Vibrotactile temporal summation: probability summation or neural integration?

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Abstract
Temporal summation, a decrease in the detection threshold that occurs when either the duration of a stimulus or the number of stimuli in a sequence is increased, has been attributed to the operations of either the mechanism of neural integration or of probability summation. Our experiments indicate that under certain conditions, both mechanisms may operate, but that the process of neural integration is an exclusive characteristic of the Pacinian (P) channel. The P channel was isolated by applying 250 Hz stimuli through a 1.5 cm² contactor to the thenar eminence of the hand and the NPII channel was isolated by applying the stimuli through a 0.01 cm² contactor. The finding that the slopes of the psychometric functions were the same within both channels indicated that probability summation could not account for temporal summation for stimulus durations less than 1 s. The finding that the threshold for the detection of multiple-pulse stimuli increased as the interpulse interval increased indicated that, for time intervals less than 800 ms, temporal summation resulted from neural integration. But for interstimulus intervals greater than 800 ms, probability summation accounts for temporal summation.

Key words: vibrotactile, temporal summation, probability summation, neural integration, tactile

Introduction
In many sensory systems, the detectability of a stimulus improves as stimulus duration increases. This phenomenon, known as temporal summation, occurs in the sense of touch under very restricted conditions. The threshold for detecting vibratory stimuli decreases as stimulus duration increases only when high-frequency stimuli are delivered through a large contactor to an area of the skin known to contain Pacinian corpuscles (Verrillo, 1965a; Green, 1976; Gescheider, 1976; Gescheider et al., 1994a, c, 1996). Under these conditions, only the Pacinian (P) channel is stimulated (Bolanowski et al., 1988). Because spatial summation, as well as temporal summation, is an exclusive property of this channel, the P channel is exceptionally sensitive when the stimulus is delivered to the skin through a large contactor. Indeed, the detection threshold of the P channel at 250 Hz is 20–30 dB below that of any other channel (Bolanowski et al., 1988). In contrast to results obtained with the P channel, the threshold is independent of stimulus duration when non-Pacinian (NP) channels are exclusively stimulated by applying stimuli to skin containing Pacinian corpuscles but through a contactor of insufficient size to stimulate the spatially summating P channel (Verrillo, 1965a; Gescheider, 1976; Gescheider et al., 1994c). Gescheider (1976) and Green (1976) also found that temporal summation is absent or nearly absent at low stimulus frequencies that exclusively excite NP channels at the observer’s detection threshold. Thus, of the four tactile information processing channels, P, NPI, NPII, and NPIII (Bolanowski et al., 1988), only the P channel, mediated by Pacinian corpuscles, has been found to be capable of temporal summation.

An important question to ask is how the temporally distributed effects of tactile stimulation determine the threshold in the P channel. A classical solution to this problem, in touch (Verrillo, 1965a; Gescheider, 1976; Checkosky and Bolanowski, 1992, 1994) as well as in other sensory modalities such as vision (DeLange, 1952; Kelly, 1961; Sperling and Sondhi, 1968; Rashbass, 1970; Roberts, 1972; Koenderink and Van Doorn, 1978) and hearing (Garner and Miller, 1947; Plomp and Bouman, 1959; Zwitheck, 1960) has been to propose that sensory systems integrate persisting neural responses to the stimulus over some critical duration of stimulus exposure. In all of the neural-integration
models that have been proposed to account for temporal summation, the magnitude of the sensory response increases over the time of stimulation and when it exceeds some threshold level, a detection response is made by the observer. Because this threshold is reached sooner with more intense stimuli, the reciprocal relationship found experimentally between the intensity of the stimulus at the psychophysical threshold and stimulus duration can be explained. To understand the proposed mechanism of neural integration, one must conceptualize an ongoing stimulus as being made up of separate brief stimulus events such as the individual cycles of sinusoidal vibration, each being capable of causing an abrupt increase in neural activity followed by a relatively gradual decay. According to Zwislocki's neural-integration theory (Zwislocki, 1960, 1965, 1969) of temporal summation, neural activity elicited by a stimulus event decays exponentially with a time constant of 200 ms. It is this residual decaying of neural activity following each stimulus event that, when added to the neural activity of the current stimulus event, results in a build up of neural activity over the duration of the stimulus presentation. A common feature of the various neural-integration models is that they are deterministic in that no attempt is made to conceptualize stimulus detection as a probabilistic event.

