The Journal of Science and Medicine
2023: Special Edition: Undergraduate Student Research
Student Articles: Corresponding Editor Mark Tommerdahl

The Role of Entrainment and Aperiodicity in Vibrotactile Discrimination

A Choi
A Abraham
UNC

The extent to which entrainment – the phenomenon in neuroscience where neurons synchronize their firing patterns to external stimuli with rhythmic or periodic features – occurs in response to aperiodic or irregular flutter stimuli remains debatable. It has been proposed by Mountcastle et al. that information is processed in a periodic manner; however, more recently, Romo et al. challenged Mountcastle's theory and proposed that flutter stimulus was encoded based on the rapidly adapting fibers, not the periodicity.[1-5] Therefore, if Mountcastle et al. is correct, the brain should be more adept at discriminating frequency between periodic stimuli than between aperiodic stimuli; conversely, if Romo et al. is correct, the brain should be equally good at discriminating frequencies between periodic and aperiodic stimuli. In this study, a two-point vibrotactile stimulation device (The Brain Gauge, Cortical Metrics, USA) was used to stimulate digits II and III of 43 participants' preferred hand to determine their difference limen (DL) for both amplitude (AD) and frequency (FD) discrimination tests, given aperiodic or periodic stimuli. The tests were performed in the following order: periodic AD, aperiodic AD, periodic FD, and aperiodic FD. The results suggest that the periodicity of the stimuli affects frequency discrimination more than amplitude discrimination and the participants were significantly better at discriminating stimuli with periodic frequencies than aperiodic frequencies. A paired, one-tailed t-test indicated that the subject DLs resulting from periodic stimuli were significantly different ($p<0.05$) from that resulting from aperiodic stimuli for frequency discrimination, while it was not statistically significant for amplitude discrimination. The results were in favor of Mountcastle's theory; however, more trials with a more controlled experimental environment may be needed to definitively conclude.

Background

The entrainment of neural activity is a well-established phenomenon in neuroscience, where neurons synchronize their firing patterns to external stimuli with rhythmic or periodic features. Flutter stimuli at the glabrous skin of the fingertips, which constitute mechanical sinusoids in the range of 5 to 50 hz, initiate the firing of the Meissner's corpuscles, which are a type of nerve endings in the skin that are responsible for sensitive touch and vibration[1,2]. Above 50 hz, the sensation begins to change from a flutter to a constant vibration. Upon stimulation, these receptors elicit the firing of the afferent neurons, which project to the primary somatosensory cortex (SI) where processing and encoding of the stimuli is performed[3]. Entrainment of neurons to external stimuli is crucial for cortical information processing of external stimuli, allowing perception of features of the external stimuli, such as frequency and amplitude. However, the extent to which this entrainment occurs in response to aperiodic or irregular stimuli remains a topic of debate.

In the 1960s, Mountcastle et al. studied monkeys' ability to discriminate differing stimuli by training the monkeys to preferentially select one stimuli over the other[1,2]. He proposed that all sensory information is processed in a periodic manner and that the brain can entrain the firing of neurons to a periodic stimulus, allowing the brain to discriminate the frequency of the stimuli[6].Therefore, he suggested that the brain may be more adept at discriminating frequency between periodic stimuli (stimuli with constant local frequency) than between aperiodic stimuli (stimuli with constant mean frequency, but not local frequency). Furthermore, lesions in the parietal cortex were shown to remove frequency discrimination in monkeys, suggesting that a mechanism to distinguish periodic, entrained activity in the somatic afferent pathway is necessary for the discrimination of frequencies[7]. This led to the widely accepted theory that the flutter stimulus frequency is encoded by the entrainment of SI neurons to the stimuli frequency.

In the late-1900s, however, a newer theory by Romo et al. emerged that the flutter stimulus was encoded based on the rapidly adapting fibers, and not the periodicity[3-5]. Monkeys were shown to discriminate between frequencies of aperiodic cortical stimuli, and the firing rate of the adapting fibers was shown to have a greater effect on frequency discrimination than the periodic entrainment of neurons [4,8]. This directly challenged Mountcastle's theory that firing patterns of neurons reflect the periodicity of the stimulus and in essence, suggested that neuronal activity is more complex and dynamic than previously thought. By selectively filtering out information – due to the rapidly adapting fibers – Romo et al. argued that neuronal activity is largely aperiodic. Romo et al. suggested that the precise timing of action potentials within individual neurons is crucial for discriminating between different frequencies, regardless of whether the stimuli are periodic or aperiodic. Therefore, he suggested that the brain should be equally good at discriminating between periodic and aperiodic stimuli, as long as the stimuli produce distinct patterns of spikes in individual neurons.

