STOCHASTIC RESONANCE IN ELDERLY TACTILE SENSATION

by

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ABSTRACT

A common symptom of ageing is an increase in vibrotactile detection thresholds, especially in the feet. A hypothesized result of this increase is dysfunction in those aspects of gait that rely on footsole cutaneous input. One way of ameliorating elevated thresholds is by the use of stochastic resonance (SR), a non-linear phenomenon where the addition of noise to a sub-threshold signal renders the signal detectable.

The effect of SR on elderly vibrotactile thresholds was investigated using 3 studies. In the first study, detection thresholds for vibration sensitivity were assessed at 4 frequencies, at 55 locations on the footsole, and in young and old participants. Results showed that there were 3 regions of sensitivity on the footsole: the ball/medial arch, the lateral border of the foot and the heel, and the toes. The ordinal pattern of regional sensitivity was age and frequency invariant.

In the second study, the effectiveness of SR at lowering vibrotactile detection thresholds from the first study was investigated using a 2 Age x 2 Signal Level x 4 Frequency x 6 Noise Level protocol. Effects were quantified using a psychophysical measure, %Corr. At the 90% signal level, 33% noise optimized %Corr. At the 80% signal level, either 50% or 66% noise produced a maximum in the %Corr measure.

In the third study, the effectiveness of SR in lowering vibrotactile differential thresholds was investigated using a 2 Age x 2 SR Condition x 2 Frequency Range x 6 Signal Level design. Results showed that the elderly have higher differential thresholds than the young, however only at hypothesized FAII mediated frequencies. Noise was found to be effective in decreasing differential thresholds in both young and elderly at the hypothesized FAI mediated range, at sub-threshold and near-threshold signal levels. At the higher frequency range, noise was only

effective in decreasing differential thresholds in younger subjects.

It has been hypothesized that elevated detection and differential thresholds may be a factor in dysfunctional gait due to impoverished cutaneous reflex engagement. Together, the results of the three experiments suggest that SR may be useful as a rehabilitative aid for functions, such as gait and grasp, which rely on vibrotactile sensation.

TABLE OF CONTENTS

List of Tables

LIST OF FIGURES

CONTRIBUTION OF THE AUTHOR

This thesis contains 3 experiments that were performed and analyzed by the candidate, Cari Wells, under the direction of the supervisory committee. This committee consisted of J.T. Inglis, Associate Professor, School of Human Kinetics, UBC; R. Chua, Associate Professor, School of Human Kinetics, UBC; L.M. Ward, Professor, Department of Psychology, UBC; and J.J. Collins, Professor, Department of Biomedical Engineering, Boston University. The conduct, analysis and documentation of each experiment were primarily the work of the candidate.

The above statement was written by the candidate, and agreed upon by the undersigned:

J.T. Inglis, Ph.D.

PREFACE

This thesis consists of 3 separate experiments that look at different aspects of aging and its effects on vibrotaction in the footsole. The chapters devoted to each experiment are written in manuscript format with the intention that the data and results be published. Because of this format, there is some repetition in the contents of the 3 chapters describing the experiments, and the chapter detailing the background. The chapter in manuscript format for the first experiment (chapter 2), entitled "Regional variation and changes with ageing in vibrotactile sensitivity in the human footsole" has been submitted to the Journal of Neurophysiology (authors: C Wells, L.M. Ward, R. Chua and J.T. Inglis). The chapter for the second experiment (chapter 3), entitled "Tactile noise lowers vibration detection thresholds in elderly feet" has been submitted to the journal Psychological Sciences (authors: C Wells, L.M. Ward, R. Chua, J.J. Collins and J.T. Inglis). The chapter for the third study (chapter 4), entitled "Stochastic resonance aids in vibrotactile frequency discrimination in young and elderly participants" has been submitted to the journal Perception and Psychophysics (authors: C Wells, L.M. Ward, R. Chua, J.J. Collins and J.T. Inglis).

The final interpretation of the results (chapter 5: General Conclusions) was intended to integrate the results from the individual experiments and show how they contribute to the understanding of the effects of age on vibrotaction, and the possible role of SR in alleviating these effects.

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1 OVERVIEW AND BACKGROUND

1.1 INTRODUCTION

A common symptom of ageing is an increase in sensory thresholds, that is, an increase in the minimum amount of a sensory phenomenon for the phenomenon to be detected. In the sense of touch, increased tactile thresholds mean that elderly have impoverished vibrotactile acuity (Verrillo, 1979), decreased Von Frey hair sensitivity (Thornbury and Mistretta, 1981) and other touch related deficits (Olausson, Norsell, Gothner and Wallin, 1997). Typically, tactile sensation impoverishment worsens distally (Rothwell, 1986) so that the extremities, specifically the hands and feet, are most affected. One hypothesized result of this impoverishment is dysfunction with those aspects of grasp, and gait and balance, that rely on cutaneous input from the hands and feet respectively (Perry, McIlroy and Maki, 2000). This dysfunction may occur because cutaneous reflexes involved in grasp and gait and initiated by cutaneous sensation, are not adequately engaged due to elevated tactile thresholds.

One way of lowering elevated thresholds, and thus perhaps alleviating dysfunctional gait, is by the use of stochastic resonance (SR). SR is a non-linear phenomenon, where the addition of noise to a sub-threshold signal makes the signal detectable. SR has been proven effective in young, healthy individuals (Collins, Imhoff and Grigg, 1996; Collins, Imhoff and Grigg, 1997; Ivey, Apkarian and Chialvo, 1998), however it has not been demonstrated in an elderly population.

There were 3 goals of this investigation, implemented in 3 experiments. The first goal was to benchmark vibrotactile detection thresholds in the footsoles of the 2 experimental populations: young and elderly people. Using these thresholds, the second goal was to determine if SR could be used to decrease thresholds in both the young and older populations. Finally, building on the first 2 goals, the third goal was to determine if SR could decrease differential thresholds in the feet. It has been hypothesized that elevated detection and differential thresholds may be a factor in dysfunctional gait due to impoverished cutaneous reflex engagement. Achieving these goals would suggest that SR may be useful as a rehabilitative aid for functions like gait, that rely on vibrotactile sensation.

To achieve the first goal, psychophysical vibrotactile thresholds were assessed for 4 different frequencies at 55 locations on the footsole, and for both experimental populations. This was done to reveal the degree of tactile impoverishment in the elderly footsole, and to determine if the degree of impoverishment varied with stimulus frequency and the location of application of stimulus. Using the results of this experiment and the literature on the role of footsole cutaneous input in gait and age induced gait dysfunction; it was possible to hypothesize gait related functional reasons for regional variation in vibrotactile thresholds, as well as how and why this function might change with age.

The second experiment used threshold levels from the first experiment to generate sub-threshold signals, which were augmented with noise in an SR paradigm. This was done to test the effectiveness of SR in lowering detection thresholds of vibration stimuli. The results of these experiments revealed that psychophysical vibrotactile thresholds of both young and old subjects were lowered using SR, and that SR was effective for all the frequencies tested. This suggests that it may be possible to parlay the signal boosting effect of noise into sensory aids for people with elevated thresholds. Specifically, by lowering detection thresholds, SR may help to engage the cutaneous reflexes that are a component of gait, and thus may improve pathological gait in the elderly.

The third experiment used sub-threshold signal levels and optimal noise levels from the first 2 experiments to determine if noise could be used to decrease differential thresholds; that is, to improve the accuracy of subjects in differentiating 2 vibrotactile frequencies. It was shown that SR *could* improve differential thresholds at certain frequencies. This is an important result, since smaller differential thresholds may mean greater activation of cutaneous reflexes during gait.

This document is organized as follows. The rest of chapter 1 contains background information on each of the major topics contributing to the experiments: sense of touch and vibrotaction, SR, SR and touch, and gait. Chapters 2, 3 and 4 discuss experiments 1, 2 and 3 respectively. Finally, chapter 5 integrates the conclusions of the 3 experiments and suggests possible future directions.

1.2 Touch

1.2.1 Physiology of Vibration Sensation

There are 4 different types of mechanoreceptors in humans responsible for encoding sense of touch: Merkel's discs, Meissner's corpuscles, Ruffini endings and Pacinian corpuscles. The receptors and their locations within the dermis are depicted in Figure 1 (Kandel, Schwartz and Jessel, 1991). These receptors are classified into 2 functional groups according to the way the associated afferent nerves fire in response to constant stimuli. The slowly adapting (SA) afferent associated receptors are Merkel disks (SAI) and Ruffini endings (SAII). These receptors's nerves respond continuously to constant stimuli. The fast adapting (FA) type afferent associated receptors are the Meissner's corpuscles (FAI) and Pacinian corpuscles (FAII). These receptors fire at the onset and cessation of the stimulus only. For all 4 receptor types, the sensitivity of the receptor is a property of the nerve terminal membrane, while the dynamic response is determined by the electro-mechanical properties of the terminal.

