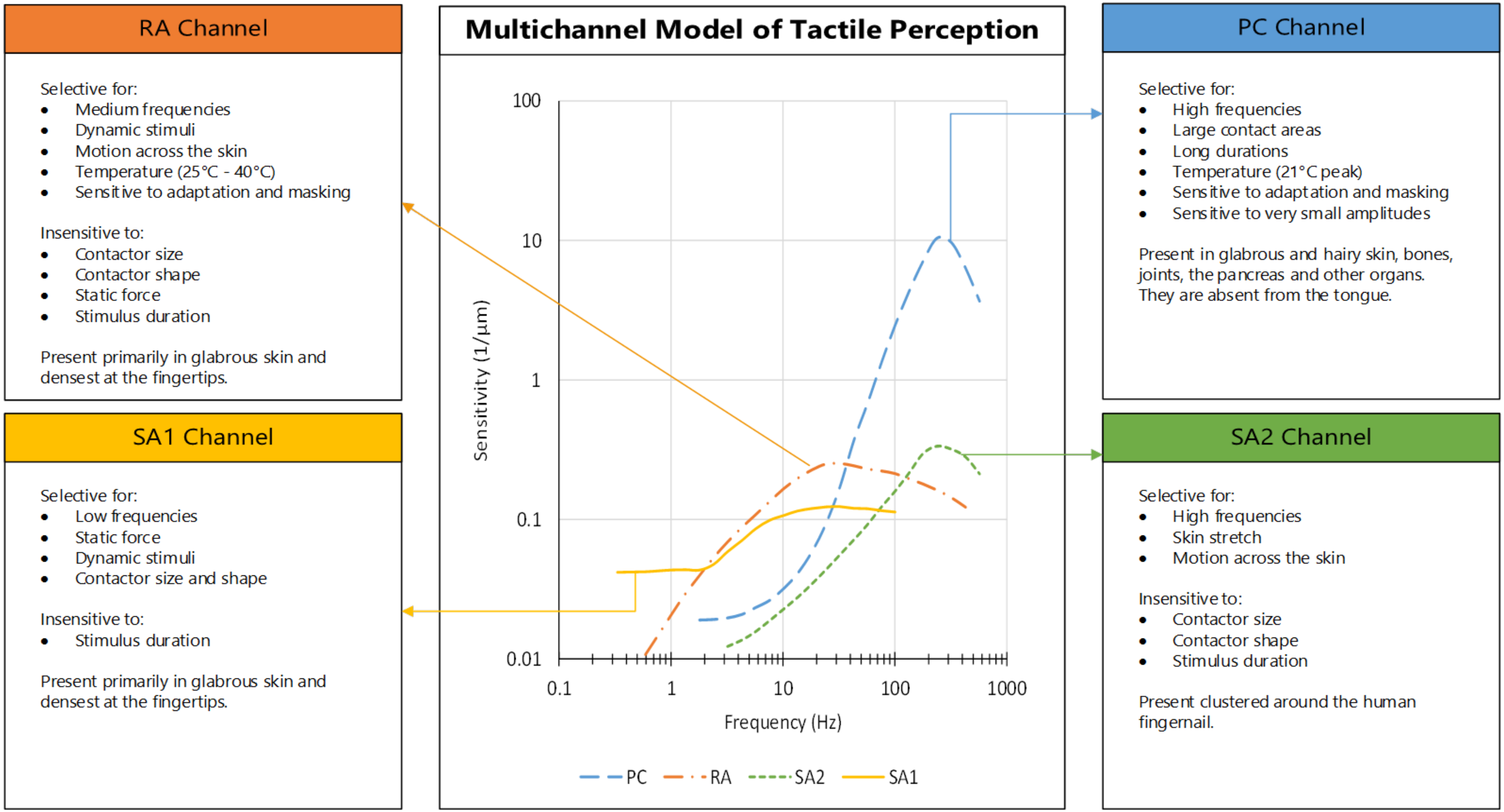

Figure 1. Summary of known effects of stimulus parameters on the four tactile channels that comprise the multichannel model of tactile sensory system (Gescheider *et al*., 2010), based on tuning curves derived by Bolanowski and colleagues (1988), Bolanowski and Verrillo, (1982), Gescheider and colleagues (1985), and Verrillo and Bolanowski (1986). Sensitivity (1/(threshold peak displacement in µm)) is plotted as a measure of the strength of the predicted channel response at a given frequency. The sensitivities of the individual channels are modulated by the factors listed.

