Temporal integration of tactile inputs from multiple sites

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Abstract. We investigated the perceived frequency elicited by two vibrating probes on the skin. Participants (n = 11) compared two probes vibrating in counter-phase (25Hz), with comparison stimuli of in-phase vibration (18 - 54Hz). They indicated which had the higher perceived frequency. Skin sites on the palm (glabrous) and arm (hairy) were tested with a range of probe separations (1 - 16cm) and amplitudes (10 - 120μm). Perceived frequency increased with decreasing separation of the probes ($F_{1,10}$ = 182.8, p < 0.001). The two skin sites did not significantly differ ($F_{1,10}$ = 3.6, p = 0.087). Perceived frequency was only minimally affected by amplitude changes between 40 and 120μm ($F_{2,20}$ = 6.4, p = 0.007, η^2_G = 0.06). Both phase and spatial separation strongly influence vibrotactile interaction between two skin locations in a manner largely independent of changes in amplitude, and of skin type.

Keywords: touch, vibration, frequency, psychophysics, human

1 Introduction

Fast adapting mechanoreceptors in the skin are uniquely adapted to respond to mechanical vibration. Recordings of FA1 and FA2 primary afferents show that their responses are precisely phase-locked to each cycle of sinusoidal vibration, providing highly reliable temporal information [1], [2]. In this study, we investigated how temporal features of vibrotactile stimulation are processed for perception of frequency for inputs that are spatially separated. It is not obvious to what extent the precise temporal information available in primary afferent trains is processed in later neural pathways, nor are the perceptual consequences of any such processing understood.

During vibrotactile stimulation, some afferents with receptive fields furthest from the center of stimulation will be poorly activated and fail to respond on some cycles [2]. This does not give rise to a lower apparent frequency in that zone, however [3], and frequency perception appears to rely on an integrated population response. Units with receptive fields close to the center of stimulation that respond on every cycle of vibration may effectively 'fill-in' the missing spikes from poorly activated units that respond intermittently, resulting in integrating inputs from multiple units [1]. If no

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one afferent is adequately stimulated, multiple weakly responding afferents might fill-in for each other, preserving the stimulus frequency in the population response.

A challenge for central nervous system (CNS) neurons to preserve the precise timing present in the periphery is that these higher order neurons receive multiple converging peripheral inputs, which travel along axons varying in conduction velocity [4]. Responses in multiple afferents caused by the same mechanical event reach the first synapse with slightly different delays (up to 15ms), reducing the temporal precision with which the vibratory signal is encoded [5].

The main goal of this study was to test to what extent frequency perception integrates temporal inputs from separate sources of afferent sub-populations. To do this, we applied vibration to the skin with two probes simultaneously, and asked participants to judge the overall frequency of the vibration. Both probes vibrated at 25 Hz, in counter-phase with each other. When two probes are located close to each other, a considerable number of afferents would be recruited by both probes, responding to indentations from each alternately, encoding a frequency of 50 Hz. Other afferents are likely to be recruited by only one probe, encoding a frequency of 25 Hz. When a greater distance separated the probes, fewer (and eventually no) primary afferents are likely to be recruited by both probes (**Fig. 1)**.

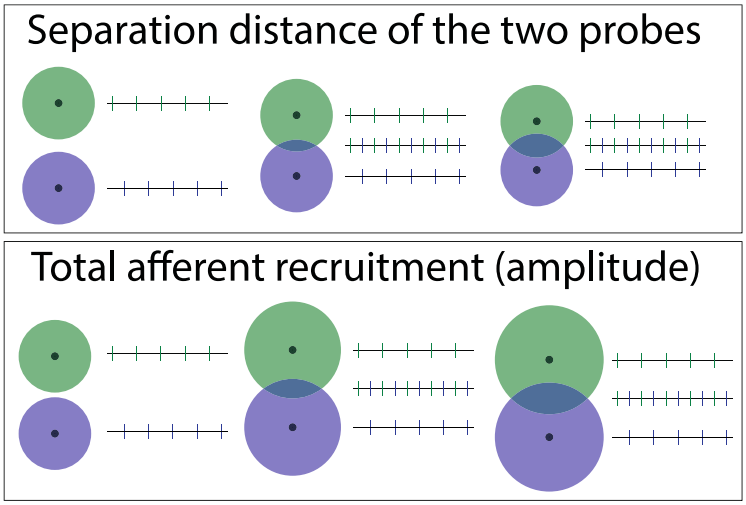

Fig. 1. Illustration of activation regions: primary afferents with their receptive fields in the shaded areas will be activated by a probe. *Top*: as the probes move closer together, more afferents respond to both. *Bottom*: as the amplitude is increased, activation areas increase. This causes more afferents to respond to both probes, but also recruits more afferents that respond to just one.