In this paper, our goals are two-fold: 1) to determine if the effects of aperiodicity of flutter stimuli are congruent for both amplitude and frequency discrimination, and 2) to attempt to validate the two theories – that of Mountcastle and that of Romo – to provide stronger support for one over the other. We hypothesize that while periodicity of the flutter stimuli has a significant effect on the subject's ability to discern stimuli of two different frequencies, it will not affect amplitude discrimination as much. To achieve this, vibrotactile stimulation was provided to digits II and III of the participants' preferred hand using a two-point stimulation device (The Brain Gauge, Cortical Metrics, USA), and discrimination tasks – frequency and amplitude discrimination with periodic and aperiodic stimuli – were provided to the participant to determine their ability to discern each counterpart stimuli as a measure of difference limen.

Methods

Participant

43 participants (27 females and 16 males), ranging from ages 18 to 32 years (avgstd: 21.8 2.3; median: 21), were recruited for the study. While a majority of the subjects were right-handed, subject handedness was not acquired as handedness was not considered to be a significant factor in the study. No participant claimed any neurological or physical deficits. All participants gave consent prior to the study and were fully disclosed of the procedures.

Tactile Stimulation

Tactile stimulation of the fingertip pulp on digits II and III of the participants' preferred hand, along with assessment of AD and FD, were conducted using a two-point vibrotactile stimulation device (The Brain Gauge, Cortical Metrics, USA). The Brain Gauge device was interfaced with a computer via USB and elicited vibrations to two 5-mm diameter cylindrical surfaces positioned at the top of the device, similar to the physical configuration of a typical computer mouse Figure 1. The time, frequency, and amplitude of the tactile stimuli to the two digits – which were positioned on the vibratory surfaces – could be programmed, and each of the two cylindrical surfaces could be independently actuated. The participant, via the Brain Gauge software, was able to respond to the test, immediately following each trial.

Experimental Design

The participants completed the battery in four discrete tasks – two amplitude discrimination and two frequency discrimination tasks. The tasks were administered in the following order: periodic AD, aperiodic AD, periodic FD, and aperiodic FD. Training tasks were also administered in-between each of the four tasks Figure 1. In a training task, the participants were given three trials with the stimuli conditions identical to those of the following task. The participants were given immediate feedback after each training trial, and the participant was forced to restart the current training task until three consecutive training trials were answered correctly. No feedback was given for the remaining tasks.

The subjects were tested in single, independent sessions, lasting approximately 15 to 30 minutes. Immediately following each trial, the participants were prompted to select the finger that received the greater intensity stimuli. The measurable outcome was the difference limen (DL) of the amplitude or frequency of each trial, for AD and FD, respectively. Five levels of differing DL for each task were administered, with each level consisting of 5-6 trials. There was approximately 3 to 5 seconds of delay after the participant’s response and the next stimulus.

In all tasks, the participants’ digits II and III were simultaneously stimulated with the programmed parameters for each condition. In AD tasks, each finger was simultaneously stimulated with a stimulus of differing magnitude in microns, but with identical frequency (25 hz) and duration(400 ms). The amplitudes of the two stimuli began at 200 microns and 400 microns (DL: 200 microns), with the amplitude of the stimulus with the greater amplitude adjusting according to the staircase procedure (also known as the up-and-down method)[9]. The finger that received the stimulus with the greater amplitude was randomized at each trial.

In FD tasks, each finger was simultaneously stimulated with a stimulus of differing frequency in hertz, but with identical amplitude (200 microns) and duration (400 ms). The frequencies of the two stimuli began at 25 hz and 35 hz (DL: 10 hz), with the frequency of the stimulus with the greater frequency adjusting according to the staircase procedure[9]. The finger that received the stimulus with the greater amplitude was randomized at each trial.

