

Signal combination in vibration perception

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Abstract

While the brain’s integration of auditory and visual inputs has been extensively investigated, the mechanisms underlying the combination of somatosensory signals remain less explored. Here, we investigated vibrotactile summation across fingers using psychophysical and electrophysiological methods. In Experiment 1, discrimination thresholds for 26 Hz vibrations were measured using a two-alternative forced-choice (2AFC) task. Thresholds exhibited a ‘dipper’ pattern when plotted against pedestal intensity. Detection thresholds decreased by approximately 1dB when all ten fingers were stimulated (‘dekadactyl’ condition) compared to when each alternate finger was stimulated (‘pentadactyl’ condition), suggesting a process of probability summation. When a target stimulus was presented to five digits and a pedestal stimulus to the remaining digits (‘dichodactyl’ condition) thresholds increased, consistent with suppression between digit representations. In Experiment 2, steady-state somatosensory evoked potential (SSSEP) signals showed approximately a 1.4-fold amplitude increase in dekadactyl compared to pentadactyl conditions, indicating a summation effect. Conversely, SSSEP amplitudes decreased when targets and masks were presented at different frequencies, providing additional evidence of suppression. These results are consistent with a model featuring inhibition between digits and reveal that the weight of suppression is intermediate between that observed in binocular vision and binaural hearing.

Keywords:

vibrotactile summation, suppression, somatosensory, computational modelling

Significance

How does the brain combine tactile inputs from multiple digits? Through psychophysical and neurophysiological methods, we show that vibrotactile processing across fingers involves both probability summation and suppression between digit representations. Discrimination thresholds improved when all ten fingers were stimulated at the same frequency but worsened with the introduction of mask stimuli between digits. EEG responses further demonstrated a summation effect when doubling the digits stimulated at the same frequency and a suppression effect when digits were stimulated at different frequencies. Modelling results suggest a unique mechanism of tactile integration, distinct from those observed in vision and audition.

Introduction

Signal combination is crucial for human perception and our interaction with the environment. Our sensory systems comprise a variety of receptors and neural pathways that detect and process a wide range of stimuli, including sight, hearing, touch, and smell. To construct a coherent and comprehensive representation of our surroundings, the brain must filter out overlapping or redundant information and avoid excessively strong signals to prevent sensory overload. Therefore, in addition to additive processes, suppressive processes are also involved in signal combination. This suppression during signal combination has been investigated both within (e.g., vision, hearing, touch, 1, 2–4) and between (e.g., visuo-tactile, audio-visual, 5, 6) modalities.

In visual and auditory perception, psychophysical studies have shown that detection performance for binocular or binaural presentation is typically between a factor of $\sqrt{2}$ and 2 better than for monocular or monaural presentation (2, 7, 8). This summation at threshold implies the existence of physiological mechanisms that combine signals across eyes or ears. Above threshold, detection performance improves when a weak fixed intensity (‘pedestal’) stimulus is added, a phenomenon known as facilitation. At higher intensity pedestals performance worsens, producing a masking effect. When plotted against pedestal intensity, the discrimination thresholds exhibit a “dipper” shape (see Figure 1b). The facilitation and masking effects arise from the brain transducing physical signals into neural responses in a non-linear manner, and are observed for many sensory stimuli (reviewed by 9).

We can directly measure the response to stimuli of different intensities by recording brain activity. One convenient method is the steady state technique, in which periodic stimulus oscillations are reflected in electromagnetic neural responses at the same frequency, which can be recorded using EEG or MEG. For instance, some EEG studies have investigated the signal combination process in visual and auditory modalities by recording steady-state brain signals (1, 2). These studies found that brain responses increased when input channels (eyes or ears) were doubled, but by less than a factor of two. Additionally, when a mask was to one channel

added instead of a signal input (i.e. oscillating at a different frequency), the signal response decreased due to suppression.

The process by which the brain combines multiple signals has attracted great interest in recent years, leading to the proposal of several computational models. The two stage model (10) successfully accounts for both binocular and binaural perception, positing that the signal from one channel (left or right) is inhibited by the other channel before being summed. The equations describing this model are defined as:

$$Stage1_L = \frac{C_L^m}{S + C_L + \omega C_R} \quad (1)$$

$$Stage1_R = \frac{C_R^m}{S + C_R + \omega C_L} \quad (2)$$

$$binsum = Stage1_L + Stage1_R \quad (3)$$

$$resp = \frac{binsum^p}{Z + binsum^q} \quad (4)$$

where *resp* is the binocular or binaural model response, C_L and C_R are the contrast signals in the left and right channels respectively, m , S , ω , p , q and Z are free parameters. In Equation 1 and Equation 2, ω is the weight of suppression from the other channel. In vision, the weight of suppression is approximately $\omega = 1$, whereas in auditory perception, suppression between the ears is dramatically weaker, with ω close to 0. Therefore, while suppression can be key to signal combination, its strength varies across different sensory modalities.

In tactile perception, some neuroimaging findings suggest there exist summation and suppression of vibration signals also. For instance, studies have recorded brain responses to vibration stimuli delivered to two fingers separately and simultaneously. Results indicated that at low levels of stimulation near the perceptual threshold, there was a facilitation or summation effect between two fingers. However, at higher levels of stimulation, a suppression effect was observed (4). Furthermore, the brain response to simultaneous vibration of two fingers is less than (approximately 50% of) the sum of the responses to individual finger stimuli (3, 4). In addition, the extent of suppression is dependent on the spatial distance between the fingers (4, 11). In some psychophysical studies, researchers measured vibration detection thresholds using various contactor sizes (12, 13). Results found that the threshold decreased as the contactor size increased, a phenomenon known as area summation. Specifically, when the contactor size was doubled, the threshold decreased by approximately 3 dB (12). These findings focused on the summation rather than suppression between inputs, because suppressive processes are minimal at low intensities near threshold. In summary, although substantial evidence suggests the existence of suppression in vibration combination, there has been relatively little

psychophysical work above threshold, and a corresponding computational model has yet to be developed.