In a probabilistic model of temporal summation, stimulus detection increases as a function of stimulus duration because random factors such as fluctuations in noise or sensory transduction may cause sensitivity to vary. The stimulus can be considered as a sequence of brief intervals in which the probability of exceeding the threshold may fluctuate from moment to moment (Watson, 1979). Stimulus detection is affected by these probabilities, and temporal summation may occur because a long stimulus is more likely to cause a sensory response to exceed the threshold than a short stimulus. Consequently, if the detection probability is held constant, as it is in psychophysical threshold measurement (e.g., 75% correct responding in a two-alternative forced-choice situation) then brief stimuli will have to be presented at higher intensities than stimuli of longer duration for the threshold to be exceeded.

Is there any evidence presently available that supports one or both of these models? The evidence is sparse for tactile sensitivity. Support for the neural-integration model has come mainly from the consistent finding (Verrillo, 1965a; Gescheider, 1976; Green, 1976; Frisina and Gescheider, 1977; Gescheider et al., 1994a, c; Gescheider and Joelson, 1983) that changes in the detection threshold as stimulus duration is increased correspond closely with quantitative predictions from Zwislocki's (1960) model of temporal summation. The results from some of these studies are seen in Figure 1 in which threshold shift in decibels relative to the detection threshold for a 1000 ms stimulus is plotted as a function of stimulus duration. The solid function is predicted from Zwislocki's (1960) theory of temporal summation. The data points are from Frisina and Gescheider, 1977 (∙); Gescheider, 1976 (∗); Gescheider and Joelson, 1983 (∗); Gescheider et al., 1994a (∨); Gescheider et al., 1994c (∗); Gescheider et al., 1996 (∆); Green, 1976 (♭) and Verrillo, 1965a (∗∗).

FIGURE 1. Threshold shift in decibels relative to the threshold for detection of a 1000 ms stimulus. In all cases, stimuli of sufficiently high frequency were applied to the skin of the hand through a relatively large contactor, resulting in isolation of the Pacinian (P) channel at the detection threshold. The solid function is predicted from Zwislocki's (1960) theory of temporal summation. The data points are from Frisina and Gescheider, 1977 (∙); Gescheider, 1976 (∗); Gescheider and Joelson, 1983 (∗); Gescheider et al., 1994a (∨); Gescheider et al., 1994c (∗); Gescheider et al., 1996 (∆); Green, 1976 (♭) and Verrillo, 1965a (∗∗).
model is that the intensity of the pulses required for detection should, because of integration of the neural activity from the two pulses, decrease as the time between the pulses becomes smaller. In contrast, the prediction, according to the probability-summation model, is that the detection threshold should not be affected by the time interval between pulses. Thus, because opposite results are predicted from the neural-integration and probability-summation models, the multiple-pulse procedure provides an ideal approach for determining which model best explains temporal summation.

When Zwischinski (1960) first conducted this experiment for the detection of tone pulses, he obtained evidence that supported the neural-integration model but failed to support the probability-summation model. Specifically, auditory sensitivity improved as the separation between the two pulses progressively decreased from 1000 to a few milliseconds. The time constant of neural integration determined by his results was 200 ms, the same as that proposed in his model. Although these results appear to constitute powerful evidence for the neural-integration model and against the probability-summation model, they have been contested by Vieimeister and Wakefield (1992) who used more modern, criterion-free psychophysical methods than the Békésy tracking method used by Zwischinski. In their study it was found that the threshold for two pulses was approximately 1.6 dB lower than for one pulse at all interpulse intervals except when the time between the pulses was less than 10 ms, in which case it was even lower. These results were interpreted as indicating that the time constant for neural integration in hearing is only 5–10 ms and that probability summation operates over the remainder of the duration of the auditory stimulus.

The purpose of the present study was to determine the roles of neural integration and probability summation in vibrotactile temporal summation.

**Experiment I: Temporal summation and the psychometric function**

In a two-alternative forced-choice detection task, the lower limit of the psychometric function is the intensity at which the observer's performance in correctly responding is just better than chance (above a probability of 0.5 of correctly responding) while the upper limit is the point at which the probability of correctly responding first becomes 1.0 as stimulus intensity is increased. In a hypothetical sensory system capable of probability summation, a very steep psychometric function would result in little reduction in the threshold, expressed in units of stimulus intensity, as the stimulus duration is changed from short to long while at the same time, the probability of detecting the stimulus would increase substantially. This concept is illustrated in Figure 2b where the threshold decreases only slightly from X to Y as the duration of the stimulus increases from 10 to 1000 ms while at the same time the probability of detecting stimulus X changes from...