2. Effects of stimulus parameters on detection

A basic principle of the multichannel model is that the channels exhibit different selectivity. This means that different channels are more likely to respond, or to respond more strongly, to a vibration with particular values of certain parameters (e.g., frequency, contactor size). It will be assumed that this property can be expressed in terms of sensitivity, a measure of channel response derived from the reciprocal of the detection threshold.

Vibrotactile detection thresholds attempt to expose the selectivity of the channels by assuming that, for a particular set of stimulus parameters, the most sensitive channel mediates detection. This assumption has been useful for investigating whether tactile channels exist. However, while a vibrotactile stimulus may primarily activate one channel, there can be smaller signals from the other channels that are not considered selective for that stimulus.

Measures of the sensitivity of all four channels provide indications of the relative activation of the tactile channels, and allow an assessment of how likely a target channel will be the one that is primarily activated. For suprathreshold stimuli, such as those often experienced in everyday life, it is most likely that several of the information processing channels are activated and that their combined activity mediates rich and detailed perception of object and surface properties like texture (Gescheider *et al*., 2010; Saal and Bensmaia, 2014). Some attempts have been made to quantify suprathreshold information processing with measures of vibrotactile intensity (Hollins and Roy, 1996), but no cohesive model has emerged. Measures of sensitivity derived from detection thresholds may be a partial guide to understanding channel activation by suprathreshold stimuli.

2.1 Frequency

All the channels display frequency selectivity (sometimes thought of as the ‘tuning curve’ of a channel). The PC channel exhibits strong selectivity for the perception of high frequencies of vibration displacement. Microneurographic studies show that the responses of Pacinian corpuscles also exhibit marked frequency selectivity, with the tuning curve changing depending on the vibration amplitude (Bolanowski *et al.*, 1988; Johansson *et al.*, 1982).

2.2 Body location

The mechanoreceptors that mediate vibrotaction are present or absent at different body locations:

- Merkel’s Discs (SA1) are found in glabrous skin, and are densest on the fingertips (Johnson *et al*., 2000; Lacour *et al*., 1991)
- Meissner's corpuscles (RA) are found primarily in glabrous skin, mostly on the fingertips (Johansson and Vallbo, 1979)
- Ruffini endings (SA2) are probably clustered around the fingernail, and are absent in macaques (Johansson and Vallbo, 1979; Johnson *et al*., 2000; Paré *et al*., 2003)
- Pacinian corpuscles (PC) are present in glabrous and hairy skin, bones, joints, the pancreas and other organs, but absent from the tongue (Andres and von Düring, 1973; Hunt, 1974; Macefield, 2005; Verrillo, 1966).

Given that innervation density (e.g., Johansson, 1978; Saal *et al*., 2017; Vega-Bermudez and Johnson, 1999b; Zotterman, 2014), CNS representation (e.g., Romo *et al*., 1993), relationship to motor function (e.g., Saal and Bensmaia, 2014; Witney *et al*., 2004), and psychophysical response (e.g., Forta *et al*., 2012) vary by body location, it might also be possible for the information processing system to differ by body location beyond differences in the density of mechanoreceptors. There might also be differences in whether, or how, the information within channels is integrated to produce sensations.

2.3 <u>Contactor size and the presence of a surround</u>

The sensitivity of the PC channel increases with increasing contact area (e.g. Verrillo, 1968), which is explained by the PC channel's ability to 'spatially summate' signals. This psychophysical evidence formed the foundation for a multi-channel model of touch perception.