Here, we combine psychophysical measurements (Experiment 1) with EEG recordings (Experiment 2) to assess human vibration perception, and fit a computational model to interpret the processes of vibration signal combination and suppression. In Experiment 1, we measure how thresholds vary across different conditions and pedestal levels using a two-interval forced-choice (2IFC) task. We find that thresholds decrease by approximately 1 dB when the number of inputs was doubled. This finding is consistent with probability summation rather than physiological summation. Our computational modelling indicated that this effect could potentially be explained without requiring suppression between digits. Consequently, in the EEG experiment, we directly measured suppression between digits. The modelling results indicated an inhibitory weight of suppression of $\omega \sim 0.5$, intermediate between the weights observed for vision ($\omega \sim 1$) and audition ($\omega \sim 0$).

Materials and Methods

Participants

Eight adult subjects participated in the psychophysics experiment, and thirty-one adult subjects participated in the EEG experiment. All participants self-reported as healthy, with no diagnosed neurological disorders, and no history of exposure to severe hand-transmitted vibration. Both experiments were approved by the Ethics Committee of the Department of Psychology at the University of York (application IDs 2277 and 2303). Written informed consent was obtained from all participants prior to conducting the experiments.

Apparatus & stimuli

Vibration stimuli were generated by a specially constructed board with ten fixed solenoids (‘tactor’ devices, from Dancer Design Ltd.) controlled by a computer (Figure 1c). Each solenoid could be independently driven by a pair of 6-channel USB sound cards to vibrate each finger. The outputs of the sound cards were amplified by a 10-channel linear amplifier, which produced a maximum output modulation of $\pm 7.5\text{V}$, for a maximum vibration amplitude of $\pm 0.375\text{N}$. All the stimuli were generated and presented using MATLAB and Psychtoolbox 3 (14, 15). Any sounds produced by the vibrations were rendered inaudible by playing a 440 Hz tone on the remaining two sound card outputs, which was delivered to participants over a pair of headphones.

EEG signals were recorded using a 64-channel electrode cap and an ANT Neuroscan (ANT Neuro, Netherlands) amplifier sampling at 1kHz. Electrodes were arranged according to the 10-20 system, and impedances were kept below $5k\Omega$. Digital triggers were sent to the EEG



Figure 1: Overview of methods details. Panel (a) illustrates the arrangements of pedestal and target stimuli in the two intervals of a trial in Experiment 1, for four stimulus arrangements (rows). Panel (b) shows an example ‘dipper’ function. Panel (c) shows the board containing the ten tactors. Panel (d) illustrates the allocation of digits into two sets. Panel (e) illustrates the stimulus conditions used in Experiment 2.

amplifier using a USB TTL module (Black Box Toolkit Ltd., UK), signifying the start of the trial. The whole head average was used as a reference for the EEG data, and the ground electrode was located at position *AFz*.

Psychophysical procedures

In Experiment 1, a two-interval forced-choice (2IFC) task was used to measure detection and discrimination thresholds. During the experiment, participants were instructed to place their ten digits on the corresponding solenoids, and a series of vibration stimuli were delivered to their hands. The digits on each hand were coded 1 to 5 from the thumb to the little finger in that order. The digits 1, 3 and 5 on the left hand and 2 and 4 on the right hand are denoted “Set A”, and the digits 2 and 4 on the left hand, and 1, 3 and 5 on the right hand are denoted “Set B” (illustrated in Figure 1d).

Each trial consisted of two 500 ms intervals: one containing the pedestal stimulus and the other containing the pedestal stimulus plus a target increment, separated by a 400 ms inter-stimulus interval. The next trial began 200 ms after the participant responded. To mask any sound produced by the solenoids and indicate the stimulus intervals, a 440 Hz beep sound was delivered through headphones simultaneously with the vibration stimuli. The order of the two intervals was randomised, and participants were required to determine which interval contained the target increment by pressing a foot pedal. Feedback was provided by a coloured square on the computer screen, with green indicating a correct response and red indicating an incorrect one. The amplitude of the target increment was determined using a pair of 3-down-1-up staircases, with a step size of 3 dB (where dB units are defined as $20 \times \log_{10}(100 \times C)$, and C is the stimulus intensity expressed as a proportion of the maximum system output), aiming to distribute trials around the detection threshold at 75% correct. Threshold measurement was terminated after either 70 trials or 12 reversals, whichever occurred first.