![Figure 2](image)

**Figure 2.** Hypothetical psychometric functions for two systems both showing the same amount of temporal summation when expressed in terms of a change in the probability of detecting the signal as its duration changes. System (b), however, because of the steep slope of the psychometric function, shows only a small threshold shift, whereas system (a), because of the shallow slope of the psychometric function, shows a large threshold shift.
In contrast, in a sensory system with a much-less-steep psychometric function (Fig. 2a), the probability of detecting stimulus X increases by this same amount, 0.75 to 0.99, but in this case, the threshold is decreased substantially from X to Y as the stimulus duration increases from 10 to 1000 ms. Thus, the degree to which probability summation can manifest itself in a decrease in threshold as stimulus duration is increased, is inversely related to the slope at the psychometric function.

The sense of touch is ideally suited for testing the probability-summation model because, within this sensory system, only the P channel exhibits substantial decreases in threshold as stimulus duration increases. The NPI and NPII channels have been found to exhibit only a slight amount of temporal summation as measured by changes in the detection threshold as stimulus duration is changed. The important question then is whether this difference in temporal summation between the P and NP channels is due to the existence of relatively steep psychometric functions in the NP channels. According to probability-summation theory, if probability summation uniformly applies to the P and NP channels, then the predicted change in the probability of correctly detecting the stimulus as its duration is changed is the same in all channels. Since the threshold shift associated with changes in stimulus duration is minimal in the NP channels and substantial in the P channel, the psychometric functions of the NP channels are predicted from the probability-summation model to be much steeper than those of the P channel. If this prediction were to be confirmed, then probability summation alone would account for temporal summation in the P channel as well as the relative lack of temporal summation in the NP channels. As a result, the need to postulate a neural-integration mechanism to account for temporal summation would be obviated.

In this experiment, the P channel was isolated by delivering 250 Hz stimuli to the thenar eminence through a 1.5 cm$^2$ contactor and the NPII channel was isolated by delivering these same stimuli to the same site through a 0.01 cm$^2$ contactor. Under these conditions, the threshold of the P channel is approximately 20 dB lower than that of the NPII channel (Bolanowski et al., 1988). Psychometric functions of both channels were determined for the detection of stimuli having durations of 10 and 1000 ms.

**Method**

**Observers**

Five observers, three females and two males, participated in this experiment. The age range of the observers was 19–22 years and all were healthy with no known neurological disorders. Prior to the experiments each observer participated in two or three 1 h practice sessions in detecting vibrotactile stimuli.

**Apparatus**

The observer and the stimulus-delivering apparatus were located within a sound and vibration proofed testing chamber. Vibratory stimuli were produced by a Ling 203-A shaker. Vibratory displacements of the skin were produced relative to a static indentation of the vibrator contactor of 0.5 mm into the skin. Sinusoidal displacements of the skin were measured with a calibrated electromagnetic linear-variable displacement transducer (Schevitz LVDT) that sensed the displacement of the moving element of the vibrator. All measurements were made with the subject's hand in the test position. The skin was stimulated by either a 1.5 cm$^2$ or a 0.01 cm$^2$ circular contactor, contoured to fit the curvature of the skin of the thenar eminence and mounted on the moving element of the vibrator. The edge of the contactor was separated from a rigid surround by a 1.0 mm gap. The rigid surround confines the stimulus to the immediate area of the contactor (Eijkman and Vendrick, 1960) by confining the spread of surface waves on the skin (Verrillo et al., 1983). Because skin temperature can affect vibrotactile sensitivity (Bolanowski and Verrillo, 1982; Verrillo and Bolanowski, 1986) skin temperature was held constant to within ± 0.5°C of 30°C by a device that circulates water of the appropriate temperature through the hollow chamber of the surround. A Lauda/Brinkman K-Z/R heating and refrigeration unit and pump controlled both the water temperature and the circulation flow rate. Skin temperature was monitored by a thermistor embedded in the surround. The observers wore ear phones through which narrow-band noise was delivered to mask the sound of the vibrator. Stimulus waveforms and timing were controlled by a MacII computer system. Vibratory stimuli had rise–fall times of 10 ms. Stimulus durations of 10 and 1000 ms were specified at the half-power points (points in time at which the power of the stimulus is at one half of its maximum level).