Surrounds have been used to limit the area of stimulation by controlling the spread of surface waves. A contactor of any size without a surround can be considered to have a large and diffuse area of stimulation. Surrounds also affect the extent to which the skin is stretched close to the surround.

The characteristics of contactors and surrounds have complex effects on the contact conditions, affecting the static force, skin indentation, and pressure distribution across the skin. For example, the area of a contactor affects the pressure gradient at its edges.

2.4 <u>Static force, skin indentation, and pressure distribution</u>

Some effects of contact conditions on vibration perception have been proposed based on the findings of neurophysiological and psychophysical studies:

SA1:

- More sensitive to points, edges and curvature than to homogenous surfaces (Goodwin *et al*., 1991; Goodwin *et al.*, 1991, 1991; Goodwin *et al*., 1997; Johnson, 2001).
- Merkel receptors respond more to increasing amplitude but respond to surface features independently of increasing indentation depth (Vega-Bermudez and Johnson, 1999b). Tactile pattern recognition, measured psychophysically, is insensitive to contact force (Johnson *et al.*, 2000).
- More sensitive to dynamic than static stimuli (Johnson *et al*., 2000; Krueger, 1970; Vega-Bermudez and Johnson, 1999b).

RA:

- Highly sensitive to motion across the skin (Johnson *et al*., 2000; Pei and Bensmaia, 2014; Srinivasan *et al*., 1990).
- Relatively insensitive to contactor size and shape, because of uniform response across receptive fields (Johnson and Phillips, 1981; Phillips and Johnson, 1981a, 1981b; Vega-Bermudez and Johnson, 1999a).
- Insensitive to static force (Johnson, 2001)

PC:

- Sensitive to skin indentation as small as 10 nm (Brisben *et al*., 1999), about 2 orders of magnitude more sensitive than RA.

SA2:

- Sensitive to skin stretch and motion across the skin (Edin, 1992; Johnson, 2001; Johnson *et al.*, 2000).

2.5 <u>Duration</u>

The PC channel is thought to summate stimulus energy temporally, exhibiting a lower threshold for longer stimuli and a raised threshold for short stimuli (Gescheider, 1976, Gescheider *et al*., 1994; Gescheider *et al*., 1999; Gescheider and Joelson, 1983; Verrillo, 1965a).

2.6 <u>Adaptation and masking</u>

Adaptation can attenuate the responses of the RA and PC channels (Verrillo and Gescheider, 1977; Gescheider *et al.*, 1979). The effects of adapting stimuli on the perception of different frequencies of vibration have been used to identify the frequency selectivity of the channels (Gescheider *et al*., 2001). The degree of adaptation of a tactile channel is taken to be proportional to its sensitivity to the adapting stimulus. High amplitude adapting stimuli may attenuate several channels to different extents.

Masking can affect vibrotactile detection thresholds in specific channels by increasing the 'noise' in the channel (e.g. Gescheider *et al*., 1983; Gescheider *et al*., 2010). Like adaptation, masking can reduce the sensitivity of an individual tactile channel if the channel is sensitive to the masking stimulus.

2.7 <u>Temperature</u>

The responses of the mechanoreceptors and the tactile channels have been found to vary as a function of skin temperature (Bolanowski and Verrillo, 1982; Gescheider *et al.*, 1997; Green, 1977; Verrillo and Bolanowski, 1986). The RA channel increases in sensitivity over the range 15 to 25°C and then plateaus between 25 and 40°C. The PC channel increases in sensitivity as the temperature of the contactor rises from 15 to 21°C, and declines from 21 to 41°C. The frequency of peak sensitivity in the PC channel increases as the skin temperature increases from 21 to 41°C.