When the probes are separated enough that no primary afferents are activated by both of them, some higher order neurons with their larger receptive fields [6] may still receive inputs from afferents responding to each of the probes. In this case, filling-in due to phase differences may still occur, but because this process is subject to varying delays of peripheral inputs, the signal may be degraded. Instead, if higher order neu-

rons are unable to sufficiently preserve the temporal precision of the periphery, neural filters may serve to temporally align the inputs to produce a perceived frequency of 25 Hz. By systematically varying the distance between the probes, we tested to what extent integration is preserved over these distances.

A secondary goal of this study was to test how the properties of different skin regions influence the integration of peripheral frequency signals. The glabrous skin of the hands and in the hairy skin of the arms differ in spatial resolution [7], sensitivity thresholds, elasticity and receptor types (e.g. hair sensitive units not found in glabrous skin) [8]. It seems likely that these differences may lead to different strategies for integrating peripheral inputs for frequency perception.

In addition, we wanted to test how the number of recruited afferents affects perceived frequency. Higher amplitude vibration will recruit additional afferents, with receptive fields further from the center of stimulation compared to a lower amplitude stimulus [2]. This increases the number of afferents responding to both probes, but also increases the number responding to only one (**Fig. 1**). If perceived frequency is dominated by the highest frequency (double the frequency of individual probes) (maximal filling-in), we might expect to see an upwards frequency shift at increasing spatial separations as amplitude increases.

2 Method

2.1 Participants

Eleven participants volunteered for the two main experiments (8 male, aged 19-33), 6 for the hairy-glabrous direct comparison experiment (all male, aged 21-43), and 8 for the double probe control experiment (7 male, aged 18-34). All participants were healthy, with no history of neurological dysfunction. The experimental protocol was approved by the human research ethics committee of Western Sydney University and conformed to the Declaration of Helsinki.

2.2 Apparatus

Vibration was delivered to the skin via two spherical probes (diameter 5mm), attached to V4 shakers (Data Physics, San Jose, USA). Vibration waveforms were generated in Spike2 (v7.07) software and converted to an analog voltage signal using a Power 1401 MkII (CED, Cambridge, UK) and a 30W amplifier to drive the shakers.

The vibration was measured using an OptocoNCDT 2200 displacement laser (Micro-Epsilon, Ortenburg, Germany). Two push buttons recorded participants' responses. These signals were acquired by the Power 1401 and recorded in Spike2.

Participants were seated with their right arm on a bench-top, supported by a pillow filled with polystyrene balls molded to the arm, which holds its shape when the air is pumped out. The probes were lowered until they just contacted the skin (causing a displacement of the probes of approximately 20 μm) and locked into position with a Mini Salon 190 Studio Stand (Manfrotto, Cassola Italy). To mask the sound of the

shakers, participants wore earplugs and listened to white noise played through noise-isolating headphones.

2.3 Vibrotactile stimuli

We used a pulsatile waveform, with each indentation having a fixed wavelength of approximately 4 ms, independent of the indentation rate (vibration frequency). Unlike with sinusoidal waveforms, even when our stimuli varied in frequency, they recruited approximately the same primary afferents. Recordings from both types of fast adapting primary afferents in glabrous skin have validated this, showing that pulsatile stimuli similar to what we used produced a reliable stereotyped response for each cycle of vibration, independent of frequency [9], [10].