1.2.2 Merkel's Disks (SAI)

Merkel's disks are located in clusters at the center of papillary ridges (see Figure 1). They are superficial receptors with small receptive fields (~2-3mm) and sense deformation in the papillary ridge in which they reside (Kandel et al., 1991). Merkel's disks are made up of small epithelial cells that surround the nerve terminal. The cell encloses a semi-rigid structure that transmits mechanical strain from the skin to the nerve ending, causing the nerve to fire. Because the structure is semi-rigid, it does not accommodate the stimulus, so a sustained, slowly adapting response is evoked. The strongest responses are evoked by punctate stimuli (Goodwin, Macefield and Bisley, 1997).

1.2.3 Ruffini Endings (SAII)

Ruffini endings are located in subcutaneous tissue, and link this tissue to folds in the skin in the nail beds and palms (see Figure 1). The receptive field is about 10mm in diameter. Stretch of the skin causes the receptor to stretch and fire. The Ruffini ending encodes skin stretch caused by pressure exerted on the skin (Edin and Johansson, 1995). The average firing rate of the nerve ending (action potentials/s) is proportional to the amount of skin stretch.

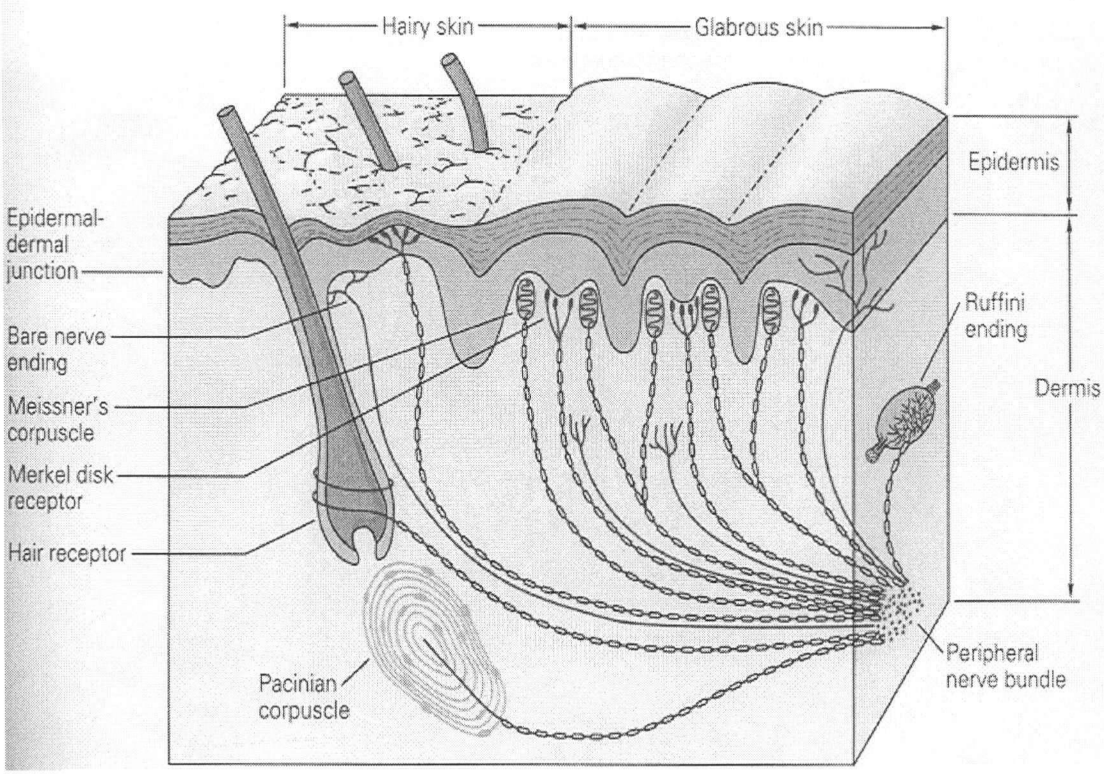


Figure 1: The 4 cutaneous mechanoreceptors. Reproduced from Kandel et al. (1991).

1.2.4 Meissner's Corpuscles (FAI)

Meissner's corpuscles are located at the edges of the papillary ridges (see Figure 1). The receptor is a globular structure filled with fluid and flattened epithelial cells. The nerve ending is entwined between the layers of cells. The receptor itself is mechanically coupled to the papillary ridge with thin strands of connective tissue, so that when the ridges deform, the receptor also deforms and causes the nerve to fire. The receptive field of the Meissner's corpuscle is 2-3mm. It is thought that the structure of Meissner's corpuscles lends itself well to encoding 2-point discrimination (Seeley, Stephens and Tate, 2000).

1.2.5 Pacinian Corpuscles (FAII)

The Pacinian corpuscle is located in the subcutaneous tissue. It consists of connective tissue lamellae that surround the nerve ending. The receptor responds to rapid indentation (vibration) but not to steady pressure, since the capsule deforms under pressure to accommodate the stimulus and the nerve stops firing. The capsule is flexibly attached to the skin so that it can sense vibration up to several centimeters away (receptive field>10cm).

While each type of mechanoreceptor preferentially encodes a different stimulus modality, all receptors are capable of encoding certain ranges of vibration. Ruffini endings (SAIIs) can encode vibration frequencies below 8 Hz; Merkel disks (SAIs) can encode 2-32Hz; Meissner's corpuscles (FAIs) can encode 8-64Hz; and Pacinian corpuscles (FAIIs) mediate frequencies from about 50Hz to about 600Hz (Johansson and Välbo, 1983).

In general, sensitivity to lower frequencies (up to ~50Hz) is mediated by Meissner's corpuscles (FAI afferents), while sensitivity to frequencies above 50Hz is mediated by Pacinian corpuscles (FAII afferents). Indentation thresholds of these 2 receptors as a function of vibration frequency are presented in Figure 2, reproduced from Kandel, et al. (1991). The 2 black parabolas indicate the detection thresholds of FAI and FAII afferents. The stippled line indications the breakpoint frequency, that is, the frequency where mediation of vibration switches from FAI afferents to FAII afferents (around 50Hz). The gray parabola shows detection thresholds across the range of human detection. This figure indicates that detection thresholds decrease with increasing frequency, with a minimum at approximately 250Hz. Above 250Hz, detection thresholds increase.

1.2.6 Ageing Touch

Bolton, Winkleman and Dyck (1966) have investigated the mechanoreceptor network associated with touch in human glabrous skin and related changes in the network to ageing. With increased age, there is a decrease in the total number of receptors. The remaining receptors are irregularly distributed, and their receptive fields vary in size and shape. In addition to receptor changes, the skin itself changes: the epidermis thins and there is a decrease in the amount of collagen and elastin in the skin (Kenshalo, 1977; Kenshalo 1978). Changes in skin mechanics would affect the transmission of vibration through the skin to the mechanoreceptors, resulting in changes to vibration sensation.

Verrillo (1979) investigated the effect of ageing on vibrotactile acuity in four groups of subjects with mean ages of 10, 21, 50 and 65 years. Results showed that all groups produced similarly shaped curves when the vibrotactile thresholds were plotted as a function of frequency (see Figure 3).

As the age group of the subjects increased however, there was a progressive loss of sensitivity in the high frequency (hypothesized FAII mediated) portion of the curve. Sensitivity in the low frequency (hypothesized FAI mediated) portion of the curve (i.e.: those frequencies whose detection thresholds that fell along the horizontal line at approximately 13μm) remained roughly constant, however higher and higher frequencies became mediated by FAI receptors.

It is clear that with age come increased detection thresholds for vibrotactile sensation. Thus, any role played by vibrotaction in gait would likely be impaired by increased thresholds. To determine the effect of age-induced impoverishment of vibration sensation on gait, it is first necessary to determine the role of vibration sensation in gait.

1.2.7 VIBRATION SENSITIVITY STUDIES

1.2.7.1 Footsole Detection Thresholds

To determine the mechanoreceptive properties of the soles of the human foot, Kekoni, Hämäläinen, Rautio and Tuveka (1989) measured vibrotactile thresholds as a function of frequency in 8 different locations on the footsole for 6 subjects. A probe connected to the moving coil of an electromagnetic vibrator (Bruel and Kjaer minishaker 4810) delivered vibratory bursts (300ms duration) of 20, 80 and 240Hz. The stimulus was delivered with a 1mm pre-indentation of the skin. To determine the thresholds, the method of limits was used with each frequency and at each site. The individual threshold values were calculated as a mean of the last 3 of 5 consecutive values.