The two types of discrimination tasks were also tested with an aperiodic condition. In periodic tasks, the stimuli to both digits consisted of a consistent sinusoidal wave with frequency f Figure 2; the time in-between each peak remained identical over time. In aperiodic tasks, the stimuli to both digits did not have a consistent sinusoidal wave with a clear frequency. However, the mean frequency of the duration of the stimuli maintained a set frequency of f; although the time in-between each peak did not stay consistent, the number of peaks in a given time period remained consistent over time. The aperiodic patterns were generated pseudo-randomly.

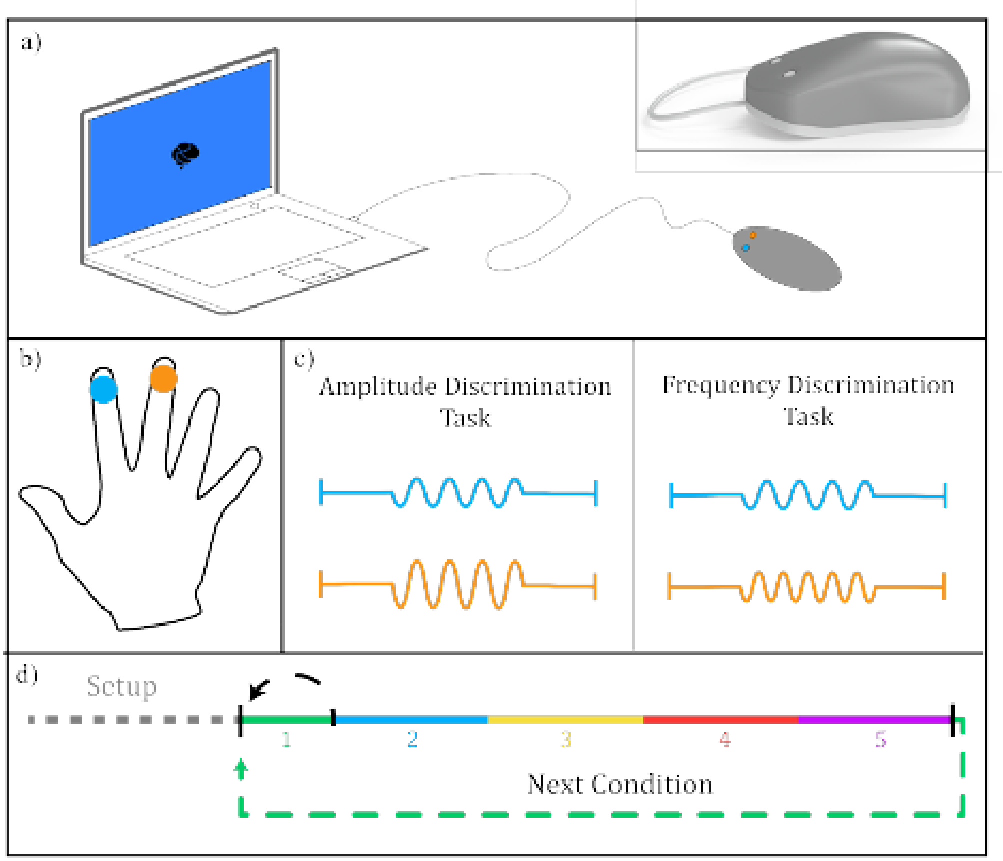

Figure 1. *Figure 1* a) The Brain Gauge device (Cortical Metrics, USA) was interfaced with a computer via USB and elicited vibrations to two 5-mm diameter cylindrical surfaces positioned at the top of the device, similar to the physical configuration of a typical computer mouse. b) Digits II and III of the participant's preferred hand were placed on top of the vibratory surfaces and stimulated. c) Qualitative example waveforms of amplitude discrimination (AD) and frequency discrimination (FD) tasks are shown. In AD, the amplitude of the stimuli was differed, while in FD, the frequency of the stimuli was differed between the two digits. d) Representation of the timeline of the experiment. The initial setup of the experimental device and software was followed by a training task (1) for the periodic AD condition. The participants were given immediate feedback after each of the 3 training trials, and the participant was forced to restart the current training task until three consecutive training trials were answered correctly. Four more sets of trials (2, 3, 4, & 5) for the condition were administered, with each set consisting of 5-6 trials. This procedure was repeated for the other conditions in the following order: aperiodic AD, periodic FD, and aperiodic FD.