We wanted to test how vibration cues, provided at spatially separated locations on the skin, influences the processing of temporal phase information present in the vibrations. To do this, we measured perceived frequency of two probes contacting nearby skin locations. The probes each vibrated at a frequency of 25 Hz, 180° out-of-phase with each other. Simply adding the signals together produces a frequency of 50 Hz, and we tested whether this occurs in frequency perception. The participants compared the frequency of this stimulus to the two probes vibrating in-phase at 18 – 54 Hz (**Fig. 2A)**. One probe always stimulated a reference location, and the other stimulated a location 1-16 cm from the reference location (**Fig. 2B**). The distances were measured center-to-center, and at a separation of 1 cm, the probes were almost touching. Participants were aware that two probes contacted their skin, but regardless of the separation, the vibration felt diffuse and was difficult to perceptually separate.

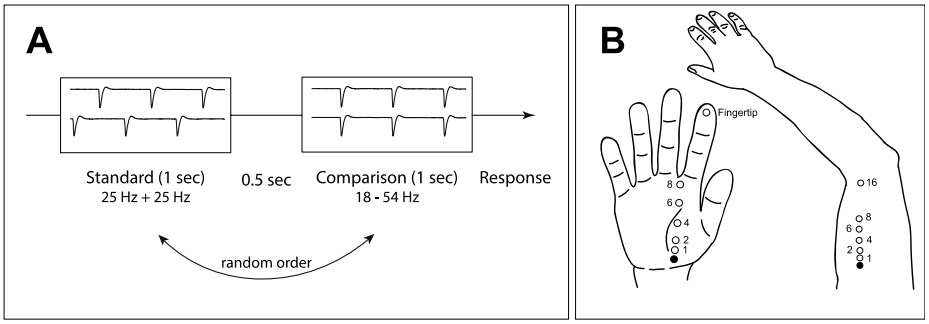

Fig. 2. A: Two-interval forced choice procedure, with the vibration waveforms of the double-probe standard and comparison stimuli. **B**: The reference location (filled circles) was always used, while the other probe varied in location (unfilled circles, cm). The 'fingertip' location on the hand, nominally 16 cm, varied between 13 and 16 cm due to differences in hand size.

To measure perceived frequency, we used the method of constant stimuli with a 2-interval forced choice paradigm (**Fig. 2A**). Participants felt a pair of vibrating stimuli, presented one after the other. For each pair, they were asked to say which stimulus felt higher frequency, the first or second (20 repeats). If they were unsure, they were told to guess. In each pair, one stimulus was the 'standard' stimulus, the two probes

vibrating out-of-phase. The other stimulus in the pair was the 'comparison' stimulus, the two probes vibrating in-phase, which varied in frequency from trial to trial. The order of the standard and comparison stimuli was randomized for each trial.

For each comparison frequency, we calculated the proportion of times the participant responded that it was higher in frequency than the standard stimulus. Logistic regression was applied to produce a psychometric function. Perceived frequency was given by the PSE (point of subjective equality), the 50% point on the regression line. This is the value of the comparison frequency that is equally likely to be judged higher as judged lower frequency than the standard.

2.4 Spatial separation in glabrous and hairy skin

We wanted to determine whether glabrous and hairy skin, with their different mechanical and receptor properties, resulted in different effects on frequency integration from spatially separated vibratory inputs (1, 2, 4, 6, 8 and 16 cm). We measured frequency perception of the two out-of-phase probes on both the glabrous skin of the palm of the hand and the hairy skin of the upper arm (**Fig. 2B**). The amplitude of vibration was always 40 μm on the hand, and 120 μm on the upper arm. These amplitudes were well above threshold and were determined in piloting to have approximately the same perceived intensity.

We also tested whether perceived frequency of vibration is the same for glabrous and hairy skin by having participants directly compare the frequency of a single probe applied to each skin region. The standard stimulus of a single probe vibrating at 23 Hz was applied to the glabrous skin of the index finger pad, and the comparison stimulus (15 – 38 Hz) was applied to the hairy skin of the arm.

2.5 Spatial separation and afferent recruitment via amplitude of vibration

We varied the amplitude of vibration to manipulate the number of afferents recruited by the stimulus, and the area of skin over which afferents were likely to respond. We wanted to test how the number of recruited afferents influenced the temporal integration of vibration cues. We measured perceived frequency for the two probes applied to the palm of the hand, with a variety of vibration amplitudes (10, 40, 80, 120 μm). A subset of the probe distances from the first experiment was used (4, 8, 16 cm).