2.8 <u>Experimental design, training, and other factors</u>

Vibrotactile thresholds can be influenced by external factors including participant demand characteristics and response bias, and by the structure of the experiment (Mills *et al*., 2016). Different psychophysical methods produce different vibrotactile thresholds (Morioka and Griffin, 2002). Training may also affect the apparent sensitivity of the tactile channels; most experiments use 'highly trained' participants with many hours of training. It is not clear how to build these effects into a model of information processing in the tactile system.

Aging reduces the sensitivity of the tactile system with the rate of loss of sensitivity greater in the PC channel than the non-Pacinian channels (Gescheider *et al.*, 1994).

Medical conditions can affect the sensitivity of the tactile system including diabetes and the hand-arm vibration syndrome (HAVS). The neurological symptoms of these conditions can be measured psychophysically with vibrotactile thresholds (Griffin, 1990; ISO 13091-1, 2001; Thomsen *et al*., 2011). Diagnosis of these disorders would be helped by a better understanding of how individual tactile channels can be selectively activated by choosing the stimulus parameters.

3. Discussion

3.1 Choosing stimulus parameters in vibrotactile psychophysics

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).

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.

3.2 Vibrotactile channel activation of stimuli recommended in International Standard 13091-1:2001

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 1 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 2) compared to a 19.2-mm diameter contactor at the thenar eminence (Bolanowski *et al.*, 1988; Figure 1). 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).

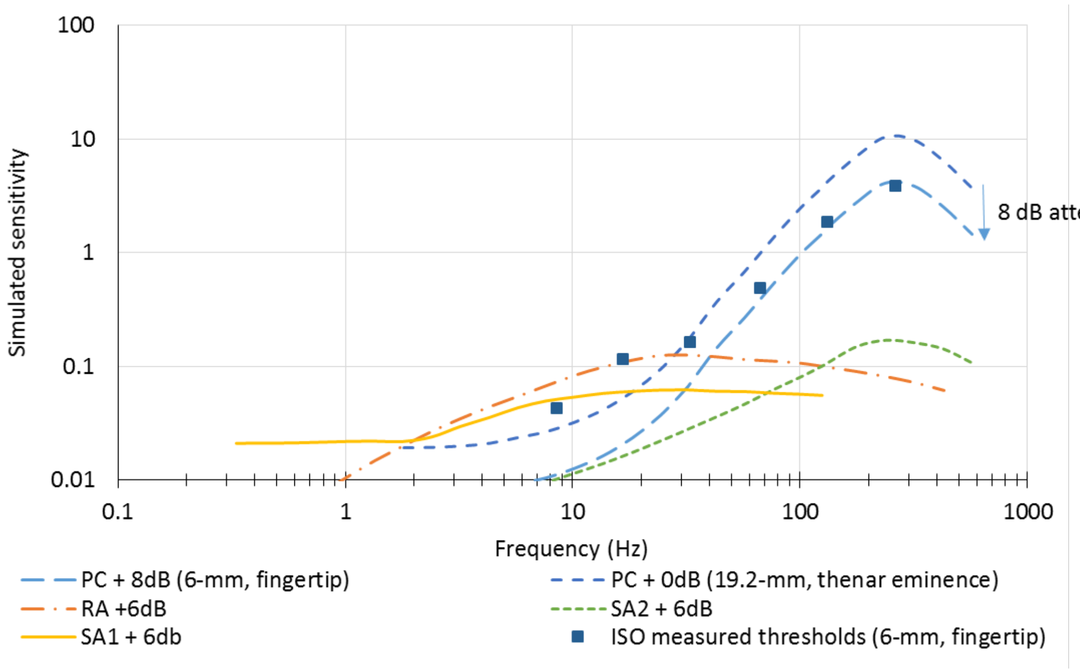

Figure 2. Channel sensitivity (1/(threshold peak displacement in μm)) with a 6-mm contactor. The PC channel is attenuated by 8 dB and the non-Pacinian channels are attenuated by 6 dB in order to fit measured vibrotactile thresholds with a 6-mm contactor (Morioka *et al.*, 2008).