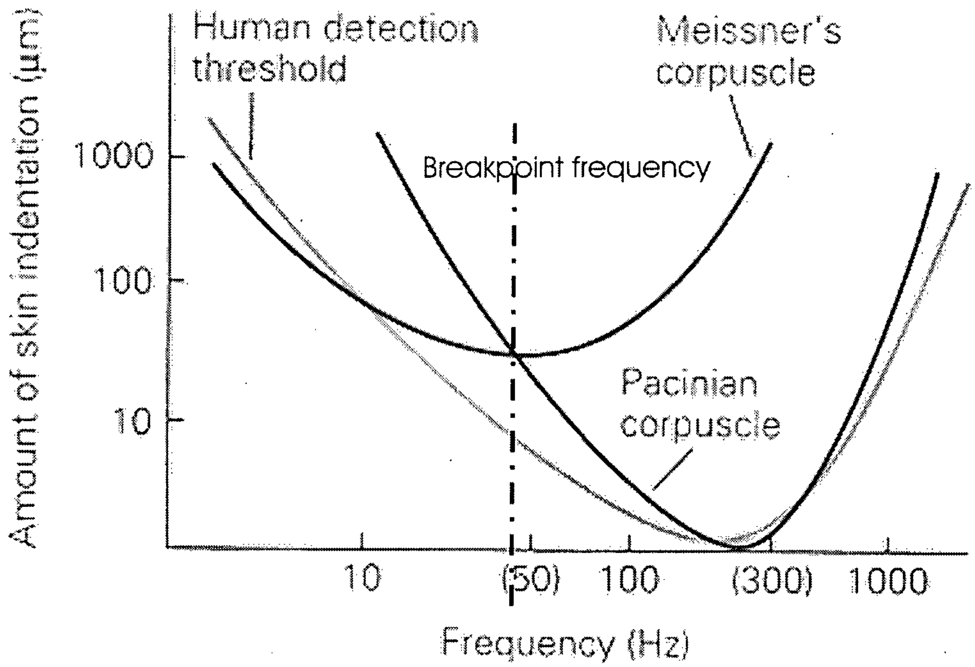


Figure 2: Vibration mediation and human vibrotactile thresholds as a function of frequency. The stippled line just below 50Hz entitled breakpoint frequency indicates the frequency at which mediation changes from Meissner's corpuscles to Pacinian corpuscles. Modified from Kandel et al. (1991).

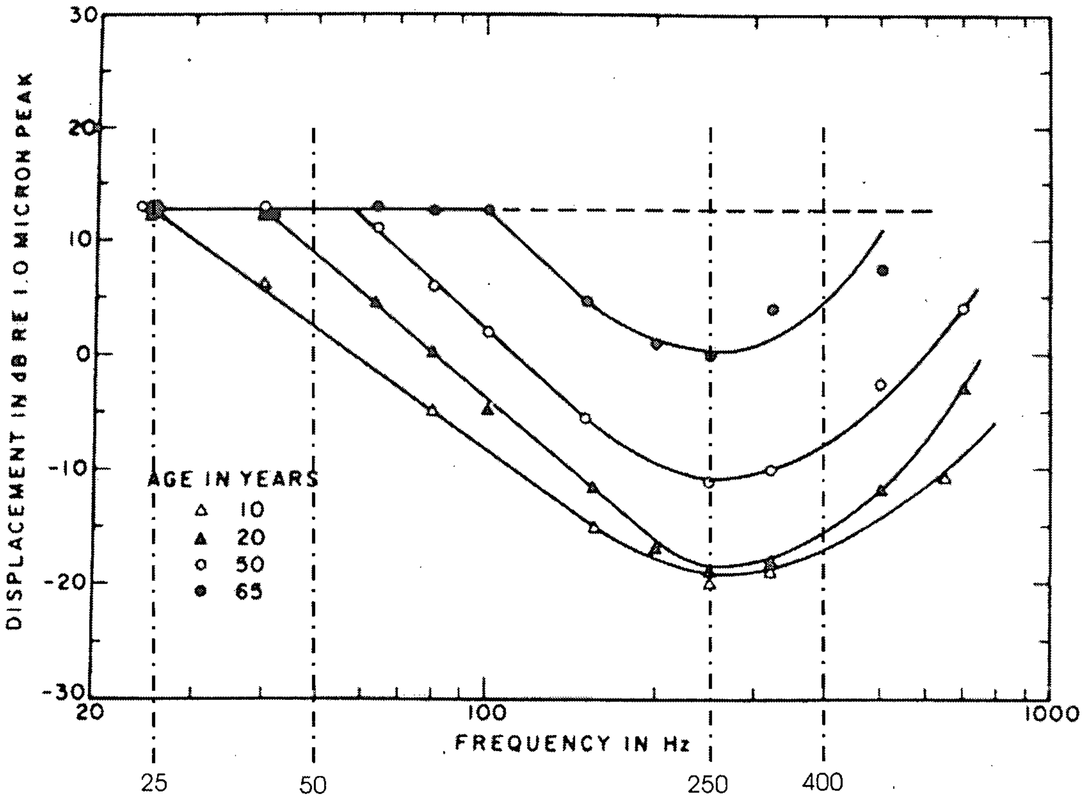


Figure 3: Changes in vibrotactile thresholds as a function of age. Each trace represents a different age group. The traces indicate that, with age, higher and higher frequencies become mediated by FAI receptors. The vertical distances between the traces indicate the differences in acuity between the age groups at a particular frequency. Stippled lines indicate the frequencies tested in the thesis experiments. Modified from Verrillo (1979).

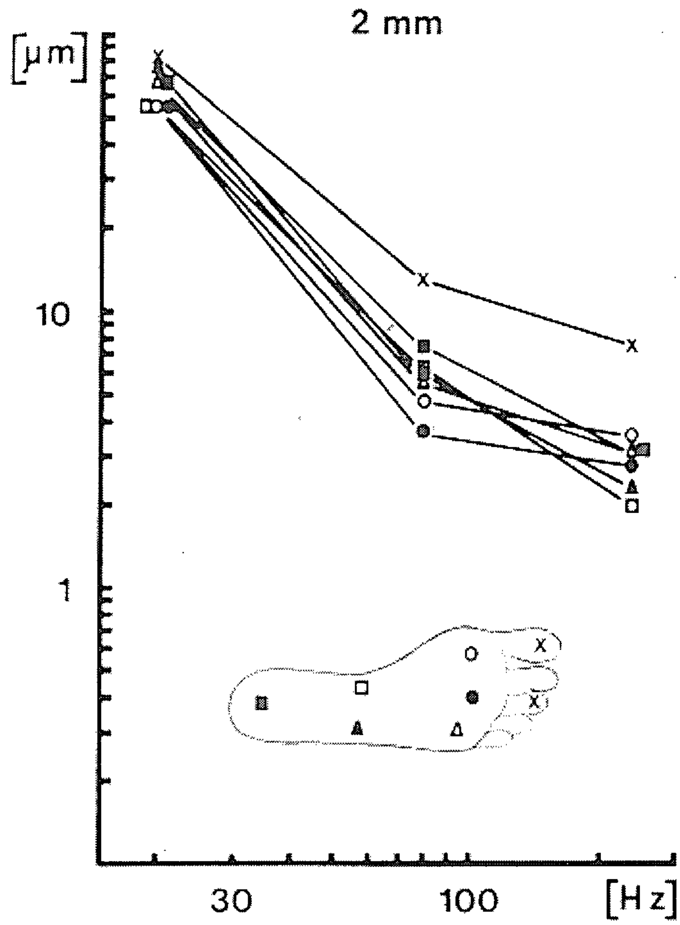


Figure 4: Vibrotactile sensitivity at 8 different locations on the foot, using a 2mm diameter probe. The markers on the drawing of the footsole indicate where the data from the above traces came from. Data from the great and third toes were pooled because no differences were observed. Reproduced from Kekoni et al. (1989).