2.6 Double-probe control experiment

In our two main experiments, we used a standard stimulus of two out-of-phase vibrating probes, and a comparison stimulus of two in-phase vibrating probes. We chose to use two in-phase probes for the comparison instead of a single probe so that the standard and comparison stimuli would have a similar subjective intensity and so that attention would be drawn to an area of the skin of similar spatial extent. In doing this, we assumed that the simultaneous stimulation of the two, in-phase probes results in

near-simultaneous afferent responses propagated through to the CNS, with little effect on perceived frequency. However, given that the two probes were sometimes as far apart as 16 cm, there could be a delay of up to ~5ms between the afferent inputs to the CNS from the two probes [11], 12% the period between indentations of the vibration. This might lead to a higher perceived frequency of the comparison stimulus than anticipated, and result in an under-estimation of the true perceived frequency of the out-of-phase standard stimulus.

To address this issue, we conducted a control experiment on both glabrous and hairy skin, comparing two in-phase vibrating probes located 16 cm apart, to a single probe at one of the two locations, (randomly varied trial-to-trial). We interleaved two experimental protocols, one in which the double-probe stimulus was the standard (25 Hz) and the single probe was the comparison (19 – 31 Hz), and vice versa.

3 Results

3.1 Spatial separation

Our results show that perceived frequency of the pair of out-of-phase probes was generally higher than the base frequency of the individual probes of 25 Hz, but lower than 50Hz, which would have resulted from a simple combination of the two signals (**Fig. 3**).

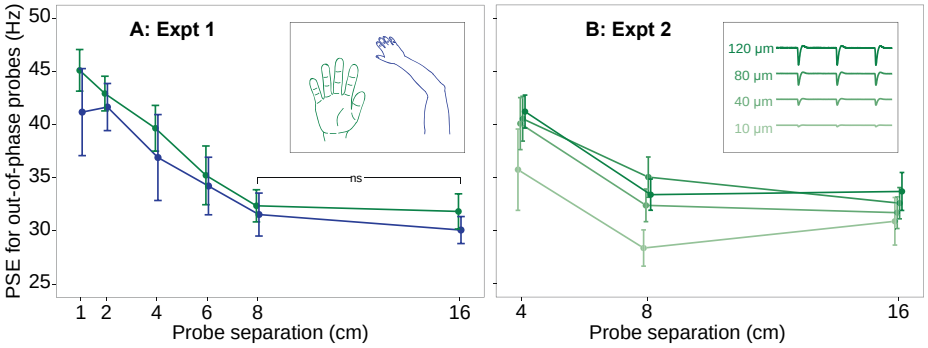

Fig. 3. Mean PSE (point of subjective equality) with 95% confidence intervals. PSE is a measure of perceived frequency for the two probes vibrating out of phase (25 Hz + 25 Hz), and is given for different probe separations. Data points are shifted horizontally to avoid overlap. **A:** Data for the glabrous skin of the hand (green) and the hairy skin of the arm (blue). **B:** Data for different vibration amplitudes (separate lines).

In general, perceived frequency was higher when the probes were closer to each other than when they were further apart. Repeated measures ANOVA analyses revealed a significant main effect of separation distance on PSE in both the skin type ($F_{5, 50}$ = 77.0, p < 0.001, η^2_G = 0.66) and amplitude ($F_{2,20}$ = 95.118, p < 0.001, η^2_G = 0.33) experiments. Between 1 cm and 8 cm probe separation the skin type experi-

ment, the PSE decreased linearly such that for each 1 cm increase, there was a decrease in mean PSE of 1.8 Hz (post-hoc linear contrast: $F_{1, 107} = 210.3$, $p < 0{,}001$, $R^2 = 0.56$). There was no significant difference between PSE at 8 and 16 cm distances (post-hoc pair-wise comparison: mean diff. = 0.7Hz, $t_{21} = 1.2$, $p = 0.248$).