**Procedure**

The test site was the thenar eminence of the right hand. This site was chosen because the channel organization is better understood on the thenar eminence than on other areas. In addition, the amount of available information on temporal summation is much greater for the thenar eminence than for any other site. Detection thresholds were measured by a two-alternative forced-choice tracking procedure (Zwislocki et al., 1958) in which the observer is presented with two sequentially presented observation intervals designated by lights, one containing a stimulus and one not. The temporal midpoint of both the 10 ms and 1000 ms stimuli occurred 600 ms after the onset of the light designation of the observation interval and 1200 ms before termination of the observation interval. The
presentation of the stimulus is distributed randomly between the two observation intervals with a probability of 0.5. The amplitude of the stimulus was decreased by 1.0 dB for every three correct responses (not necessarily consecutive) and was increased by 1.0 dB for every error. The method converges on the amplitude resulting in 75% correct responses. The amplitude of the stimulus is recorded when the performance of the observer is maintained at this criterion and the variability in the tracking record does not exceed 2.0 dB above or below the mean for at least 30 responses. Thresholds were expressed in dB referenced to 1.0 μm peak displacement amplitude.

To determine the psychometric function, nine stimuli, separated in intensity by 1.5 dB, were each presented 60 times in a randomized order within a testing period. The nine intensities consisted of four values below the observer’s tracked threshold, one at the tracked threshold, and four above the tracked threshold. The threshold was measured at the start of each session by the two-alternative forced-choice tracking method described above. On each trial, a stimulus was randomly presented in one of two successive observation intervals. The observer was required to report which observation interval contained the stimulus. Psychometric functions, in
which the proportion of correct responses is plotted as a function of stimulus intensity, were obtained at signal durations of 10 and 1000 ms for the P channel and for the NPII channel. The P channel was isolated by delivering 250 Hz stimuli through a 1.5 cm$^2$ contactor, whereas the NPII channel was isolated by delivering stimuli of the same frequency through a 0.01 cm$^2$ contactor (Verrillo, 1963, 1965a; Gescheider, 1976; Gescheider et al., 1985; Bolanowski et al., 1988).

**Results and Discussion**

Psychometric functions for each of the five subjects are shown in Figure 3 for the 1.5 cm$^2$ and the 0.01 cm$^2$ contactors. It is clear that, in each case, using the 1.5 cm$^2$ contactor resulted in a psychometric function for the stimulus duration of 1000 ms that was substantially lower on the intensity axis than that obtained at a duration of 10 ms. The separation of the psychometric functions at the 0.75 point averaged 11.7 dB. In sharp contrast, when the contactor size was 0.01 cm$^2$, the amount of temporal summation, defined as the threshold difference between the 10 and 1000 ms stimuli, averaged only 1.5 dB. The absence of, or near absence of, temporal summation when high-frequency stimuli are delivered through very small contactors has consistently been reported in earlier studies (Verrillo, 1965a; Gescheider, 1976; Gescheider et al., 1994c).

The finding that thresholds are substantially affected by changes in the duration of high-frequency stimuli when the contactor is large but not when it is small, has been interpreted as an indication that the P channel is capable of temporal summation but the NPII channel is not.

The difference in the amount of temporal summation observed using the two contactors was also clearly illustrated when the data of the five observers were normalized and combined (Fig. 4). The normalization procedure required that in each of the four contactor size–stimulus duration conditions, the average tracked threshold of the five subjects be substituted for the tracked threshold of each subject. This value became the middle value of the psychometric function. The remaining eight intensity values of the psychometric function were 1.5, 3.0, 4.5, or 6.0 dB above and below this middle value. The average proportion of correct responses was then computed for each of the nine intensity values of the psychometric function.

It can be seen from the smooth curves drawn through the data points (Fig. 4) that, for the P channel stimulated by the 1.5 cm$^2$ contactor, the probability of detecting it changed from 0.75 to 0.81. Thus, temporal summation, defined as an increase in the probability of detecting a stimulus as its duration is lengthened, is substantially greater in the P than in the NPII channel. Because thresholds, only in the P channel, decreased greatly when stimulus duration was changed from 10 to 1000 ms, the slopes of the psychometric functions would have had to be much steeper in the NPII channel than in the P channel for the probability of stimulus detection to have increased by the same amount in both channels. The slopes of the psychometric functions did not significantly differ as indicated by an analysis of variance and consequently we must conclude that the results fail to support the probability-summation model of vibrotactile temporal summation. Therefore, it is important to examine the alternative neural-integration model.