The pedestal and target stimuli were presented under four conditions (illustrated in Figure 1a) and at eight pedestal levels (0, 1, 2, 4, 8, 16, 32, 64%), with the pedestal level expressed as a percentage of the maximum vibration. In the “pentadactyl” condition (meaning five-fingered in Greek), the pedestal and target stimuli vibrated only “Set A” (analogous to the stimulation of one eye or one ear). In the “dekadactyl” (ten-fingered) condition, the pedestal and target stimuli vibrated both “Set A” and “Set B” (analogous to the stimulation of both eyes or both ears). Comparing the “pentadactyl” and “dekadactyl” conditions reveals the summation effect of doubling the number of inputs. In the “dichodactyl” condition (named for consistency with dichoptic conditions in vision experiments, where different stimuli are shown to the two eyes), the pedestal stimulus vibrated “Set A” and the target stimulus vibrated “Set B”, permitting the measurement of masking effects across digits. The “half-dekadactyl” condition involved vibrating all ten digits for the pedestal stimulus, while only “Set A” vibrated for the target stimulus, enabling measurement of summation (by comparison with the dekadactyl condition) while controlling the number of digits receiving the pedestal stimulus (10). In all conditions, the vibration frequency for both pedestal and target stimuli was 26 Hz. “Set A” and “Set

B” were counterbalanced across trials. Each pedestal level was tested in a single block lasting approximately 15 minutes and repeated three times. The entire experiment took around 7 hours per participant, resulting in a total of 60438 trials (7555 per participant on average), and was completed over multiple days.

EEG procedures

After EEG cap set-up, participants in Experiment 2 were exposed to a series of vibrations under six different conditions (illustrated in Figure 1e) at five intensity levels (4, 8, 16, 32, 64%). Steady-state somatosensory evoked potential (SSSEP) signals were recorded throughout the experiment. During each trial, participants received an 11-s vibration with a 3-s interstimulus interval, and were required to keep their hands still until designated break periods. The “Set A” and “Set B” allocations were the same as those used in the psychophysical experiment (see Figure 1d) and were counterbalanced across trials. The order of conditions was randomised, and each condition was repeated twice for each set, resulting in a total of 120 trials. The entire experiment lasted approximately 30 minutes, split into four 7-minute blocks with rest breaks between blocks.

Two different frequencies were used: 26 Hz (F1) and 23 Hz (F2). F1 is considered the primary frequency, as SSSEP responses are greatest around 26Hz when vibration is delivered to the hands (16). Using two distinct frequencies enables measurement of both the separate responses to each frequency and the interactions between them. In the “pentadactyl” condition, F1 only vibrated “Set A”; in the “dekadactyl” condition, F1 vibrated both “Set A” and “Set B”; in the “dichodactyl” condition, F1 vibrated “Set A” while a mask at 26 Hz with an intensity level of 32% vibrated “Set B”. These three conditions contributed to the observation of summation and suppression effects at the same frequency.

In the remaining three conditions, a second frequency (F2) was introduced to investigate interactions between different frequencies. In the “cross-pentadactyl” condition, F2 vibrated “Set A”, providing a comparison with the “pentadactyl” condition and serving as a baseline for other cross-frequency conditions. In the “cross-dekadactyl” condition, F1 vibrated “Set A” and F2 vibrated “Set B”, permitting measurement of suppression effects between different frequencies. In the “cross-dichodactyl” condition, F1 vibrated “Set A” while the F2 mask (intensity level of 32%) vibrated “Set B”, again to measure suppression between digits (see Figure 1e for a diagram of all conditions).

Data analysis

For both experiments, off-line analysis and statistical testing was performed in Python 3. For psychophysical data, the *psignifit* 4 package (17) was used to estimate thresholds (at 75%

correct) and slope parameters of the psychometric functions by fitting a cumulative Gaussian. We then converted the slope parameter (σ) to equivalent Weibull β values using the approximation $\beta = 10.3/\sigma$.

For EEG data, all preprocessing was conducted using MNE-Python (18). For each trial, the initial 1000 ms post-stimulus presentation was discarded to eliminate onset transients. The remaining 10 s were Fourier transformed and the amplitudes were averaged across repetitions and participants. Amplitudes exceeding ± 3 standard deviations from the mean were excluded. After removing one outlier, data from 30 participants remained for calculating the intensity-response functions and performing statistical analysis. The average amplitudes from six electrodes ($F1$, $F2$, Fz , $FC1$, $FC2$, FCz) were then averaged to plot the amplitude spectra and intensity-response functions. The primary dependent variables were the Fourier amplitudes at 26 Hz and 23 Hz.

Computational modelling

The psychophysical data were fitted using the two stage model of (10), as outlined in equations 1-4, with 7 free parameters (m , S , ω , p , q , Z and k). The final parameter (k) determines the threshold criteria, such that the model response in the target interval must exceed that in the null interval by k for threshold to be reached. It is proportional to additive noise in the model. We also considered a modified model, in which the summation process described by Equation 3 involved an additional exponent:

$$binsum = (Stage1_L^\mu + Stage1_R^\mu)^{1/\mu} \quad (5)$$

The Minkowski exponent (μ) is implicitly 1 in Equation 3, but was free to vary in our second model.

To fit the EEG data, we used a simpler model described by Equations 1-3, but omitting the output nonlinearity described by Equation 4, which serves primarily to determine the shape of the dipper function in psychophysical studies, but is not required for EEG data (1). The output was instead defined as:

$$resp = R_{max} \times binsum + k \quad (6)$$

where R_{max} is a scaling parameter on the output, and k again represents additive noise. The simpler model had 5 free parameters (m , S , ω , R_{max} and k). We used a downhill simplex algorithm to minimize the squared error between model and data. Fitting for each model was repeated 100 times from random starting vectors, and the parameters that gave the best numerical fit were selected.

Data and code availability

All experiment code, raw data, processed data and analysis code are available at the project repository: <https://doi.org/10.17605/OSF.IO/M79D2>. The linked GitHub repository also contains a fully computationally reproducible version of this manuscript in Quarto format.