The model in Figure 2 was used to investigate whether the stimulus parameters recommended in ISO 13091-1:2001 are likely to selectively activate their target tactile channel (Figure 3). 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 3 suggests 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 3 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 3 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 3 C).

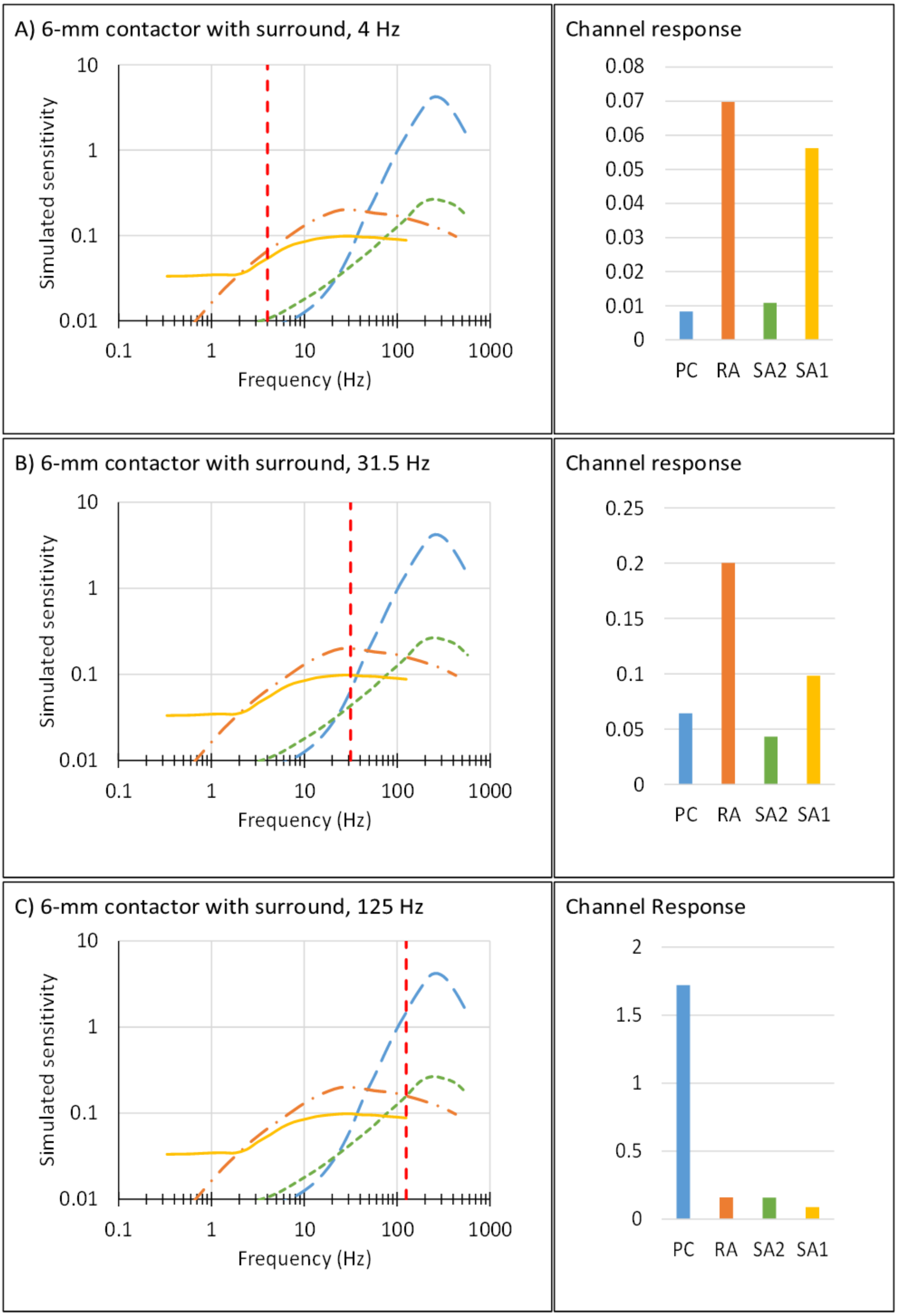

Figure 3. Predicted channel sensitivity (1/(threshold peak displacement in µm)) to vibration parameters specified in ISO 13091-1:2001. (A) illustrates the channel response to a 4-Hz stimulus designed to activate the SA1 channel. (B) shows channel sensitivity to a 31.5-Hz stimulus designed to activate the RA channel. (C) shows channel sensitivity to a 125-Hz stimulus designed to activate the PC channel.

4. Conclusions

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.

5. References

Andres, K. H. and von Düring, M. (1973). Morphology of Cutaneous Receptors. In *Somatosensory System* (pp. 3–28). Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-65438-1_2

Bolanowski, S. J., Gescheider, G. A., Verrillo, R. T. and 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. and Verrillo, R. T. (1982). Temperature and criterion effects in a somatosensory subsystem: a neurophysiological and psychophysical study. *Journal of Neurophysiology*, *48*(3), 836–855.

Brisben, A. J., Hsiao, S. S. and Johnson, K. O. (1999). Detection of Vibration Transmitted Through an Object Grasped in the Hand. *Journal of Neurophysiology*, *81*(4), 1548–1558.

Edin, B. B. (1992). Quantitative analysis of static strain sensitivity in human mechanoreceptors from hairy skin. *Journal of Neurophysiology*, *67*(5), 1105–1113.

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

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. and Bolanowski, S. J. (1999). Vibrotactile temporal summation: probability summation or neural integration? *Somatosensory and Motor Research*, *16*(3), 229–242.

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

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

Gescheider, G. A., Frisina, R. D. and Verrillo, R. T. (1979). Selective adaptation of vibrotactile thresholds. *Sensory Processes*, *3*(1), 37–48.

Gescheider, G. A. and Joelson, J. M. (1983). Vibrotactile temporal summation for threshold and suprathreshold levels of stimulation. *Perception and Psychophysics*, *33*(2), 156–162.