3.2 Integration of afferent inputs in glabrous and hairy skin

Skin type did not appear to impact perceived frequency of the out-of-phase probes. A repeated measures ANOVA revealed no significant main effect of skin type ($F_{1,10} = 3.6$, $p = 0.087$, $\eta^2_G = 0.08$), nor was there a significant interaction between skin type and separation distance ($F_{5, 50} = 0.7$, $p = 0.593$, $\eta^2_G = 0{,}01$). Although the mean PSE for hairy skin appears lower than for glabrous skin (**Fig. 3A**), this difference was not significant, and it was not consistently the case for individual participants (**Fig. 4A**). These results indicate that the mechanical and neural differences in the two skin regions have negligible influence on how temporal phase of the two probes is combined at different separations.

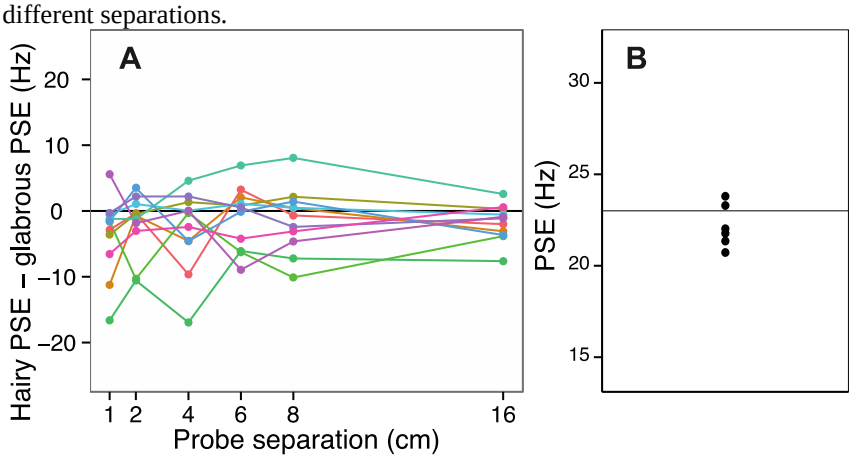

Fig. 4. A: Difference in perceived frequency between hairy and glabrous skin for the two out-of-phase probes. Separate lines for each participant (n = 11). **B:** PSE for a single probe vibrating at 23 Hz on glabrous skin when directly compared to vibration on hairy skin (n = 6).

Similarly, when vibration applied to hairy and glabrous skin sites was directly compared, perceived frequency was similar (**Fig. 4B**). A 23 Hz stimulus applied to the glabrous skin produced a PSE of 22.2 ± 1.2 Hz (mean ± 95% CI) when compared to various vibration frequencies on the hairy skin.

3.3 Afferent recruitment via amplitude of vibration

We found that amplitude had a small influence of perceived frequency of the out-of-phase probes. A repeated measures ANOVA found a significant main effect of amplitude on PSE ($F_{3,30} = 17.5$, $p < 0.001$, $\eta^2_G = 0.42$), and a significant interaction effect with probe separation ($F_{9,60} = 4.3$, $p = 0.001$, $\eta^2_G = 0.13$).

The effect of amplitude appears to be primarily due to lower perceived frequencies at amplitudes of 10 µm compared to higher amplitudes (**Fig. 3B**). The vibration at 10 µm is close to detection thresholds, and this is reflected in the higher variance of PSE measurements (SD = 5.2Hz) compared to higher amplitudes (SD = 4.7, 4.3 and 4.3 Hz for 40, 80 and 120 µm, respectively). For this reason, we conducted a contrast analysis comparing PSE at 10 µm to all higher amplitudes. This revealed a significant difference ($F_{1,10}$ = 20.5, p = 0.001) with a moderate effect size (η^2_G = 0.24). When we excluded the 10 µm data to evaluate the effect of varying amplitude between 40 and 120 µm, amplitude was still significant ($F_{2,20}$ = 6.4, p = 0.007), but with a considerably smaller effect size (η^2_G = 0.06).

3.4 Double probe control experiment

If the double probe stimulus were perceived as higher frequency than a single probe, we would expect that when the double probe was used as the standard, that the PSE would be higher than when the single probe was used as the standard. However, this wasn't the case and the PSE was close to the 25 Hz standard stimulus, regardless of whether it was delivered with double or single probes (**Fig. 5**). On the glabrous skin, the difference in PSE was 1.2 ± 4.5 Hz (mean diff ± 95% CI). On the hairy skin, it was 3.5 ± 5.9 Hz. Pooling data from both sites to maximize statistical power, a paired samples t-test revealed no significant difference between PSE for a double-probe standard vs. a single-probe standard (t_{11} = 1.6, p = 0.139).