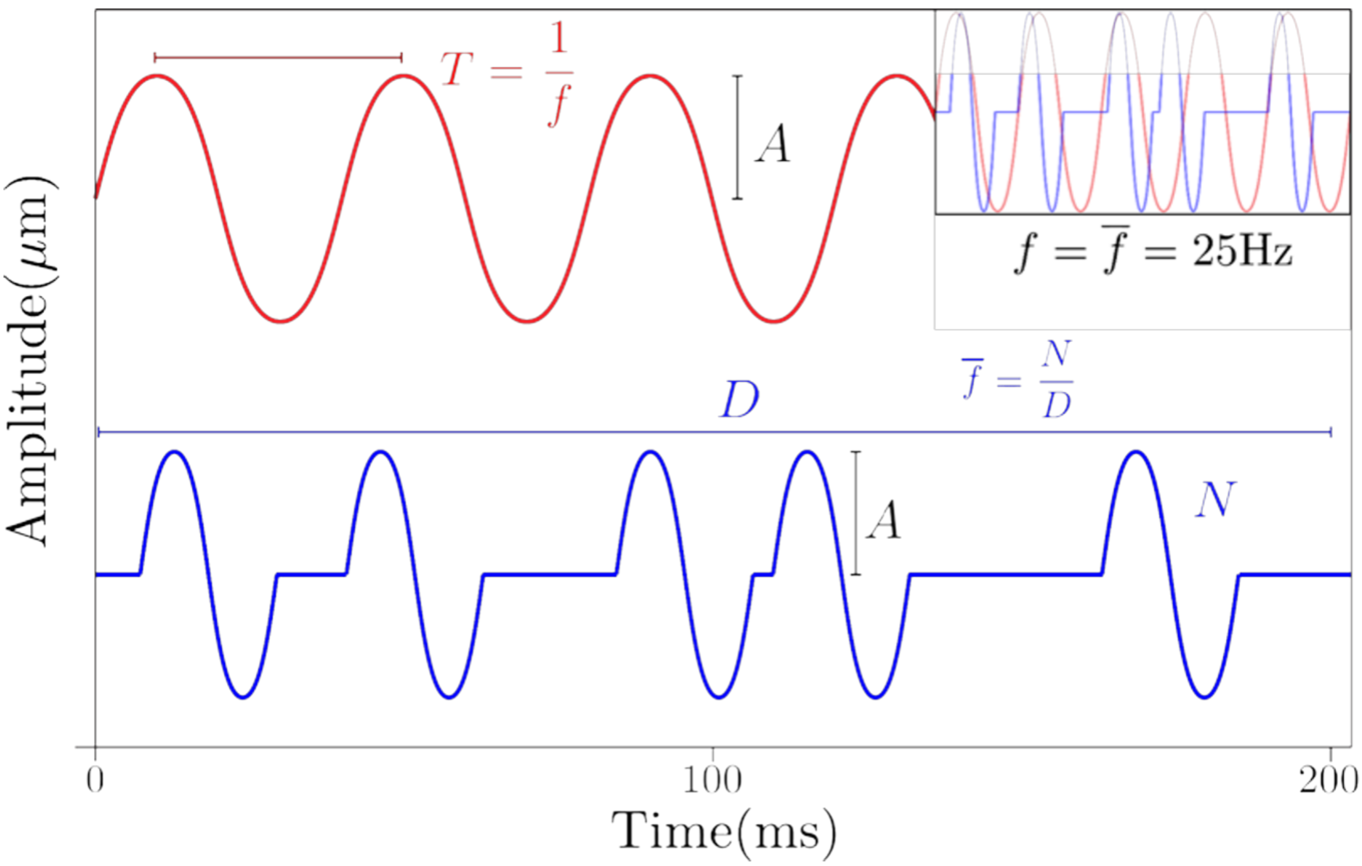

Figure 2. *Figure 2* Amplitude (m) vs. Time (ms) graph for periodic (red) and aperiodic (blue) stimuli. For a set frequency of 25 Hz, for instance, the periodic and aperiodic stimulus maintain a constant frequency *f* and a mean frequency of , respectively, throughout the entire duration of the stimulus of 200 ms, where . The number of waves N in both periodic and aperiodic stimuli are equal in a time duration D. In the top right corner, the two graphs are interposed. The appearance of the aperiodic waves was randomized, while keeping the mean frequency constant.