Gescheider, G. A., O'Malley, M. J. and Verrillo, R. T. (1983). Vibrotactile forward masking: Evidence for channel independence. *The Journal of the Acoustical Society of America*, *74*(2), 474–485.

Gescheider, G. A., Sklar, B. F., Van Doren, C. L. and 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, G. A., Thorpe, J. M., Goodarz, J. and Bolanowski, S. J. (1997). The effects of skin temperature on the detection and discrimination of tactile stimulation. *Somatosensory and Motor Research*, *14*(3), 181–188. https://doi.org/10.1080/08990229771042

Gescheider, G. A., Wright, J. H. and Verrillo, R. T. (2010). *Information-Processing Channels in the Tactile Sensory System: A Psychophysical and Physiological Analysis*. Psychology Press.

Goodwin, A. W., John, K. T. and 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. and Bisley, J. W. (1997). Encoding of object curvature by tactile afferents from human fingers. *Journal of Neurophysiology*, *78*(6), 2881–2888.

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

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

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

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

International Organization for Standardization. (2001). ISO 13091-1:2001 - Mechanical vibration -- Vibrotactile perception thresholds for the assessment of nerve dysfunction -- Part 1: Methods of measurement at the fingertips. Retrieved 21 July 2016, from http://www.iso.org/iso/catalogue_detail.htm?csnumber=32509

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., Landström, U., Lundström, R. and 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. and Vallbo, A. 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. 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

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

Krueger, L. E. (1970). David Katz's Der Aufbau der Tastwelt (The world of touch): A synopsis. *Perception and Psychophysics*, *7*(6), 337–341. https://doi.org/10.3758/BF03208659

Lacour, J. p., Dubois, D., Pisani, A. and 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

Macefield, V. G. (2005). Physiological characteristics of low-threshold mechanoreceptors in joints, muscle and skin in human subjects. *Clinical and Experimental Pharmacology and Physiology*, *32*(1–2), 135–144. https://doi.org/10.1111/j.1440-1681.2005.04143.x

Mills, S. R., Morioka, M. and Griffin, M. J. (2016). Limitations of vibrotactile thresholds. Presented at the 51st United Kingdom Conference on Human Responses to Vibration, Institute of Naval Medicine, Gosport, PO12 2DL, England.