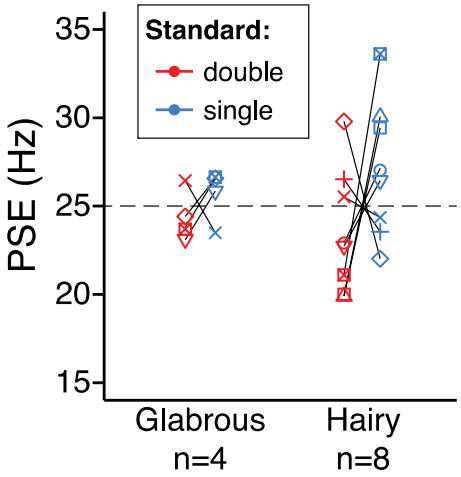

Fig. 5. PSE measured either with a standard stimulus composed of two probes vibrating in phase (double) compared to a single probe vibrations (red); or with a single-probe standard stimulus compared to double-probe stimuli (blue). The black lines link each participant's PSEs (different symbols) for the double and single probe standards. A dashed line indicates the 25 Hz frequency of the standard stimulus.

4 Discussion

We showed that frequency perception integrates temporal cues from spatially separated sources of afferent inputs, provided by two probes vibrating out-of phase. As expected, perceived frequency of the out-of-phase probes was higher for smaller sepa-

rations. Spike trains of individual primary afferents encode stimulus information with very precise timing [1], [2]. However, the temporal dispersion of spikes from different afferents when they reach the next synapse on the pathway to cortex may cause a reduction in temporal resolution [4]. We anticipated that perceived frequency would reflect the maximal stimulus integration, depending on whether or not any individual primary afferents were activated by both probes.

However, our results indicate that common activation of primary afferents by the two probes was not a critical determinant of perceived frequency. Firstly, there were no differences between glabrous and hairy skin. With different mechanical properties, receptor types, thresholds and response properties, it is surprising that perceived frequency decreased with increasing separation in a nearly-identical fashion for the different skin types. Secondly, even when the two probes were undoubtedly activating many of the same primary afferents at the shortest separation of 1 cm, perceived frequency did not reach 50 Hz, which would be the result if the signals from the two probes were fully combined with maximal filling-in.

One possible explanation is that perceived frequency may be a result of combining competing frequency channels related to primary afferent inputs that contribute to the encoding of one or another frequency. Even at the closest separation of the probes, some afferents with receptive fields at the far edges of the stimulated area would have been activated by only one probe, providing a relatively low frequency input signal (25 Hz). As the probe separation increases, afferents activated by only one probe contribute a greater proportion of the input signals.

This is also consistent with our observation that amplitude has little effect on perceived frequency. As amplitude is increased, more afferents are recruited with receptive fields further apart from the centre of stimulation [2]. This simultaneously leads to more afferents responding to both probes, and more afferents responding to just one probe. This wouldn't substantially change the balance between frequency channels and thus would have a relatively small net effect.

One limitation of the competing frequency channels explanation is that even at separation distances up to 16 cm, perceived frequency was typically higher (> 30 Hz) than the frequency with which the individual probes vibrated (25 Hz). Although it's possible that transmission of vibration through the skin or bone may have caused some primary afferents to be activated by both probes, this is unlikely to be a strongly weighted input. Because of this limitation, it is unlikely that a simple average of the discharge rate from the afferent population is used to determine perceived frequency.

An alternative explanation is that integration of inputs to determine the perceived frequency may occur after processing that localises the two probes. Top-down processes may contribute to the separation of inputs as having different origins [12]. This is consistent with the smooth decline in perceived frequency as probe separation increased. As the distance between the probes increases, it becomes less plausible that these out-of-phase sensory input signals are caused by the same real-world event.

In conclusion, some central summation of vibration frequency occurs for separately stimulated sub-populations of primary afferents. The degree of summation is insensitive to mechanical and peripheral features irrelevant to the vibration frequency, except spatial separation. This may reflect top-down filters that use the degree of

spatial and temporal coincidence to determine the extent to which peripheral inputs are integrated.

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