**Experiment II:**

Detection of multiple pulses in the P channel

In this experiment, the subject was required to detect stimuli consisting of a series of brief (10 ms) 250 Hz vibratory pulses delivered through a 1.5 cm$^2$ contactor to the P channel. Assuming that random fluctuations in the neural responses to the individual pulses are statistically independent, the probability-summation model predicts that the detection threshold will decrease as the number of pulses increases, but be independent of the time between them. According to the neural-integration model, when pulses are separated by small time intervals of a few
milliseconds, there is optimal opportunity for the decaying neural response to the first pulse to add to the neural activity generated by a subsequent pulse. However, this is not the case when pulses are separated by much greater time intervals. If the detection threshold is exceeded when the neural response achieves a specific level, then a direct relationship should exist between the time between pulses and the threshold. Furthermore, according to neural-integration theory, the detection threshold is predicted to decrease as the number of pulses is increased, but only when the time interval between pulses is sufficiently short to permit the occurrence of neural integration.

**Method**

**Observers**

Four observers, two females and two males, who served in experiment I participated in this experiment. Prior to the experiment, each observer was given two or three 1h practice sessions in which multiple pulses with variable interpulse intervals were detected.

**Apparatus**

The apparatus was the same as that used in experiment I.

**Procedure**

As in experiment I, the test site was the thenar eminence of the right hand and 250 Hz stimuli were delivered through a 1.5 cm$^2$ contactor. Stimuli consisted of either a single 10 ms pulse with duration measured at the half-power point having a 10 ms rise--fall time or multiple 10 ms pulses of the same amplitude separated by a variable time interval. The multiple-pulse stimuli consisted of either two or four pulses and the interpulse interval was varied over the range of 13–800 ms specified at the half-power point between pulses. Using the two-alternative forced-choice tracking procedure, the observers’ task was to determine on each trial which of two observation intervals designated by a red light followed immediately by a green light contained the vibratory stimulus. In the interval containing the stimulus, the first pulse was presented 400 ms after the onset of the observation interval and the observation interval was terminated 1300 ms after the presentation of the last pulse in the series. The threshold was specified as the amplitude of the pulse or pulses in a multipulse stimulus that was necessary for the observer to correctly detect the stimulus 75% of the time. Within each session, the threshold was first measured for detecting a single pulse, followed by threshold measurements for multiple-pulse stimuli at various interpulse intervals. The session ended with the measurement of a second single-pulse threshold.

The multiple-pulse stimulus presented within a session consisted of either two or four pulses. Four sessions were conducted using two-pulse stimuli and four sessions using four-pulse stimuli.

**Results and Discussion**

The average results of the four observers are shown in Figure 5. Thresholds for the detection of multiple pulses, expressed in decibels relative to the threshold for detecting a single pulse, are plotted as a function of the time between pulses. Thresholds for detecting multiple pulses are lower than for detecting a single pulse, illustrating the existence of temporal summation. The threshold shift for detecting two pulses relative to detecting one pulse when the interpulse interval was 13 ms is approximately $-3.0$ dB (3.15 dB), which suggest that, at such a small interval of time between pulses, the system perfectly integrates stimulus energy. In this case, the energy of each of the two pulses needed for detection is approximately half of that needed with a single pulse. At this same short interpulse interval, the threshold for detecting four pulses was nearly 6.0 dB (5.6 dB) lower than the threshold for detecting a single pulse, again suggesting near perfect integration of energy. The energy needed for stimulus detection in each of the four pulses is approximately one-quarter that needed for a single pulse. These results are consistent with the finding that a doubling of stimulus duration from 10 to 20 ms results in an improvement in the detection threshold by 3.0 dB, while increasing the duration of the stimulus by a factor of four to 40 ms lowers the threshold by 6.0 dB (Verrillo, 1965a; Gescheider, 1976; Gescheider et al., 1994a, c).
It is evident from Figure 5 and from a replotting of the data (Fig. 6) that the improvement in the threshold as the number of pulses in the stimulus increases is critical because it is only when the pulses are close together in time that their neural responses can add together. According to Zwislocki's neural-integration model, neural activity after termination of a pulse decays exponentially with a time constant of 200 ms. The decaying neural activity adds to the neural activity resulting from a subsequent pulse causing an increase in the magnitude of the neural response as the number of pulses increases. Thus, the detection threshold should be lowered as the number of pulses in a multiple-pulse stimulus increases only when the time between pulses does not exceed the time over which neural activity of the individual pulses decays.

The smooth curves seen in Figure 5 describe the threshold shifts predicted from Zwislocki's (1960) theory of temporal-auditory summation and are in remarkably good agreement with our data. These predicted threshold shifts were calculated from equations that describe the summation of successive neural responses.