Results

Summation and suppression effects on vibration thresholds

In Experiment 1, participants were required to report which interval included the target stimulus. The average thresholds across 8 participants for each condition and pedestal level are shown in Figure 2a. A 4 (condition) \times 8 (pedestal contrast) repeated measures ANOVA with Bonferroni-corrected post-hoc tests was used to assess statistical differences between factors. Results found significant main effects of condition ($F = 233.52$, $p < 0.001$, $\eta_G^2 = 0.651$, Greenhouse-Geisser corrected) and pedestal level ($F = 70.87$, $p < 0.001$, $\eta_G^2 = 0.83$, Greenhouse-Geisser corrected), as well as a significant interaction between the two factors ($F = 22.06$, $p < 0.001$, $\eta_G^2 = 0.419$, Greenhouse-Geisser corrected). When plotting the thresholds against pedestal level, except for the dichodactyl condition (green diamonds), the other three conditions exhibited a dipper shape. Specifically, at low pedestal levels (0.5 to 2%), thresholds decreased with increasing pedestal level, indicating a facilitation effect. When the pedestal level exceeded 2%, thresholds increased due to a masking effect, resulting in approximately parallel handles across the pentadactyl (blue circles), dekadactyl (red squares) and half-dekadactyl (orange triangles) conditions. At detection threshold (pedestal level = 0%), the threshold for the dekadactyl condition was around 1 dB lower than for the pentadactyl condition, with no significant difference. This weak summation between digits is lower than that typically attributed to physiological summation, suggesting the presence of probability summation instead (19, 20).

Above detection threshold, thresholds in the dekadactyl condition were significantly lower than those in the pentadactyl condition ($p < 0.05$, except at 8%, $p < 0.01$), with the exception of pedestal levels at 2% and 16%. On average, the thresholds decreased by a factor of approximately 1.27 (2.1 dB). Additionally, thresholds in the half-dekadactyl condition, where the pedestal stimulus vibrated 10 digits, but the target stimulus only vibrated 5 digits, were significantly higher than those in the dekadactyl condition at pedestal of 0.5% ($p = 0.01$), and 2% to 32% ($p < 0.001$). These findings could be interpreted as a summation effect when the target inputs were doubled. However the psychometric function is linearised from the bottom of the dip onwards, which might increase the effects of probability summation. We return to this point in the modelling section. In the dichodactyl condition, thresholds increased across all pedestal levels, with thresholds elevated by a factor of 7.19 (17.14 dB) at the highest pedestal level (32%). This result is consistent with a suppression effect when adding a mask between

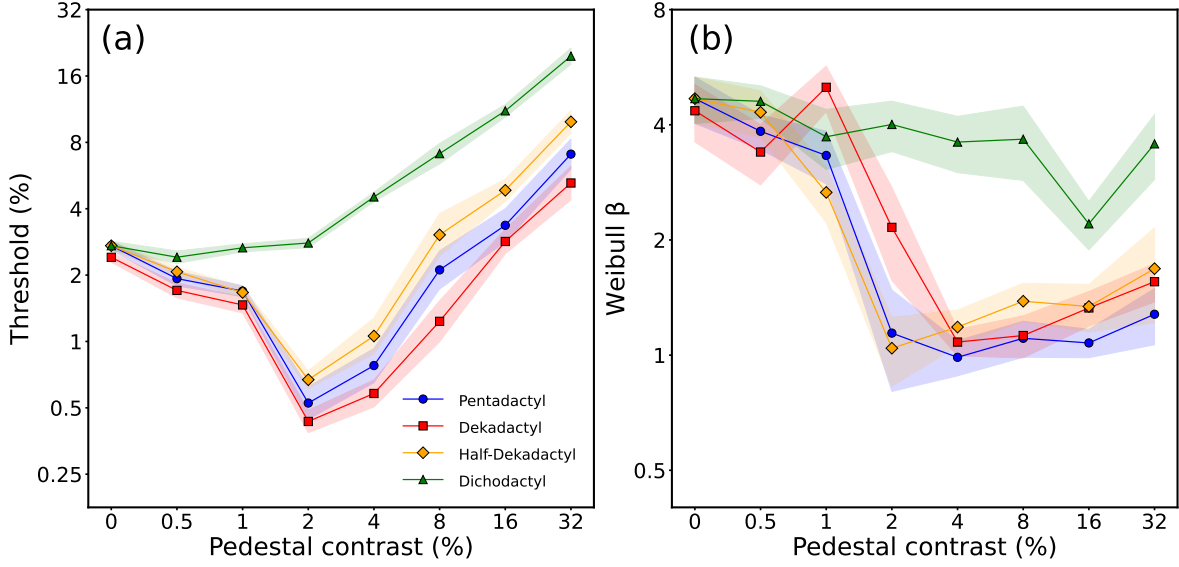


Figure 2: Thresholds (a) and psychometric slope values (b) from Experiment 1. Data are averaged across $N=8$ participants, with shaded regions indicating ± 1 SE across participants.

digits, where the target stimulus could only be detected when it approached the pedestal intensity.

The slopes of the psychometric function for each condition are illustrated in Figure 2b. At detection threshold, all conditions exhibited relatively steep slopes, around $\beta = 4$. At low pedestal levels (0 to 4%), except for in the dichodactyl condition (green triangles), the slopes decreased with increasing pedestal level, approaching $\beta = 1$ at a pedestal level of 4%. At higher pedestal levels (4% to 32%), the slopes for these three conditions remained shallow, consistent with previous studies using the same paradigm (10, 21). In contrast, the slopes in the dichodactyl condition remained steep across all pedestal levels, with slight variations in the range $2 < \beta < 5$. This pattern differs from those observed in dichoptic masking in vision (10, 22), where slopes were steep at detection threshold, became shallow at lower contrast levels, and then became very steep again at higher contrast levels. The very steep slopes ($\beta \sim 6$) in dichoptic masking are attributed to mandatory physiological summation between the eyes (23). Therefore, the approximately constant slopes observed in the dichodactyl condition suggest that mandatory physiological summation between digits may not occur here.