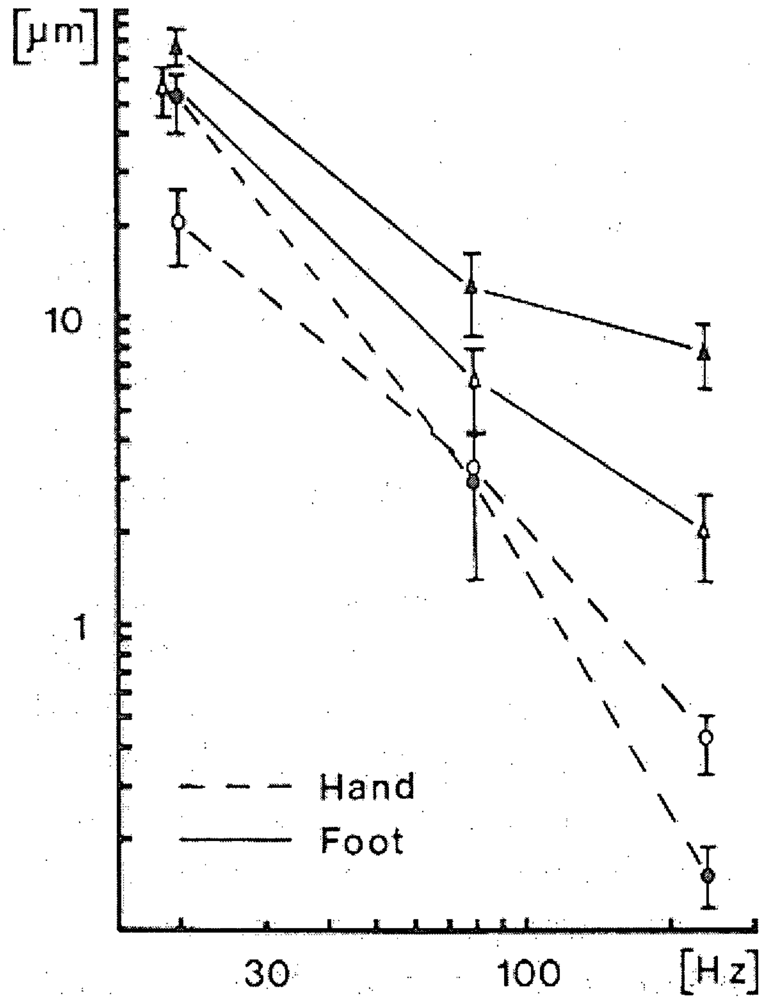


Figure 5: Difference in thresholds between hand and foot. The traces represent pooled data from 4 subjects. The 2 solid traces represent data from the inner mid-foot (open triangles) and the big toe (filled triangles). The 2 stippled traces represent data from the tip of the middle finger (open circles) and the thenar eminence (filled circles). Reproduced from Kekoni et al. (1989).

Figure 4, reproduced from Kekoni et al. (1989) plots threshold vs. frequency. The shape of the curves was the same for all subjects: for all frequencies, the highest thresholds were located at the toes and the heel. The variation in average threshold from one point to another was largest at the highest frequency (240Hz – an FAII mediated frequency (Verrillo, 1979)). At the lowest frequency (20Hz – an FAI mediated frequency (Verrillo, 1979)) threshold values were more uniform.

Figure 5, also from Kekoni et al. (1989), is a plot of threshold on the thenar eminence of the hand vs. the foot. At the higher vibration frequencies, the palm and fingertip are more sensitive than any of the locations on the foot; at 240 Hz vibration, the footsole thresholds are 10X those of the hand.

That the thresholds in the hands and feet were the same order of magnitude at low frequencies suggests that the mechanics of information transmission are similar in both locations. The low sensitivity of the foot for high frequency vibration may be due to less dense enervation of FAII afferents, but more likely is due to the thick skin of the footsole impeding the transmission of low amplitude, high frequency vibration. This would produce higher thresholds (Perry et al., 2000).

1.2.7.2 Differential Thresholds

While detection thresholds are usually expressed in terms of the minimum amplitude of indentation that can be detected, differential frequency thresholds are expressed in terms of the minimum difference in frequency of vibration that can be detected. Several researchers have investigated differential threshold in humans and monkeys. In psychophysical studies in humans, the ability to discriminate vibrotactile stimuli of different frequencies is typically quantified using one of 2 measures: the differential threshold, or the Weber fraction. The differential threshold is the difference in 2 frequencies required before identification of the higher or lower one can be made at some particular accuracy level, usually 75%. The Weber fraction is the differential threshold divided by the frequency at which the differential threshold is measured. Both measures are indications of the differential sensitivity of a sensory system; however they are generally only reliable in the mid ranges of operation of the system.

In a study by Goff (1967), "upward differential thresholds" in humans were determined at 20dB and 35dB above threshold; that is, the differential threshold for a standard frequency, and a comparison frequency which was always higher. The upward differential thresholds were found to increase with increasing frequency. Weber fractions for vibrotactile stimuli at a level 20dB above the detection threshold ranged from about 0.32 at 25Hz, to 0.55 at 200Hz. Weber fractions were lower for the 35dB intensity level.

Mountcastle, Talbot, Sakata and Hyvärinen (1969) used a confidence-rating scheme in conjunction with signal detection theory to determine frequency discrimination. The researchers found that frequency discrimination on the finger was poor at intensities close to detection threshold, but improved asymptotically with increasing amplitude to 10dB. At 20dB, the Weber fraction was about 0.11 and did not change as a function of frequency over the range of 5-200Hz. These results were replicated by Mountcastle, Steinmetz and Romo (1990).

Rothenberg, Verrillo, Zahorian, Brachman and Bolanowski Jr. (1977) looked at differential thresholds and Weber fractions for 40Hz vibrations on the thenar eminence, the fingertip and the forearm. They determined Weber fractions of between 0.1 and 0.3, suggesting that different areas of the body have different acuities for vibrotactile discrimination.

1.3 STOCHASTIC RESONANCE

Animal sensory systems, made up of sensory receptors and neurons, are biological signal detection systems. These systems transform environmental events, like compression waves in the air, into sensory events, like hearing a tone. In addition to environmental signals, sensory systems must take into account the presence of background "noise". This noise is ongoing, spontaneous activity that is uncorrelated with the target signal. Noise is normally considered detrimental to signal detection, like hearing a conversation. Recent research, however, shows that sometimes noise actually *aids* in the detection of weak signals SR (Gammaitoni, Hänggi, Jung and Marchesoni, 1998).

How does SR work? Simply put, every signal detection system is made up of four fundamental components. First, the detection threshold, which is the minimum amount of signal needed to signify an event; second, the input to the detection system, which is the event in the environment to be detected; third, the record of the detection, or the output of the system; and finally noise. These 4 components, and the SR phenomenon at the neuronal level are illustrated in Figure 6.

All panels show a detection threshold (1), an input signal (2), the output of the system, (activity of the nerve) (3), and noise (4). In a sensory neuron, the detection threshold is the amplitude of a signal above which there is enough power in the wave to generate impulses in the associated nerve (3). Below this level, there is not enough power, no nerve activity results, and no sensation is felt. These components, and the effect of different levels of noise on a sub-threshold signal, are illustrated in Figure 6. In panel A, the signal is sub-threshold and does not produce any output. In panel B, a small amount of noise is added to the signal, so that it exceeds threshold only when high and produces output correspondingly. In panel C, excessive noise is added to the signal, and the output reflects the noise rather than the phase of the signal. An optimal amount of noise, such as that shown in panel B makes the sub-threshold signal detectable without swamping the signal.

In order to determine what this optimal amount of noise is, a measure is needed that quantifies the effect of noise on the sensory system's ability to detect signals. This effect can be quantified in many ways: signal-to-noise ratio (the ratio of the amplitude off the signal to the amplitude of the noise – abbreviated SNR) (Douglass, Wilkens, Pantazelou and Moss, 1993; Levin and Miller, 1996), Fisher information (the expectation of the second derivative of the log likelihood (Greenwood, Ward, Russel, Neiman and Moss, 2000; Stemmler, 1996), % correct measure (the ratio of correct trials of a task to the total number of trials – abbreviated %Corr) (Collins et al., 1996; Collins et al., 1997; Richardson, Imhoff, Grigg and Collins, 1998) and the cross-correlation coefficient (the normalized power norm -- abbreviated C1) (Collins, Chow and Imhoff, 1995; Collins, Chow, Capela and Imhoff, 1996; Collins, Imhoff and Grigg 1996) .

For all of these measures, the higher the value of the measure, the greater the ability of the system to detect a signal. No matter which measure is used however, SR has a characteristic effect on the value of the measure: with increasing noise, the measure increases quickly to a maximum value, and then slowly declines. This is illustrated by Figure 7. The maximum value of the measure is produced by the optimal amount of noise for the system.

The purpose of the information measures is to relate the output of the sensory system to the signal input, quantifying the effects of different levels of noise on the output of the sensory system. In the psychophysical protocols of experiments 2 and 3, the output of the sensory system, that is, the participant's response, will be related to the signal input using the %Corr measure.

1.3.1 Using %Corr to assess SR

Collins et al. (1997) and Richardson et al. (1998) have used %Corr to measure the effects of noise in psychophysical studies (see Equation 1). These studies used a one-interval forced choice (1IFC) protocol: participants were presented with a single stimulus that contained either noise only, or noise plus signal, and subjects were asked to identify whether or not the stimulus contained a signal.

$$\%Corr = \frac{N_{Correct}}{N_{TotalTrials}} \qquad \text{Equation 1}$$

where $I_{ncorrect}$ is number of correctly identified trials and $N_{TotalTrials}$ is the total number of trials.

There are several aspects of these experiments that could be refined to better determine the exact mechanism of SR. First, in the 1IFC paradigm, the noise only stimuli and the noise *plus* signal stimuli contained unequal amounts of energy. Thus, it is possible that participants were able to detect the greater energy of the later stimulus, rather than being better able to detect the signal itself. This produces an SR effect; however it is not possible to ascertain whether participants, while detecting the greater energy introduced by the signal and therefore its presence, are better able to detect any information contained in the signal.