The neural response to the second of two equally intense stimulus pulses ($N_2$) can be computed, knowing the neural response to the first pulse ($N_1$), from the equation

$$N_2 = N_1 + N_1 e^{-5t}$$  \hspace{1cm} (1)

in which $t$ is the interpulse interval in seconds and $-5$ is the value needed for a 200 ms time constant in an exponential decay of neural activity. In computing the neural responses for multiple-pulse stimuli consisting of four pulses of equal intensity, the value of $N_4$ is first computed from $N_1$ by equation (1) and $N_3$ is computed from $N_2$ by

$$N_3 = N_1 + N_2 e^{-5t}$$  \hspace{1cm} (2)

and finally $N_4$ is computed from $N_3$ by

$$N_4 = N_1 + N_3 e^{-5t}$$  \hspace{1cm} (3)

These equations were used to compute the predicted size of the neural responses needed to exceed an arbitrary fixed threshold level when the number of stimulus pulses was either one, two or four and the interpulse interval was varied. Assuming that the neural response was directly proportional to the energy of the stimulus pulse that elicited it, the predicted threshold shifts (TS) in decibels for detecting a multiple-pulse stimulus relative to the threshold for detecting a single pulse were calculated from the equation

$$TS = -10 \log \left( \frac{N_s}{N_m} \right)$$  \hspace{1cm} (4)

where $N_s$ is the magnitude of neural response required for a single pulse to be detected and $N_m$ is the required magnitude of the neural response to each pulse in a multiple-pulse stimulus.
Figure 7. Illustration of Zwislocki's (1960) proposed process of neural integration for the response to single- and multiple-pulse stimuli. The neural threshold has an arbitrary value of 10. Predicted threshold shifts, based on the required size of the neural responses to a single pulse (a) and to multiple pulses (b–d), are plotted as a function of interpulse interval for the detection of (b) a two-pulse stimulus with an interpulse interval of 400 ms, (c) a two-pulse stimulus with an interpulse interval of 40 ms and (d) a four-pulse stimulus with an interpulse interval of 40 ms.
Figure 7 is a graphic illustration of the calculation of the neural responses to a single pulse (a) and to two pulses with interpulse intervals of either 400 ms (b) or 40 ms (c) and to four pulses with interpulse intervals of 40 ms (d). It is evident that, because the neural response to an individual stimulus pulse adds to the exponentially decaying neural response to the previous pulse, the level of neural activity builds with each successive pulse and eventually reaches the detection threshold. Notice that, as a result of neural integration, the required magnitude of the neural response to the first pulse, as well as the incremental neural response to each successive pulse, decreases as the interpulse interval decreases and the number of successive pulses increases. Predicted threshold shifts calculated from equation (4) are shown plotted as a function of the interpulse interval.

The assumption required in calculating predicted threshold shifts in the stimulus intensity domain from a theoretical model of temporal summation formulated in the neural domain is that the amplitude of the neural response, at the level within the nervous system at which temporal summation operates, is a linear function of stimulus energy. This assumption is supported by the results of psycho-physical studies in which subjective magnitude judgements are found to be linearly related to stimulus energy over a range of intensities from threshold to 10–15 dB above threshold (Verrillo and Chamberlain, 1972; Verrillo, 1974; Gescheider, 1976; Gescheider et al., 1994b). It must be pointed out, however, that because the firing of action potentials tends to become entrained to sinusoidal stimuli, their frequency of firing is not proportional to stimulus energy (e.g., Bolanowski and Zwischlocki, 1984). Thus, it would appear that the neural input to the temporal integrator cannot be the neural response from a single Pacinian corpuscle (Checkosky and Bolanowski, 1994). Instead, the input to the temporal integrator must consist of activity from multiple Pacinian fibers or of the activity of neurons within the central nervous system that are themselves driven by Pacinian inputs. The fact that the threshold shifts in the stimulus domain, seen in our present experiment and plotted in Figure 5, can be predicted accurately from a neural-integration model with characteristics specified within the neural domain, also strongly suggests that, in the tactile system, the neural responses that determine the threshold must be linearly related to stimulus energy.

An inspection of Figure 5 reveals that although the neural-integration model accounts extremely well for nearly all the results, an exception is seen for the four-pulse stimulus with an interstimulus interval of 800 ms. In this case, the threshold is somewhat lower than the predicted result. Calculation from the model indicates that the threshold for detecting a four-pulse stimulus should be only 0.09 dB lower than that for detecting a single pulse. However, the average measured threshold was 0.97 dB lower. Perhaps it is only at such long interpulse intervals that the statistical variation of the neural responses to separate pulses becomes uncorrelated so that probability summation can occur.