Summation and suppression effects on neural responses

The average amplitude spectra and scalp distributions for four conditions of Experiment 2 are shown in Figure 3a-d. The steady-state EEG signals were strongest at fronto-central electrodes

for both frequencies, aligning with findings from previous studies involving finger vibration (24, 25). Therefore, we averaged the EEG responses across six electrodes ($F1$, $F2$, Fz , $FC1$, $FC2$, FCz) to calculate intensity-response functions at both 23 Hz and 26 Hz.

In the pentadactyl and dekadactyl conditions, where a 26 Hz stimulus was used, we observed a peak at 26 Hz in both Figure 3a and b, with a stronger activity at the fronto-central region in the dekadactyl condition. A similar pattern was observed in the cross-pentadactyl condition, where a 23 Hz stimulus resulted in a peak at 23 Hz (Figure 3c). In the cross-dekadactyl condition (Figure 3d), when two different frequencies were simultaneously presented, peaks were observed at the original frequencies (26 Hz ($F1$) and 23 Hz ($F2$)) as well as at specific intermodulation frequencies (20 Hz ($2 \times F2 - F1$) and 29 Hz ($2 \times F1 - F2$)). Additionally, the distribution of activity across the scalp was similar in the cross-dichodactyl and cross-dekadactyl conditions.

Responses as a function of vibration intensity showed monotonic increases for most conditions (Figure 3e,f). Two 6 (condition) \times 5 (intensity) repeated measures ANOVAs with Bonferroni-corrected post-hoc tests were conducted on the EEG amplitudes at each frequency separately. At 26 Hz, significant main effects of condition ($F = 67.32$, $p < 0.001$, $\eta_G^2 = 0.309$, Greenhouse-Geisser corrected), intensity level ($F = 66.6$, $p < 0.001$, $\eta_G^2 = 0.288$, Greenhouse-Geisser corrected), and a significant interaction effect ($F = 25.61$, $p < 0.001$, $\eta_G^2 = 0.115$) were observed. In the pentadactyl condition (blue circles), EEG amplitudes increased monotonically with increasing intensity level (Figure 3e). In the dekadactyl condition (red squares), doubling the inputs led to significantly stronger responses at intensity levels of 8% ($p < 0.01$), 16% ($p < 0.001$), and 32% ($p < 0.001$). Compared to the pentadactyl condition, average amplitudes increased by a factor of 1.41 across all intensity levels, indicating a sub-linear summation effect. In the dichodactyl condition (green triangles), the target stimulus was presented to Set A, while a fixed vibration at 32% of maximum intensity was presented to Set B, resulting in a high baseline response, and responses that increased with intensity level. At higher intensity levels (32 to 64%), the responses in the dichodactyl condition approximated those in the dekadactyl condition. In the cross-dekadactyl (pink pentagons) and cross-dichodactyl (black diamonds) conditions, two different frequencies were presented simultaneously. Instead of summing, they suppressed each other, leading to weaker responses compared to the pentadactyl condition, with a significant difference observed between the pentadactyl and cross-dichodactyl conditions at the 16% intensity level ($p < 0.001$).

At 23 Hz (Figure 3f), we also found significant main effects of condition ($F = 68.27$, $p < 0.001$, $\eta_G^2 = 0.402$, Greenhouse-Geisser corrected), intensity level ($F = 33.07$, $p < 0.001$, $\eta_G^2 = 0.069$), as well as a significant interaction effect ($F = 28.98$, $p < 0.001$, $\eta_G^2 = 0.255$, Greenhouse-Geisser corrected). Further evidence of suppression was observed in the cross-dekadactyl condition (pink pentagons), where simultaneous 23 Hz and 26 Hz stimuli led to significantly reduced responses compared to the cross-pentadactyl condition (yellow triangles) at intensity levels of 16%, 32%, and 64% (all $p < 0.001$). In the cross-dichodactyl condition (black diamonds), a stronger initial response to the mask at 4% target level decreased with increasing target intensity levels ($F = 14.27$, $p < 0.001$, $\eta_G^2 = 0.33$, Greenhouse-Geisser corrected), indicating