Second, the %Corr measure in a 1IFC protocol is not free of criterion effects (Swets, 1996). In the 1IFC paradigm where participants are asked to choose whether or not a signal was

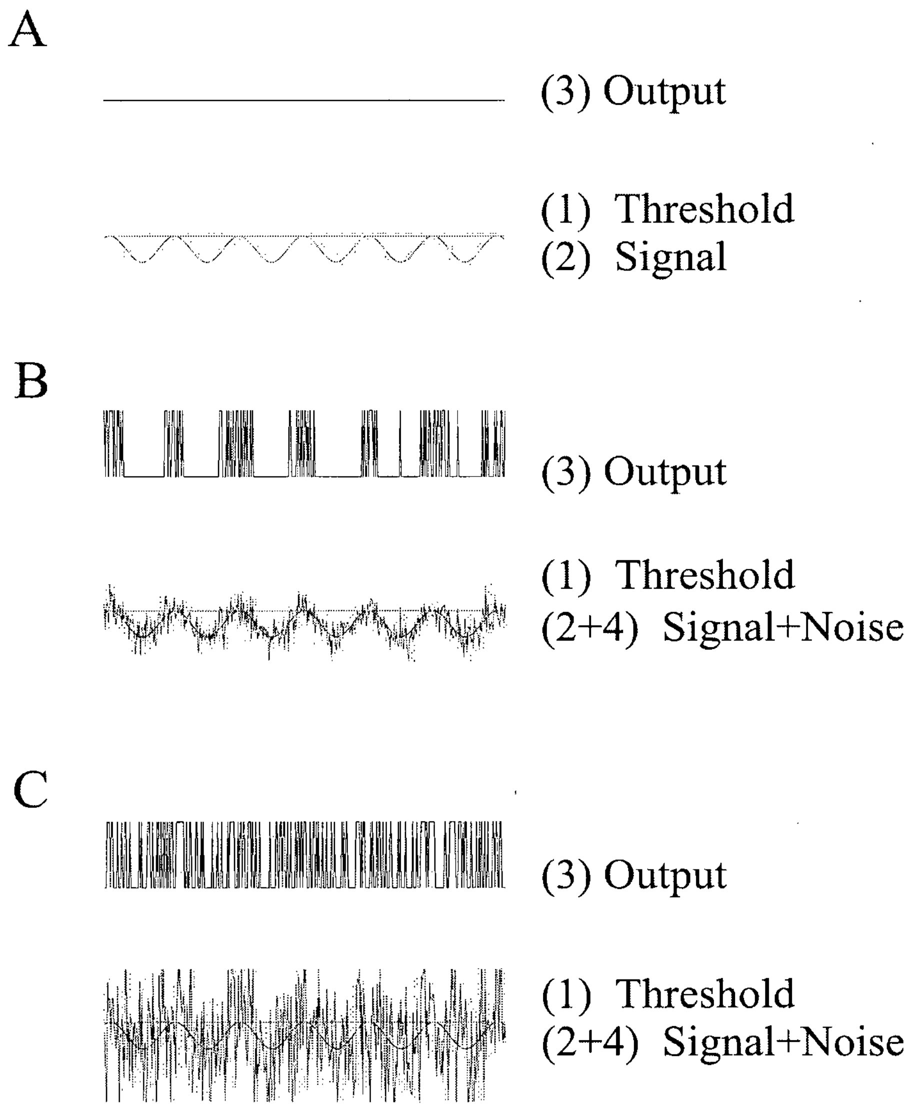


Figure 6: The SR phenomenon at the neuronal level. Panel A) shows a sub—threshold signal with no added noise. There is no activity in the neuron. Panel B) shows a sub-threshold signal with a bit of noise. The neuron fires, but only when the signal is closest to threshold. Panel C) shows a sub-threshold signal with excessive noise. The neuron fires regardless of the phase of the signal.

present, their answer was affected by where they set their decision criterion. If the criterion is set non-optimally, then any SR effect shown would be an effect of SR on the criterion, rather than the physical threshold. In a study designed to determine the effects of noise on threshold, it is critical that the threshold not be confounded by the participant's bias.

While energy and criterion affect the information measure used to quantify the SR, so too can the "color" of noise used (Nozaki, Mar, Grigg and Collins, 1999). Typically, the noise used in SR experiments is "white", that is, noise containing all frequencies, with each frequency having equal power. This produces a sharp, high peak in the information measure, however the range of noise values (i.e.: the range of standard deviations) which produce improvements is small. By using "pink" noise (the power at each frequency is determined by 1/frequency), one can increase the range of noise values at which SR is produced, however the peak in the information function is lower, thus there is a trade-off between the benefit produced by the added noise, and the range of useable noise values.

1.4 SR and Touch

The SR phenomenon in the sense of touch has been investigated using animal models at a physiological level, and using human participants in psychophysical investigations. Both types of investigations are valuable, because they allow for the determination of the SR mechanism at the level of the neuron, and at a higher, functional level. While animal research is not directly relevant to the current investigations, it is included here for completeness.

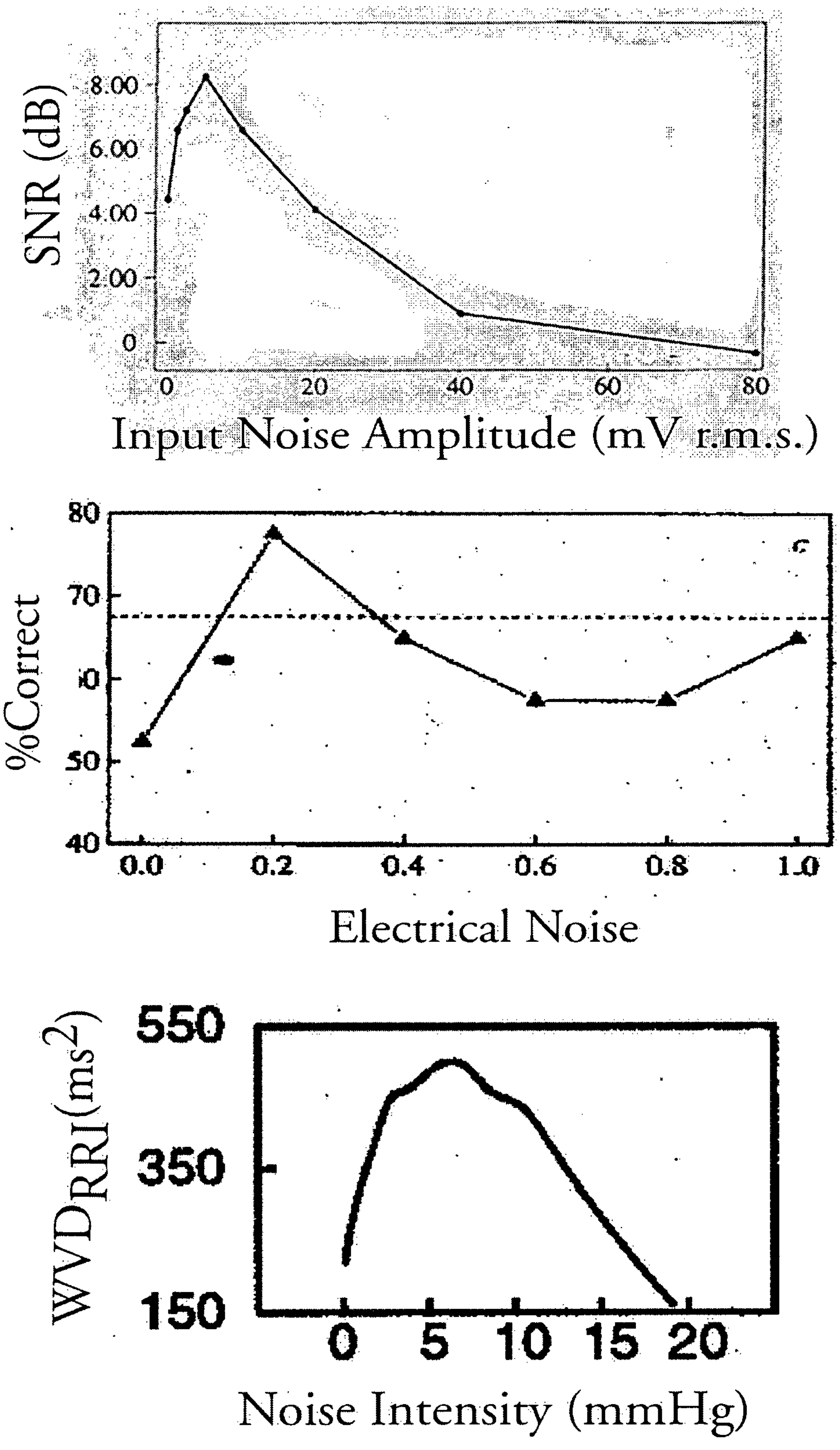


Figure 7: The signature of SR. Top panel: SNR (Levin and Miller 1996). Middle panel: %Corr (Richardson et al., 1998) and Bottom panel: cardiac inter-beat intervals (Hidaka, Nozaki and Yamamoto, 2000).