**Experiment III:**
**Detection of multiple pulses in the NPII channel**

As in experiment I, the NPII channel was isolated by delivering a 250 Hz stimulus through a 0.01 cm² contactor to the thenar eminence. The purpose of this experiment was to determine whether the detection threshold in the NPII channel is affected by the number of pulses in a stimulus and the time between pulses. It was predicted that, unlike the results obtained for the P channel, in this non-summating channel, neither of these variables would affect the detection threshold.

**Method**

**Observers**
The same four observers employed in experiment II were employed in this experiment.

**Apparatus**
The apparatus was the same as that used in experiment II with the exception that the stimulus was delivered through a 0.01 cm² contactor.

**Procedure**
The procedures were the same as those used in experiment II with the exception that the number of pulses in a stimulus was either one or four and the interpulse intervals used in this experiment were 13, 400 or 800 ms. Within each session, two single-pulse thresholds, one at the start and one at the end of the session, were measured. Between these two measurements one threshold for the detection of multiple-pulse stimuli presented at each of the interpulse intervals was measured.

**Results and Discussion**

Presented in Figure 8 are the threshold shifts for the detection of multiple-pulse stimuli relative to thresholds for single pulses plotted as a function of the interpulse interval. For the purpose of direct comparison, the four-pulse results for the P channel obtained in experiment II are also shown. It is evident that the responses of the two channels to changes in the number of pulses and to changes in the interpulse interval are dramatically different. Whereas the sensitivity of the P channel is greatly affected by changing the interpulse interval and the number of pulses, the sensitivity of the NPII channel is not.
In revealing a lack of temporal summation in the NPII channel, the results of the multiple-pulse experiment are in agreement with the results of experiment I and those of prior studies (Verrillo, 1965a; Gescheider, 1976; Gescheider et al., 1994c) where the detection threshold for high-frequency stimuli delivered through a small contactor was minimally affected by stimulus duration. One exception to this general finding is the observation that when sinusoidal stimuli presented to the skin through a small contactor (0.01 cm²) are delivered against a vibratory noise background, the detection threshold decreases as the duration of the stimulus increases (Gescheider et al., 1985, 1994c). It has been suggested that, in the presence of background noise, temporal summation in the NPII channel results from probability summation (Gescheider et al., 1994c). Noise may introduce fluctuation in the channel’s sensitivity of sufficient magnitude that probability summation in the detection process can operate over the time of exposure to the stimulus. If this hypothesis proves to be correct, then the lack of substantial amounts of probability summation, in the absence of external noise in either the P or NPII channel may be the result of minimal variability over time in the sensitivity of the channel.

**Experiment IV**

Experiment IV was conducted because of a concern for why so little, if any, evidence was found for probability summation in the detection of multiple-pulse stimuli. The detection threshold of any system in which sensitivity varies over time should be lower when multiple pulses rather than single pulses are presented, provided the fluctuations in the neural responses of each pulse of a multiple-pulse stimulus are sufficiently large and statistically independent. If changes in the sensitivity of the P or NPII channels are rapid enough to occur within a period of 800 ms or less, then thresholds at interpulse intervals of 800 ms or more would be expected to be lower for the detection of multiple-pulse than single-pulse stimuli, even though neural integration, according to Zwischen’s (1960) model, is essentially absent at these relatively long time intervals. To test this hypothesis, it is essential for an observer to focus attention over the entire observation interval to determine if a pulse had been presented at any time within a period as long as several seconds. In experiment IV, an attempt was made to maximize this possibility by presenting four 10 ms indicator lights separated by the interpulse interval during each of the two observation intervals of the two-alternative forced-choice tracking task. On each trial, the four pulses of a multiple-pulse stimulus were presented during the four light flashes in one or the other of the two observation intervals. In this way the temporal position within the observation interval in which a pulse was presented was exactly specified to the observer.

Because there was only a slight suggestion in experiment II that probability summation may have operated when the interpulse interval was 800 ms, the range of interpulse intervals was expanded to include a value of 1200 ms. The rationale for this decision was to give probability summation, if it exists, the best possible chance to reveal itself. The effect seen at 800 ms in experiment II may have been small because it resulted from partial rather than complete probability summation. Partial probability summation could occur when the correlation between the neural responses to the individual pulses is less than 1.0 but not zero. Only when the correlation is zero can probability summation be complete. It was thought that the use of an interpulse interval of 1200 ms might lower the correlation to a level at which large amounts of probability summation would be exhibited. Thus, it was predicted that, if probability summation operates on the P channel, threshold shifts for detecting multiple-pulse stimuli should be greater when the interpulse interval is 1200 ms than when it is 800 ms.