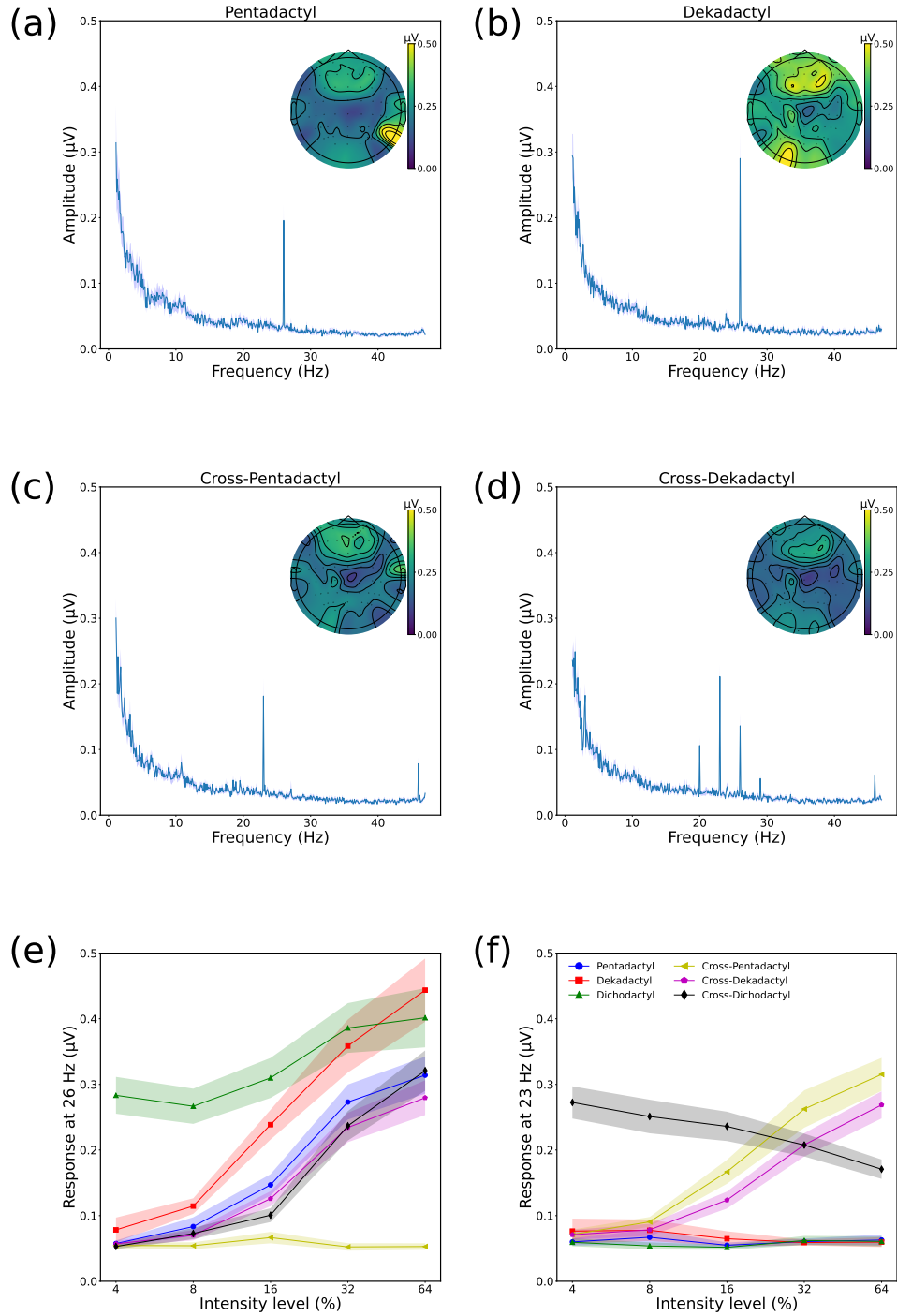


Figure 3: Results of the EEG experiment. Panels (a-d) show Fourier spectra and inset scalp topographies for a subset of four conditions at the highest intensity. Panels (e,f) show intensity-response functions for all conditions at 26Hz (e) and 23Hz (f). Data are averaged across $N=30$ participants, and shaded regions indicate ± 1 SE across participants.

a masking effect and suppression between digits. As expected, the three conditions involving only a 26 Hz vibration did not show any measurable responses at 23 Hz (Figure 3f).

Computational modelling results

We began by fitting the data of Experiment 1 using the model of Meese et al. (10), with seven free parameters including the weight of suppression between channels (ω in Equation 1 and Equation 2). Because the combination across channels is linear (following an initial transducer stage), we refer to this as the Linear summation model. The model gave a reasonable fit, as shown in Figure 4a, with an RMS error of 1.79dB (see Table 1 for parameter values). However, two systematic shortcomings are apparent. At detection threshold, the model overestimates the amount of summation (notice the red curve is below the data points for the first three pedestal levels). Also, suppression between channels is relatively strong ($\omega = 0.817$), but this results in the slope of the dichodactyl condition (green curve) being steeper than in the empirical data (green triangles).

To address these shortcomings, we added a further parameter to the model - an exponent at the summation stage (see Equation 5). The Minkowski summation model provides a much more satisfactory fit (see Figure 4b), with an RMS error of 0.89dB, and no obvious systematic issues with the fit. The Minkowski exponent was estimated at $\gamma = 15.484$ - substantially greater than the implicit value of $\gamma = 1$ in the Linear summation model, and consistent with the low levels of summation at threshold in the data. Several other parameter values also differ between the models (see Table 1), most notably the weight of suppression (ω) reduces to near-zero. With this architecture, threshold elevation in the dichodactyl condition is caused by the MAX-like operation from the high Minkowski exponent (a true MAX operator would have an exponent of $\gamma = \infty$), meaning that explicit suppression is not required. However, this does not necessarily mean that there is no suppression at all - since psychophysical responses are assumed to be based on the most sensitive subset of neurons relevant to a given task, it is possible that they directly tap mechanisms that are suppression-free. Our EEG data measure responses from the whole neural population, and so we next model these results to obtain a more general estimate of suppression.

The model used to fit the EEG data omits the output nonlinearity (Equation 4), and adds a scaling parameter (R_{max}), resulting in 5 free parameters. It produced an excellent account of the results at both temporal frequencies, and across all 6 stimulus conditions (see Figure 4c,d), with an RMS error of $0.02\mu V$. The model correctly captures the sub-linear summation between channels (i.e. the red curve in Figure 4c is less than a factor of two greater than the blue curve), and the suppression evident in the cross-dekadactyl and cross-dichodactyl conditions. The weight of suppression ($\omega = 0.518$) was intermediate between the two dipper models, as well as being in between previously published values for vision ($\omega = 1$; (1)) and hearing ($\omega = 0$; (2)).