1.4.1 ANIMAL MODELS

One popular method of quantifying the body's physical response to touch is by the use of a tuning curve. A tuning curve is a measure of a receptor's responsiveness across a range of stimulus values. For example, a frequency-response tuning curve is a measurement of an individual receptor's responses to stimuli at different frequencies.

Traditionally, tuning curves only illustrate supra-threshold behaviour because, by definition, tuning curves quantify responses and thus require supra-threshold stimuli. When stimuli are sub-threshold or too weak to generate firing in a receptor, tuning characteristics have not been available. Ivey et al. (1998) combined sub-threshold signals and noise, and compared the resulting tuning curves with those generated using traditional, supra-threshold stimuli. In order to generate the tuning curves, fibers from the tibial nerve of the rat were isolated and neuron activity from single mechanoreceptor afferents was recorded using monopolar hook electrodes. The receptive field associated with each afferent was on the glabrous skin of the foot and was stimulated mechanically with waveforms comprised of various frequency sine waves plus increasing levels of white noise. Responses were recorded from RA and SA receptors. In addition to plotting tuning curves for afferents, C1 (Collins et al., 1996), was calculated for each signal and noise level. The addition of optimal levels of noise produced the SR signature in both RA and SA fibers. Furthermore, optimal noise caused an expansion of the frequencies to which the RA receptors responded, and lowered the thresholds of SA fibers.

The SR induced activity of peripheral neurons is correlated with the activity of neuronal ensembles at the spinal and cortical levels. This phenomenon has been shown by Manjarrez, Rojas-Piloni, Mendez, Martinez, Velez, Vazquez and Flores (2002). Simultaneous recordings of spinal and cortical evoked potentials were made in anaesthetized cats who's hind paws were stimulated at frequencies between 0 and 30Hz. The researchers found that all animals showed distinct, internal SR behaviour, with a mean coherence between the signal and the internal neuronal activity of 0.43. This suggests that SR is not just a peripheral artifact, but may be a mechanism by which the CNS detects weak signals.

Collins et al (1996) used a similar protocol to that of Ivey et al. (1998) in their investigation of aperiodic stochastic resonance (ASR), that is, SR where the stimulus is not a periodic signal like a vibration. This work built on their previous theoretical work showing that ASR was effective in model neurons (Collins et al., 1995).

In this experiment by Collins et al. (1996), 12 rat SAI afferents from the medial aspect of the thigh were isolated and the afferents and associated skin were excised. The skin over the mechanoreceptor was stimulated with a 60 second aperiodic signal produced by an indenter arm attached to the shaft of a DC motor. The amplitude of the signal was near threshold for the individual neuron (<10 action potentials per 60s). Noise in the form of random vibration of the indenter arm was superimposed on the signal. While the underlying signal was the same for each trial, the superimposed noise was not: different levels of noise were added to the signal in random order.

When the correlation coefficient C1 was calculated for each neuron, 11 of the 12 neurons tested showed the SR signature: as input noise variance increased, the coherence of the neuron spiking with the input increased rapidly to a peak, and then declined slowly. This experiment was important because it demonstrated that SR could be used to improve detection of ecological, aperiodic inputs in a biological setting.

1.4.2 Human Experimentation

Ivey et al. (1998) used a psychophysical protocol in a preliminary investigation of SR in the sense of touch in humans. Three human subjects were presented with a two-interval-forced-choice (2IFC) paradigm and asked to determine which of 2 time epochs contained (1) vibrotactile noise alone or (2) the same noise plus a small sine wave of a given frequency, either 3 or 30 Hz. The amplitude of the sine wave was adjusted during successive trials; the stimulus was applied to the fingertip.

For the 3Hz stimulation, there was a non-zero amplitude noise region in which thresholds for discrimination of the sine wave were lower than with no noise, a clear indication of SR. For the 30Hz trials, no such region was found. The authors stated, however, that although the noise amplitudes tested were not effective in producing SR for the 30 Hz signal, other amplitudes might have been. This suggested that noise enhancement of sense of touch is possible at low frequencies.

Like Ivey et al. (1998), Collins et al. (1997) tested SR in the fingertip, however the stimulus used was a rectangular ramp pulse. In the Collins et al. protocol, either noise alone or sub-threshold vibrotactile signal *plus* noise, were presented on the glabrous skin of the fingerpad of each participant's right middle finger. Stimuli were presented one at a time at 5-second intervals, and the subjects were required to say whether or not they detected a stimulus. The stimuli were low pass filtered (cut-off frequency: 30Hz) in order not to excite FA receptors. Each trial run consisted of 20 presentations, 10 signal *plus* noise and 10 noise only. The sequence of the presentations randomized. The percentage of trials for which the participants correctly identified the signal as present was quantified using the %Corr measure. According to this measure, 9 of the 10 participants exhibited SR behaviour: as input noise amplitude increased, the %Corr measure also increased to a maximum value. As noise variance increased further, the %Corr decreased, sometimes to a value lower than the no-noise case (a phenomenon called noise masking).

Liu, Lipsitz, Montero-Odasso, Bean, Kerrigan and Collins (2002) used a similar 1IFC protocol to test the effectiveness of vibrotactile SR on older adults, patients with stoke and patients with diabetic neuropathy, all conditions which elevate vibrotactile thresholds. The older participants were tested on the middle digit of their right hand, while the stroke patients were tested on the middle digit of their affected hand. Diabetic neuropathy patients were tested on the middle digit of their right hand, and on the first metatarsal head of the left foot. Liu et al. found that the vibrotaction detection threshold was decreased by the use of SR in 9 out of the 12 older participants, in 4 out of the 5 participants with stroke, and for all 8 participants with diabetic neuropathy on both the finger and foot. This work suggests that SR may be useful in lowering thresholds in the elderly, and those with elevated threshold due to illness.

Richardson et al. (1998) used the same protocol as Collins et al. (1997) on 11 subjects; however instead of using vibrotactile noise to augment the signal, they used electrical noise applied through the probe. In this investigation, the %Corr measure of 9 of 11 subjects exhibited SR behaviour. Since the electrical noise increased the ability of participants to detect a sub-threshold mechanical stimulus, this showed that cross-modality SR is possible.

These results using cross-modality noise were extended to the elderly (Dhruv, Niemi, Harry, Lipsitz and Collins, 2002). The researchers tested the ability of participants to detect Semmes-Weinstein monofilaments (fine touch sensitivity) on the first metatarsal phalangeal joint, with and without the addition of electrical noise. The addition of noise lowered the monofilament threshold in 5 of the 9 subjects tested. These results may be important if and when a practical SR aid is developed because an electrical implementation of noise would likely be easier than a mechanical implementation.

The SR induced activity of peripheral neurons is correlated with the activity of neuronal ensembles at the cortical level in humans. Manjarrez, Diez-Martinez, Mendez and Flores (2002) demonstrated the occurrence of SR in electroencephalographic (EEG) activity in humans, elicited via vibration delivered to the finger at 2.5Hz. The results of the experiment showed that EEG responses evoked by the vibration in the region overlying the somatosensory cortex were optimized by the addition of particular levels of noise. Further, all subjects showed this SR phenomenon.

All of the above studies showed that SR can lower tactile thresholds in the hands of humans, suggesting that SR may be of use in lowering vibrotactile thresholds in the footsole. The result may be improved gait performance in those aspects of gait that have been affected by elevated thresholds.

1.5 GAIT

1.5.1 THE ROLE OF CUTANEOUS INPUT FROM THE FOOTSOLES IN GAIT

The importance of cutaneous input from the footsole to properly functioning gait has been demonstrated experimentally by looking at dysfunctional gait caused by cutaneous deficits in 2 different populations. The first population consists of subjects with naturally occurring cutaneous deficits like the elderly (Verrillo, 1979), those with diabetes and post-operative surgery patients (Hämäläinen, Kekoni, Rautio, Matikainen and Juntunen (1992). The second population consists of healthy subjects for whom cutaneous input from the footsoles has been temporarily diminished or ablated using techniques like anesthesia, hypothermic anesthesia (Perry et al., 2000), or ischemia (Diener, Dichgans, Guschlbauer and Mau, 1984). Comparisons of the results of experiments have lead to speculation that these 2 populations have gait pathologies due to their decreased cutaneous sensation in the footsoles. SR may alleviate these pathologies by improving cutaneous sensation.

While some of the frequencies thought to play a possible role in gait in these studies being presented are outside the range of frequencies investigated in our experiment, these frequencies are likely important in standing balance, a possible application of SR. Thus, the studies investigating these frequencies are included here for completeness.