**Method**

**Observers**

One of the female observers who participated in the first three experiments also participated in experiment IV. Three other observers ranging in age from 18 to 22 years also participated in this experiment. All observers were given two or three practice
sessions in detecting single-pulse and four-pulse stimuli under the observation light conditions of the present experiment.

**Apparatus**

The apparatus was the same as that used in previous experiments.

**Procedure**

The procedure was essentially the same as that used in experiment II when four-pulse and single-pulse stimuli were employed, with the exception that, within each observation interval, 10 ms yellow indicator lights were flashed at times when a pulse could be presented. In the case of a single-pulse stimulus, the 10 ms indicator light was presented 400 ms after the onset of each of two observation intervals designated by a 1700 ms red light immediately followed by a 1700 ms green light. The observer's task was to determine which of the two observation intervals contained the stimulus. For four-pulse stimuli, the first of four indicator lights was presented 400 ms after the onset of each of the two observation intervals and the other three lights followed at a rate corresponding to the interpulse interval of the pulses. As was true for single-pulse stimuli, the observer's task was to determine which of the two observation intervals contained the stimulus. Multiple-pulse thresholds were measured at interpulse intervals of 13, 100, 400, 800 and 1200 ms.

**Results and Discussion**

Plotted in Figure 9 are the thresholds for the detection of four-pulse stimuli expressed in decibels relative to the threshold for detecting a single pulse. The results obtained in experiment II for four-pulse stimuli presented without indicator lights are also shown. Essentially the same results were obtained with or without indicator lights with interpulse intervals ranging from 13 to 800 ms. In both experiments a small amount of probability summation may be evident at an interpulse interval of 800 ms where the threshold for detecting the four-pulse stimulus is about 1.0 dB lower than the threshold for detecting a single pulse. In experiment IV the threshold shift was 2.1 dB when the interpulse interval was 1200 ms. According to Zwislocki's model of temporal summation, significant amounts of neural integration should not be possible for stimuli separated by 800 ms or more and thus the lower threshold for detecting four-pulse stimuli presented at these long interpulse intervals would appear to be the result of probability summation.

The results of our experiments support the hypothesis that neural integration accounts for temporal summation for time intervals less than 800 ms and that some probability summation seems to occur at time intervals of 800 ms or longer. Below 800 ms, sensitivity improves as the interpulse interval decreases, indicating that the neural effects of each pulse can be better integrated when the pulses are close together in time than when they are far apart. The absence of probability summation at these interpulse intervals may be because random fluctuations in the detection threshold are not fast enough for the variability in the sensitivity for detecting the individual pulses in a multiple-pulse stimulus to be uncorrelated. In contrast, longer interpulse intervals, although too long for neural integration to occur, may be sufficiently long for probability summation to occur because fluctuations of the sensitivity for detecting the individual pulses become statistically independent.

**Conclusions**

The results of this study indicate that vibrotactile temporal summation, defined as an increase in sensitivity as either the duration of a continuous stimulus or the number of pulses in a multiple-pulse stimulus is increased, can be accounted for almost entirely by a mechanism of neural integration. The finding that the slopes of the psychometric functions in the temporally sumimating P channel and the non-summatng NPII channel were the same is contrary to the hypothesis that temporal summation in the P channel results from probability summation. If probability summation had operated equally in both channels, then the psychometric function would have had to be very steep in the NPII channel for thresholds to be only slightly affected by changes in stimulus duration.
The hypothesis that probability summation operates in the P channel but not in the NPII channel is not supported by the finding that the threshold for detecting multiple-pulse stimuli decreased as the time between pulses decreased. Nor is this hypothesis supported by the finding that the size of the decrease in threshold occurs as the number of pulses increases, decreases as the time interval between the pulses increases. That the time interval between pulses has such profound effects on stimulus detectability is, however, entirely consistent with a neural-integration model of temporal summation. It is only when the interpulse interval is 800 ms or longer that probability summation, rather than neural integration, accounts for the lower thresholds for detecting multiple-pulse stimuli than for detecting single pulses. In contrast, for interpulse intervals less than 800 ms, predictions from Zwischen’s theory of neural integration are in close quantitative agreement with the experimental results.

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References