Results

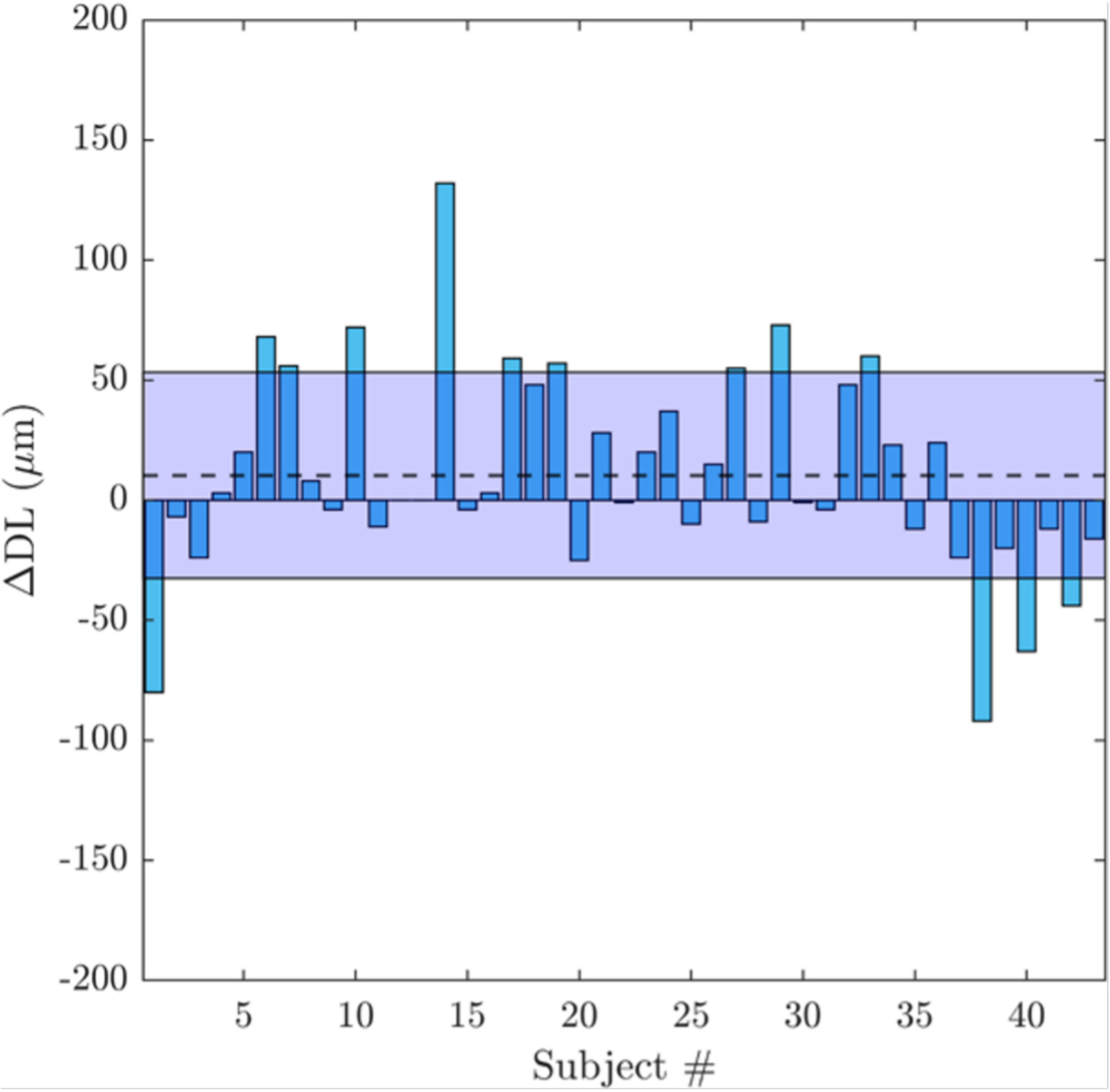

Figure 3. *Figure 3* DL (m) of AD Tasks vs. Subject. 43 subjects' data were included. DL was computed by subtracting the participants' periodic AD DL from that of the aperiodic AD. The average DL was 10.37 m (dashed lines), with a standard deviation of 42.89 m (outline of blue box). The absolute DLs for aperiodic and periodic AD were 57.37 m and 47.00 m, respectively, with a standard deviation of 33.95 m and 29.23 m.