1.5.2 DECREASED SENSATION CONTRIBUTES TO DYSFUNCTION IN GAIT

To study the influence of cutaneous footsole input on compensatory stepping, Perry et al. (2000) used hypothermic anesthesia to minimize cutaneous footsole information. Prior to the start of the protocol, subjects had their feet cooled in ice water for 15 minutes. This resulted in a 10° decrease in skin temperature and an increase in vibration detection threshold at 2 frequencies: 100Hz and 3Hz. Subjects were then required to stand on a moveable platform, and postural perturbations were induced via 3 levels of unpredictable platform accelerations in 4 directions (forwards, backwards, and both lateral directions). Six subjects wore blindfolds during testing, 4 did not.

As a result of cooling the feet, the investigators found a 68% increase in the 100Hz vibration threshold at a metatarsal site (to 6.9+/-4.0μm from 4.1+/-1.1μm, p=.036) with a similar though not significant trend for 3Hz at the heel. The investigators found 3 significant direction dependent effects of cooling on recovery stepping. First, during backwards stepping, the center of mass (the location of the center of mass of the subject, projected onto the floor – abbreviated CoM) approached the posterior limit of the base of support (the transverse area of the body projected onto the floor – abbreviated BoS) at foot-off more closely than during control conditions. This was associated with a delay in foot-off that initiated the backwards recovery step. Second, during forward stepping, there was an increase in the frequency of multiple step recoveries and an increased rate in loading subsequent to heel contact of the recovery steps. Finally, during lateral stepping, there was a change from the usual crossover step recovery to a sideways shuffle.

The main effect on backward stepping supports the hypothesis that one role of the plantar cutaneous mechanoreceptors is to sense the relationship between the CoM and the BoS. The larger excursion of the CoM within the BoS than in control trials might have been caused by the trend for higher thresholds at 3Hz in the heel. SAI afferents, those afferents possibly responsible for encoding change in pressure and postural regulation due to movements below 5Hz, and FAI or FAII afferents were presumably affected by the cooling. It was postulated that the absence of similar effects in the forward and lateral directions might be due to joint proprioception in the toes not having been affected by cooling.

The main effect of multiple step recoveries on forward stepping supports the hypothesis that plantar cutaneous mechanoreceptors contribute to the detection of foot contact and control of subsequent weight transfer. Since there was no difference in cooled vs. uncooled conditions with respect to automatic postural responses (APR), step distance, or timing of CoM motion during multiple step recoveries, the investigators concluded that instability arose subsequent to foot contact, not before. This was supported by the fact that the increased rate of loading occurred subsequent to foot contact during cooled trials, implying an inability of the subjects to control foot landing. The authors hypothesized that FAIs and FAIIs were affected by cooling (increased vibration threshold), causing problems encoding transient events such as foot off and foot contact.

The main effect of a sideways shuffle in lateral stepping supported the hypothesis that cutaneous mechanoreceptors contribute to stability during the single limb stance phase of gait (i.e.: when one foot is in contact with the ground and the other is not). The cooling resulted in a 2-fold reduction in the time of single limb support. Most likely the hypothermic anesthesia affected SAI afferents that sense borders or discontinuities in pressures or patterns (Kandel et al., 1991). It has been hypothesized that this induced dysfunction is a result of a skin effect only, because muscle afferent nerves, being larger, are less influenced by cooling (Wu and Chiang, 1997).

In a study by Santos Perry, Menzildzic and Patla (1999) on the roles of vision and cutaneous input to gait termination, six subjects had their feet chilled to induce hypothermic anesthesia. The degree of anesthesia was assessed using von Frey hairs, and maintained at 2 times the room temperature threshold. Subjects were required to walk down an 8m walkway. During random trials, participants were signaled via an audio tone to stop abruptly. Vision was occluded on half the trials. The dependent variables of interest were the times of onset of gait termination and gait termination completion. As a result of the experimental conditions, the onset of gait termination was delayed by 31ms in the non-vision condition. This suggested that visual and cutaneous information play specific roles in gait termination: while vision is involved in the initial slowing down of the CoM in its forward progression, the mechanoreceptors in the foot provide feed forward information about CoM movement during single stance support. This cutaneous information could be encoded by SAI afferents that mediate pressure information.

Using the same protocol, Perry, Santos, Menzildzic and Patla (1999) investigated the effects of reduced cutaneous sensation in one of the mechanisms used to terminate gait: the increased breaking force in the first step after being signaled to stop. The investigators found a trend for increased loading rate following the initial contact of the first step of the hypothermic trials (un-cooled trials: 11.9kN/s, cooled trials: 12.7 kN/s; p=.092). This indicated that the CoM had *not* been slowed down prior to initial foot-contact. There are 2 possible explanations for this. First, the hypothermic anesthesia diminished the sensitivity of the SAI receptors, so information about the CoM movement was not available to the nervous system. Second, the FAII receptors that encode information about transient events like initial foot contact were disabled by the hypothermic anesthesia, thus information about braking force (or lack thereof) at foot contact was not available to the nervous system.

Magnusson, Enbom, Johansson and Pyykko (1990) also used hypothermic anesthesia to investigate the significance of pressor input from the feet in postural control. Body sway was investigated, in which sway was induced by vibrators strapped to the belly of the gastrocnemius muscle (vibration amplitude: 0.4mm, vibration frequency: 20, 40, 60, 80 and 100Hz). In addition to vibration frequency, 2 other factors were manipulated: there were vision and no vision trials, and hypothermic and un-cooled trials. The effects of the manipulations of the center of pressure (CoP) were recorded using a force plate. Magnusson et al. (1990) found that hypothermia caused greater body sway in terms of both excursion and velocity. While velocity of sway was greater with eyes closed, both vision conditions showed the effect. The researchers concluded that SAI receptors were incapacitated by cooling.

Supporting the hypothesis that decreased sensory input from the footsole causes impaired balance and gait in the elderly, Murray, Kroy, Ross and Clarkson (1969) noted that walking in the elderly does not resemble that of someone with a nervous system pathology. Rather, it resembles the guarded gait of someone who has a reduced ability to use sensory information.

1.5.3 IMPROVED SENSATION ALLEVIATES DYSFUNCTIONAL GAIT

It has been shown that impoverishment of tactile sensation on the footsole produces gait dysfunction. This body of research is complemented by other investigations showing that *increased* plantar sensation awareness can improve gait dysfunction.

Maki, Perry, Norrie and McIlroy (1999) tried to increase awareness of the CoM relative to the base of support BoS in elderly subjects since this is thought to be a critical variable controlled by the nervous system in maintaining upright stance (Dietz, Golhofer, Klieber and Trippel, 1992). Awareness of the foot surface boundaries, and hence the BoS, was facilitated by outlining the border of the foot sole of subjects with 3mm diameter plastic tubing. The protocol was performed on 7 young subjects (26-31 years) and 14 older subjects (65-73 years) who had partial sensory loss. The sensory loss was quantified by the 100Hz vibration threshold at the 5^{th} metatarsal head (young: 2.5+/-2.5μm, older: 9 to 86μm, median 24μm) and at the heel (young: 7.5+/-9μm, older: 10 to 100μm, median 39μm). The researchers examined the reactions of subjects to continuous pseudo-random platform displacements with their feet in place, and to unpredictable postural perturbations evoked by sudden translation of the platform in one of four directions (anterior, posterior and both lateral directions). Experiment conditions were vision/no vision and facilitated plantar sensation/normal sensation.

Maki et al. (1999) found that the facilitation improved the efficiency of 3 aspects of postural reactions. First, there was a reduced frequency of extra steps needed to recover from the unpredictable postural displacements. This may have been because the tubing facilitated awareness of the CoM with respect to the BoS via the SAI receptors, so that the nervous system was better able to slow down the forward progression of the CoM (Perry et al., 2000). In addition, the tubing may have facilitated the ability of the FAII afferents to encode information about loading rates at foot contact, so that braking force could be increased to slow down the CoM faster (Perry et al.). Maki et al. suggested that the facilitation might provide older adults with more control over compensatory stepping.

Second, the subjects had improved postural control during "feet-in-place" reactions: the younger subjects used a stepping strategy to recover on few trials, and both young and older subjects showed less excursion of the CoP towards the limits of the BoS. Similar to the extra steps recovery experiment, the facilitation helped the SAI receptors better encode information about the limits of the BoS, and thus provided the nervous system with a more accurate representation about the CoM location relative to the BoS.

Finally, there was a reduced rate of loading after foot contact in the facilitated trials. The investigators suggested that the tubing improved the subjects's ability to sense and control foot contact via facilitation of the FAIIs, and sense and control weight transfer, via facilitation of the SAIs (Perry et al., 1999; Santos et al., 1999).

Because the tubing was effective at improving dysfunctional gait, it may be that SR is also effective, by improving cutaneous sensation via lowered thresholds. The possible effectiveness of SR at improving cutaneous sensation on the footsole was investigated using 3 experiments. The goal of the first experiment was to determine vibrotactile detection thresholds on the footsole. These thresholds were used to establish whether there was in fact acuity loss in the elderly, and which levels of signal would be used to try and demonstrate SR in experiments 2 and 3.