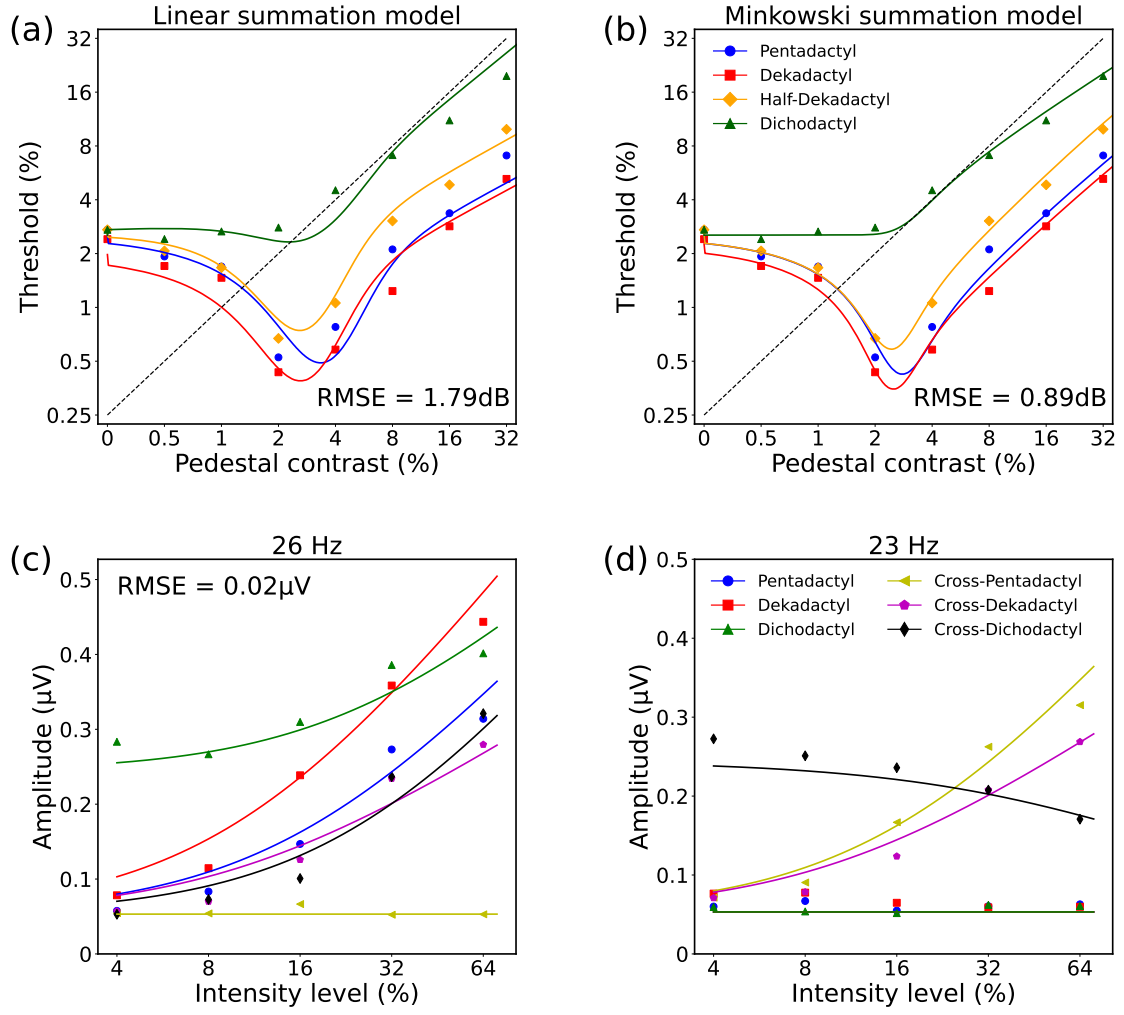


Figure 4: Summary of model fitting. Panel (a) shows the fit of a model in which summation is linear (following an early transducer), and panel (b) shows the fit of the Minkowski summation model. Panels (c) and (d) show the best model fit to the EEG data at 26Hz (c) and 23Hz (d).

Table 1: Summary of fitted model parameters for three computational models. Brackets indicate fixed values, and dashes denote parameters not included in a given model.

Model	R_{max}	p	q	m	S	Z	ω	k	γ	RMSE
Linear summation	-	9.845	8.845	1.416	0.067	106.408	0.817	0.264	(1.0)	1.79
Minkowski summation	-	19.149	16.0	1.081	0.976	0.039	0.004	0.142	15.484	0.89
EEG model	0.053	-	-	1.263	25.955	-	0.518	0.139	-	0.02

Discussion

In this study, we present evidence supporting the processes of signal summation and suppression in vibrotactile signal combination. In the psychophysical experiment, we observed that doubling the inputs resulted in a slight reduction in detection and discrimination thresholds, indicating a weak summation effect. Additionally, adding a masking stimulus led to increased discrimination thresholds, indicating a suppression process. Furthermore, the EEG experiment demonstrated that adding the same frequency increases brain activity, whereas adding a different frequency decreases it. These findings provide further evidence of the summation and suppression effect between digits. Our computational model fitting results show two vibrotactile inputs suppress each other before being combined, and the weight of suppression between digits is around $\omega = 0.5$, which is intermediate between the corresponding values observed in visual (1) and auditory (2) signal combination. Overall, our results suggest the presence of suppression in vibrotactile signal combination, with a suppression effect distinct from that observed in visual and auditory signal combination. In the remainder of this discussion, we consider the underlying mechanisms of vibrotactile signal combination and the differences across sensory modalities.