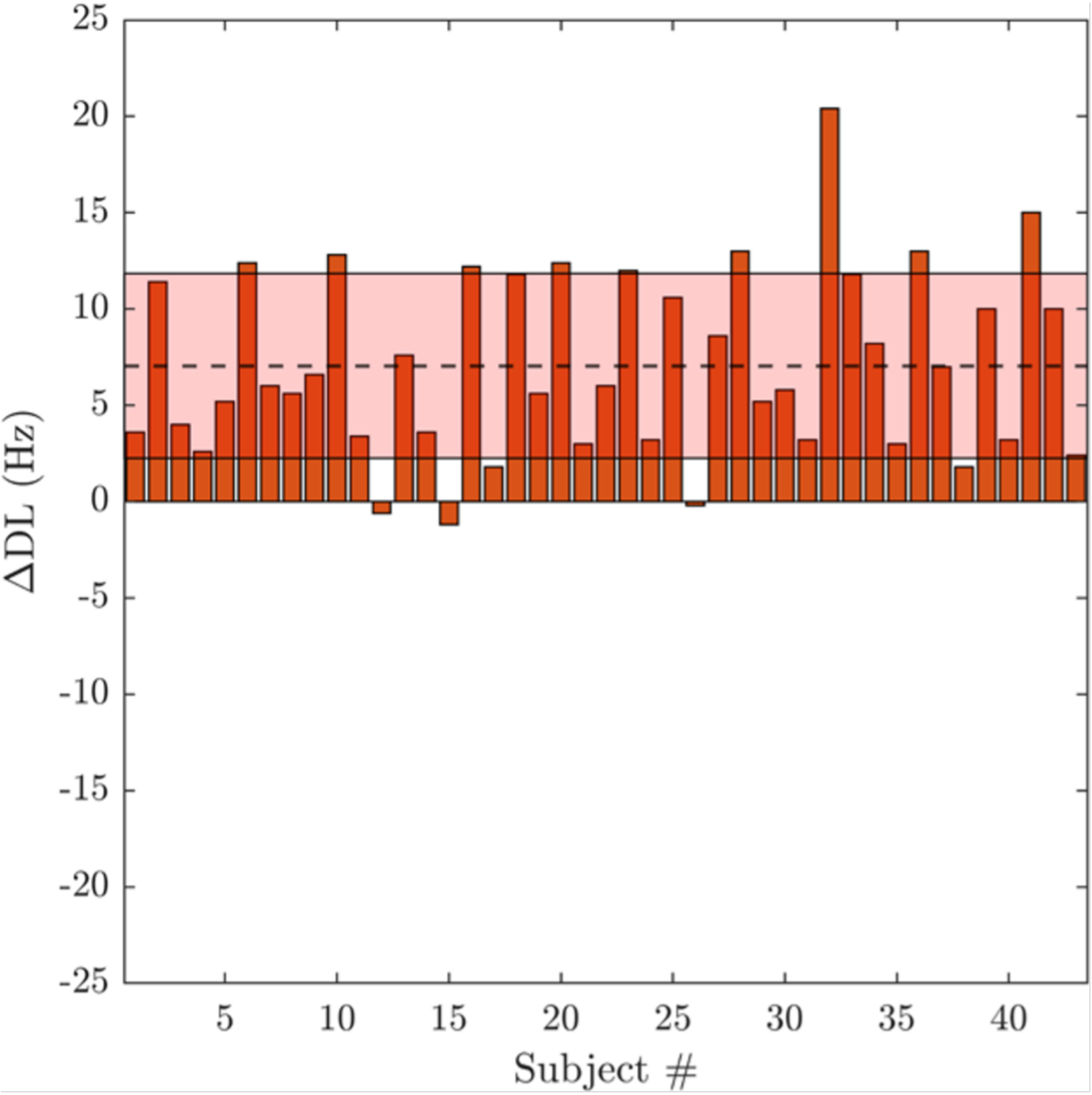

Figure 4. *Figure 4* DL (Hz) of FD Tasks vs. Subject. 43 subjects' data were included. DL was computed by subtracting the participants' periodic FD DL from that of the aperiodic FD. The average DL was 7.05 Hz (dashed lines), with a standard deviation of 4.80 Hz (outline of red box). The absolute DLs for aperiodic and periodic FD were 10.47 Hz and 3.43 Hz, respectively, with a standard deviation of 3.87 Hz and 2.45 Hz.