Morioka, M. and 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.

Morioka, M., Whitehouse, D. J. and Griffin, M. J. (2008). Vibrotactile thresholds at the fingertip, volar forearm, large toe, and heel. *Somatosensory and Motor Research*, *25*(2), 101–112. https://doi.org/10.1080/08990220802045574

Mowbray, G. H. and Gebhard, J. W. (1958). *Man's senses as informational channels*. DTIC Document. Retrieved from http://oai.dtic.mil/oai/oai?verb=getRecordandmetadataPrefix=htmlandidentifier=AD0630025

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

Pei, Y.-C. and Bensmaia, S. J. (2014). The neural basis of tactile motion perception. *Journal of Neurophysiology*, *112*(12), 3023–3032. https://doi.org/10.1152/jn.00391.2014

Phillips, J. R. and Johnson, K. O. (1981a). Tactile spatial resolution. II. Neural representation of bars, edges, and gratings in monkey primary afferents. *Journal of Neurophysiology*, *46*(6), 1192–1203.

Phillips, J. R. and Johnson, K. O. (1981b). Tactile spatial resolution. III. A continuum mechanics model of skin predicting mechanoreceptor responses to bars, edges, and gratings. *Journal of Neurophysiology*, *46*(6), 1204–1225.

Romo, R., Ruiz, S. and Crespo, P. (1993). Cortical Representation of Touch. In *Neuroscience: From Neural Networks to Artificial Intelligence* (pp. 154–170). Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-78102-5_9

Saal, H. P. and Bensmaia, S. J. (2014). 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., Delhaye, B. P., Rayhaun, B. C. and Bensmaia, S. J. (2017). Simulating tactile signals from the whole hand with millisecond precision. *Proceedings of the National Academy of Sciences*, 201704856. https://doi.org/10.1073/pnas.1704856114

Srinivasan, M. A., Whitehouse, J. M. and LaMotte, R. H. (1990). Tactile detection of slip: surface microgeometry and peripheral neural codes. *Journal of Neurophysiology*, *63*(6), 1323–1332.

Thomsen, N. O. B., Cederlund, R., Speidel, T. and Dahlin, L. B. (2011). Vibrotactile sense in patients with diabetes and carpal tunnel syndrome. *Diabetic Medicine: A Journal of the British Diabetic Association*, *28*(11), 1401–1406. https://doi.org/10.1111/j.1464-5491.2011.03308.x

Vega-Bermudez, F. and Johnson, K. O. (1999a). SA1 and RA receptive fields, response variability, and population responses mapped with a probe array. *Journal of Neurophysiology*, *81*(6), 2701–2710.

Vega-Bermudez, F. and Johnson, K. O. (1999b). 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. (1963). Effect of contactor area on the vibrotactile threshold. *The Journal of the Acoustical Society of America*, *35*(12), 1962–1966.

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). Specificity of a cutaneous receptor. *Perception and Psychophysics*, *1*(3), 149–153. https://doi.org/10.3758/BF03210047

Verrillo, R. T. (1968). A duplex mechanism of mechanoreception. *The Skin Senses*, 139–159.

Verrillo, R. T. and 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. and Gescheider, G. A. (1977). Effect of prior stimulation on vibrotactile thresholds. *Sensory Processes*, *1*(4), 292–300.

Witney, A. G., Wing, A., Thonnard, J.-L. and 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

Zotterman, Y. (2014). *Sensory Functions of the Skin in Primates: With Special Reference to Man*. Elsevier.