Our findings are consistent with previous studies (12, 26, 27) that suggest doubling inputs can reduce the vibration detection threshold. However, the summation effect observed in our study is weaker than that reported in these studies, which found a 3 dB reduction in detection threshold when using vibrations above 40 Hz and doubling the contactor size. This discrepancy may be attributed to the different vibration frequencies used in the studies. Some psychophysical studies have proposed that four distinct mechanoreceptive channels mediate vibration perception: Pacinian (P), Non-Pacinian I (NP I), Non-Pacinian II (NP II), and Non-Pacinian III (NP III) (27, 28). Each channel has unique characteristics and responds to specific frequency ranges. For instance, the P channel is more sensitive to higher frequencies (e.g., greater than 40 Hz) and is the only channel that possesses the property of spatial summation (26, 28, 29). In contrast, vibrations between 2 and 40 Hz are mediated by the NP I channel, which has been shown not to exhibit spatial summation (27, 28, 30). Consequently, the weak summation effect observed in our study may be attributed to the 26 Hz vibration, which is determined by the NP I channel that lacks spatial summation. Additionally, unlike the study by (12), which used varying contactor sizes to stimulate random areas within a test region—thereby preventing participants from knowing the exact location of stimulation, our study specifically involved the stimulation of individual digits, with participants aware of

which digits were being stimulated. This methodological difference likely contributed to the observed discrepancy between the studies.

The results of the EEG experiment are consistent with those of the psychophysical study. Doubling the digits at the same frequency elicited stronger brain responses, though the increase was less than twofold. These findings correspond with previous studies, demonstrating that brain responses to concurrent stimuli at the same frequencies are stronger than those elicited by individual stimuli, suggesting a summation effect between inputs (4, 31, 32). However, the observed response is less than the anticipated summed response, generally falling between 10% and 50% of the expected value, signifying a suppression effect between inputs (4, 33). In contrast, adding a different frequency or a masking stimulus resulted in a reduction in brain activity. These results provide further evidence of suppression between digits and are consistent with previous neuroimaging studies investigating the interaction between different frequencies (34, 35). For instance, (34) examined the suppression effect by vibrating two fingers at the same (18 Hz) or different frequencies (18 vs. 22 Hz, 18 vs. 26 Hz). Their findings revealed that the event-related potential (ERP) and SSSEP responses to simultaneous stimulation of both fingers were significantly lower than the linear summation of individual responses, with no difference in suppression based on frequency variation. This ruled out the hypothesis that suppression is due to neuronal occlusion from overlapping cortical areas, as stronger suppression would be expected at the same frequency if this were the case (4, 36). Instead, the results support the alternative explanation of lateral inhibition, where activation of one cortical neuron suppresses neighbouring neurons' activity (37–41). This inhibitory mechanism has been extensively observed in both animal and human studies (3, 4, 11, 42, 43).

Another interesting finding is that we observed an intermediate suppression between vibrotactile stimuli compared with vision and audition. In visual perception, the forward-facing positioning of the eyes results in substantially overlapping visual fields. To merge these overlapping inputs from each eye (monocular vision) into a cohesive single image (binocular single vision), neural signals from both eyes must exhibit strong mutual inhibition to achieve 'ocular invariance', ensuring the constancy of perception through one or both eyes (44). This is congruent with recent findings indicating that some neurons in the primary visual cortex are monocularly excitable, responding exclusively to the dominant eye, while binocular stimulation can suppress their activity (45). In contrast, the lateral placement of the ears results in minimal overlap between auditory inputs, reducing the necessity for strong interaural inhibition to integrate these signals into a unified percept, as is required in visual processing. Instead, binaural perception benefits from the comparison and integration of these disparate inputs to localise sound sources and discern subtle differences in timing and intensity (46, 47). Although prior evidence supports the existence of binaural suppression (2, 48, 49), the extent of this suppression may differ depending on hemispheric laterality (50, 51).

Tactile perception involves the stimulation of each of the ten fingers individually, creating a more complex signal integration compared to binocular or binaural perception. The primary somatosensory cortex (SI) is divided into four distinct Brodmann areas (BA 3a, 3b, 1, and 2), each responsible for mapping different parts of the body surface. Evidence suggests that

receptive field of each finger is arranged in somatotopic order in BA 3b, while in BA 1/2, they are arranged in clusters with large overlap (32, 36, 52). Although SSSEPs reflect activity across the whole scalp, EEG (35, 53) and MEG (11, 32, 54) studies also support overlapping finger representations in SI. Notably, the overlap between adjacent fingers is greater than between non-adjacent ones, indicating that suppression between fingers depends on their spatial proximity. Additionally, hand posture plays a significant role in signal summation and suppression. For instance, a study (55) found that a “CLOSE” posture (thumb and index finger positioned as if to pick something up) produces stronger suppression than an “OPEN” posture (hand fully open). In the present study, finger posture and inter-finger distance were controlled by placing the fingertips in a fixed position on solenoids, suggesting that the amount of suppression may vary depending on finger arrangements or hand posture. Furthermore, studies have shown that blind individuals exhibit stronger somatosensory evoked potentials compared to sighted individuals, potentially indicating an expanded S1 region (56, 57). This suggests that use-dependent cortical reorganisation may occur across different body regions, and the amount of suppression may vary depending on the body part involved.

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