Aperiodic vs. Periodic	p-value
Amplitude Discrimination	0.06
Frequency Discrimination	2 x 10e-12

Table 1. *Paired, one-tailed t-test results for aperiodic vs. periodic instances of AD and FD.* The threshold value for statistical significance was set at 0.05.Statistically significant p-values at of 0.05.

Discussion

In this study, the goals were to 1) determine if the effects of aperiodicity of flutter stimuli are congruent for both amplitude and frequency discrimination and 2) attempt to validate the two theories – that of Mountcastle and that of Romo – to provide stronger support for one over the other. Subjects' digits II and III were stimulated with either aperiodic or periodic stimuli to determine their difference limen values for both amplitude and frequency discrimination. The acquired periodic difference limen values were subtracted from the aperiodic difference limen values () for both amplitude and frequency discrimination tests and plotted, as shown in Figures 3–4, respectively. The mean DL for amplitude discrimination (10.3742.89 m) and frequency discrimination (7.054.80 Hz) were both positive, suggesting that participants in both amplitude and frequency discrimination tests were better able to discriminate with periodic stimuli than with aperiodic stimuli. However, the large standard deviation of the amplitude discrimination DL, suggests that there may not have been much difference at all in discriminating amplitude, regardless of the periodicity of the given stimuli. The frequency discrimination test resulted in a smaller standard deviation, suggesting that the periodicity of the stimuli affected the frequency discrimination test more than the amplitude discrimination test. This makes sense since periodicity of the stimuli directly affects its frequency, not its amplitude.

If Mountcastle's theory that firing patterns of neurons reflect the periodicity of the stimulus was correct, there would be a significant difference in the difference limen for aperiodic versus periodic frequency discrimination tests. However, if Romo's theory –that the precise timing of action potentials within individual neurons is crucial for discriminating between different frequencies, regardless of whether the stimuli are periodic or aperiodic – was correct, the difference limen for either aperiodic or periodic frequency discrimination should have no significant difference. In Table 1, a paired, one-tailed t-test was performed comparing aperiodic and periodic stimuli DL for amplitude and frequency discrimination tests. With a statistical significance threshold at 0.05, frequency discrimination showed that its DL between aperiodic and periodic stimuli were significantly different (p = 2E-12), while amplitude discrimination did not show any significant difference (p = 0.06) in DL. This challenges Romo's theory, since periodicity of the stimuli had a significant impact on the participants' abilities to discern differing frequencies. These results support Mountcastle's theories and suggest that firing patterns of neurons do in fact reflect the periodicity of the stimulus by entrainment; hence, with aperiodic stimulus, the firing patterns also become aperiodic, rendering the brain unable to determine aperiodic frequency, but able to discern periodic frequency. Furthermore, the result of the t-test also supports the claim that periodicity of the stimuli impacts frequency discrimination more than amplitude discrimination.

While steps were taken to minimize error in this study, more studies must be done to yield far more accurate results. For instance, although the participants were given clear instructions during the experiment, it was impossible to control the environment and alertness of the participants as each participant took the experiment alone at their leisure. A randomized ordering of the trial conditions between participants – instead of a strict order of periodic AD, aperiodic AD, periodic FD, and aperiodic FD – may eliminate effects due to training and fatigue. The number of times the participants were allowed to redo the training task for a particular test was unlimited and uncontrolled for, which may have led to emotional frustration during the task that followed.

Conclusion

In this study, difference limen values of periodic and aperiodic frequency and amplitude discrimination tests were used to determine the consequences of stimulus periodicity. The results of this study suggested that while periodicity of a given stimuli affected frequency discrimination significantly, it had little to no effect on amplitude discrimination, directly aligning with our hypothesis. With a statistically significant difference between the difference limen values of aperiodic and periodic stimuli in frequency discrimination, we conclude that our results align with

Mountcastle's theory and challenges that of Romo's. More trials must be completed with better control of extraneous and confounding factors in the study to conclude with absolute certainty.

Acknowledgements

We acknowledge and thank Dr. Mark Tommerdahl for our discussions and experimental planning, as well as for providing The Brain Gauge, all of which proved vital to the completion of this study.

Contributions

A.M.C. and A.J.A. performed the experiments under the guidance of Dr. Mark Tommerdahl. A.M.C wrote the text. A.J.A. made the figures.

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