2 EXPERIMENT 1

2.1 ABSTRACT

Age-related plantar sensation insensitivity results in pathology of those aspects of gait that are dependent on vibration sensation. This dysfunction could lead to falls, the major cause of accidental deaths in people over age 75.

Because of the important role of vibration sensation in gait, the present study investigated the degree to which plantar vibration sensation decreases as a function of age, and if this change is dependent on frequency and on the location of vibration application on the footsole. This study will allow us to infer how the gait related functions of different areas of the footsole may be affected by age-induced vibration insensitivity.

Thresholds for vibration detection were assessed at 4 frequencies (25Hz, 50Hz, 250Hz, 400Hz), at 55 locations on the footsole, and in 2 groups of participants: young (mean age=26 years, 2 months +/- 3 years 3 months) and old (mean age=88 years 8 months, +/- 5 years 4 months). Using clustering techniques to group the 55 locations into regions with similar threshold values, it was determined that there were 3 distinct regions of sensitivity on the footsole: the ball/medial arch, the lateral border of the foot and the heel, and the toes. The ordinal pattern of regional sensitivity was age and frequency invariant; however specific values of detection thresholds for the regions changed as a function of these factors. Detection thresholds for FAI mediated frequencies (25Hz for young subjects, 25 and 50Hz for older subjects) were age invariant. The thresholds for FAII mediated frequencies (50, 250 and 400Hz

for young subjects, 250 and 400Hz for old subjects) were lowest at 250 Hz for both age groups.

From the discussions of the relationship between foot region sensitivity and foot region function, and the possible role of vibration sensation in gait, it was hypothesized that decreased vibrotactile acuity due to age may result in changes to those aspects of walking and balance control that rely on FAII frequency sensation.

2.2 INTRODUCTION

It has been hypothesized that vibrotactile information from the glabrous cutaneous receptors of the human footsole plays an important role in locomotion, specifically, in regulating balance and equilibrium in stepping (Yang and Stein, 1990; Duysens, Tax, Murrer and Dietz, 1995; Perry et al., 2000). Furthermore, it has also been speculated that decreased cutaneous sensation, a natural result of ageing (Verrillo, 1979), may cause dysfunction in gait (Perry et al.). To establish the contribution made by vibrotactile information from this region, it is important first to determine vibrotactile thresholds for the footsole and to see if these thresholds change with age, since vibrotactile acuity determines the range of cutaneous information available to control balance and equilibrium in standing and walking.

In humans, vibrotactile sensation in the glabrous skin of the footsole is encoded by mechanoreceptors that are associated with 4 different types of afferent nerve fibres (Johansson, Landstrom and Lundstrom, 1982). Recently using microneurography, it was determined that all four types of receptors and afferents exist in the human footsole (Kennedy and Inglis, 2002), although their distribution and thresholds of activation were different from those described for the hand (Johansson and Vallbo, 1983).

Plantar vibrotactile thresholds have been investigated in several studies. Kenshalo (1986) measured vibration sensitivity at 2 frequencies (40Hz, 250Hz) in young and older participants. Kekoni et al. (1989) measured vibration thresholds at 7 different locations on the plantar surface of the foot (heel, lateral mid-foot, medial mid-foot, lateral ball, mid-ball, medial ball and toes) and at 3 different frequencies (20, 80 and 240Hz). Nurse and Nigg (1999) looked at plantar sensitivity at 4 different locations on the plantar surface of the foot (heel, lateral arch, medial ball and hallux) at 30 and 125Hz vibration. These studies established normative vibration threshold values for the frequencies and locations tested; however these investigations were restricted to a young population only (Kekoni et al.: n=6, age=23-36 years; Nurse and Nigg: n=15, age=26.2 years, sd=6.28years), or, to only one location on the footsole (Kenshalo: young: ages 19-31, older: ages 55-84; tested on the thenar eminence and an unspecified location on the footsole). As a result, no conclusions could be drawn from these data about how plantar sensitivity across the whole foot changes with age, and what implications this may have for the control of walking and running.

In a psychophysical investigation of vibrotactile acuity as a function of age, Verrillo (1979) measured thresholds in four groups of subjects, each group having a different mean age (10, 21, 50 and 65 yrs). While testing was done on the glabrous skin of the hand (the thenar eminence) and is therefore not directly applicable to gait, the 3 main may have homologues in the glabrous skin of the foot. The first result showed that low frequency thresholds (FAI mediated) were age invariant. Second, high frequency thresholds (FAII mediated) increased as a function of age. Third, the "break-point frequency" that is, the frequency at which it was hypothesized that mediation switched from FAI to FAII, also increased as a function of age, with the result that higher and higher frequencies were mediated by FAIs. A similar pattern of frequency mediation has been demonstrated for 2 age groups (young: ages 19-31 years; older: ages 55-84 years), however at only one unspecified location on the plantar surface of the foot, and at only 2 frequencies (40, 250Hz) (Kenshalo, 1986).

As a means of investigating the effect of diminished vibrotactile sensation on balance control in walking, Perry et al. (2000) increased thresholds by cooling the footsole, and observed the ensuing effects of this on locomotion. Since vibration information may be important in gait, using cooling as an aging analogue to diminish or ablate information may cause similar dysfunction. The result of the cooling was that participants who were subjected to unexpected perturbations used non-normative strategies to recover their equilibrium. For example, perturbations in the forward direction caused an increase in multiple step recoveries, rather than a single step recovery. The experimenters hypothesized that when FAIIs were incapacitated by cooling (vibrotactile threshold on the 1^{st} metatarsal-phalangeal joint at 100Hz increased to 6.9+\-4.0 from 4.1+\-1.1μm, pre-cooled condition), participants were unable to detect foot contact and control weight transfer. This strategy was similar to that used by elderly individuals (average age=69 years) with measurable loss of vibration sensation at 100Hz (Maki et al., 1999).

In light of the research suggesting a role for cutaneous footsole information in controlling gait, and a decline in cutaneous function with age, the purpose of the present study was to determine by how much plantar vibration sensation decreases as a function of age, and if this change is also dependent on frequency and on the location of vibration application on the footsole. Whereas the loads applied to the plantar surface of the foot are higher than threshold during gait, this study of thresholds is a first step towards inferring how the gait-related functions of different areas of the footsole may be affected by age-induced vibration insensitivity, and whether this insensitivity translates into gait dysfunction in the elderly.

2.3 METHODS

2.3.1 SUBJECTS

A total of 12 participants were involved in this study: 6 in a young age group (mean age=26 years, 2 months +5 years 7 months /- 3 years 3 months, 4 men and 2 women) and 6 in an old age group (mean age=88 years 8 months, + 5 years 4 months /-15 years 3 months, 2 men and 4 women). The number of participants was similar to that used in 2 previous studies (Verrillo, 1979; Kekoni et al., 1986). Participants were self-reported free of neurological disease, were non-smokers and moderate drinkers. While some participants in both age groups were taking medication regularly, none of the medications have been shown to affect the sense of touch.

2.3.2 EXPERIMENT PROTOCOL

All research was done using methods approved by the University of British Columbia Office of Research Services and Administration Behavioural Research Ethics board. Vibrotactile thresholds were determined for 4 different frequencies at 55 locations on the right footsole (Figure 8). The 55 locations were spread across the footsole in an 11x5 point grid in order to assess thresholds in all areas of the foot. To ensure that the same relative locations were tested on all participants, the participants first outlined their foot onto graph paper. The outline was scanned, and the footsole depicted in Figure 8 was sized to fit the outline. The sized footsole figure was then printed and holes poked in the paper where the test points were. The sized footsole was then laid over the participants footsole, and ink used to mark the locations of the test points.

The 4 frequencies tested, 25, 50, 250 and 400Hz, were chosen for several reasons. First, if frequency mediation changes as a function of age as suggested by Verrillo (1979), then an Age x Frequency x Threshold Level interaction will be apparent between 25Hz and 50Hz. Furthermore, 25 and 50Hz capture the major frequency content at heel strike during walking (Munro Abernethy, Paul, Rose, Simon, Pratt and Radin, 1975; Paul, Munro, Abernethy, Simon, Radin and Rose, 1978; Voloshin and Wosk, 1980; Wosk and Voloshin 1981). Second, the work by Verrillo shows that 250Hz is the frequency at which vibration thresholds are lowest, and 400Hz was the maximum frequency which we could test using our equipment set-up. Finally, this range of frequencies fits the range of physiological response in human cutaneous receptors and allows a comparison of sensitivity between the glabrous skin of the hand and that of the foot (Johansson et al., 1982).

2.3.3 Equipment, Instrumentation and Stimuli

The subjects lay face down on a portable massage table with their right foot supported in a padded restraint to expose the footsole (Figure 8). The foot was strapped to the restraint using soft webbing. The footsole was tested in this position (i.e. unloaded) because it gave the experimenter access to the entire footsole, making it possible to perform the protocol in a timely and accurate way.

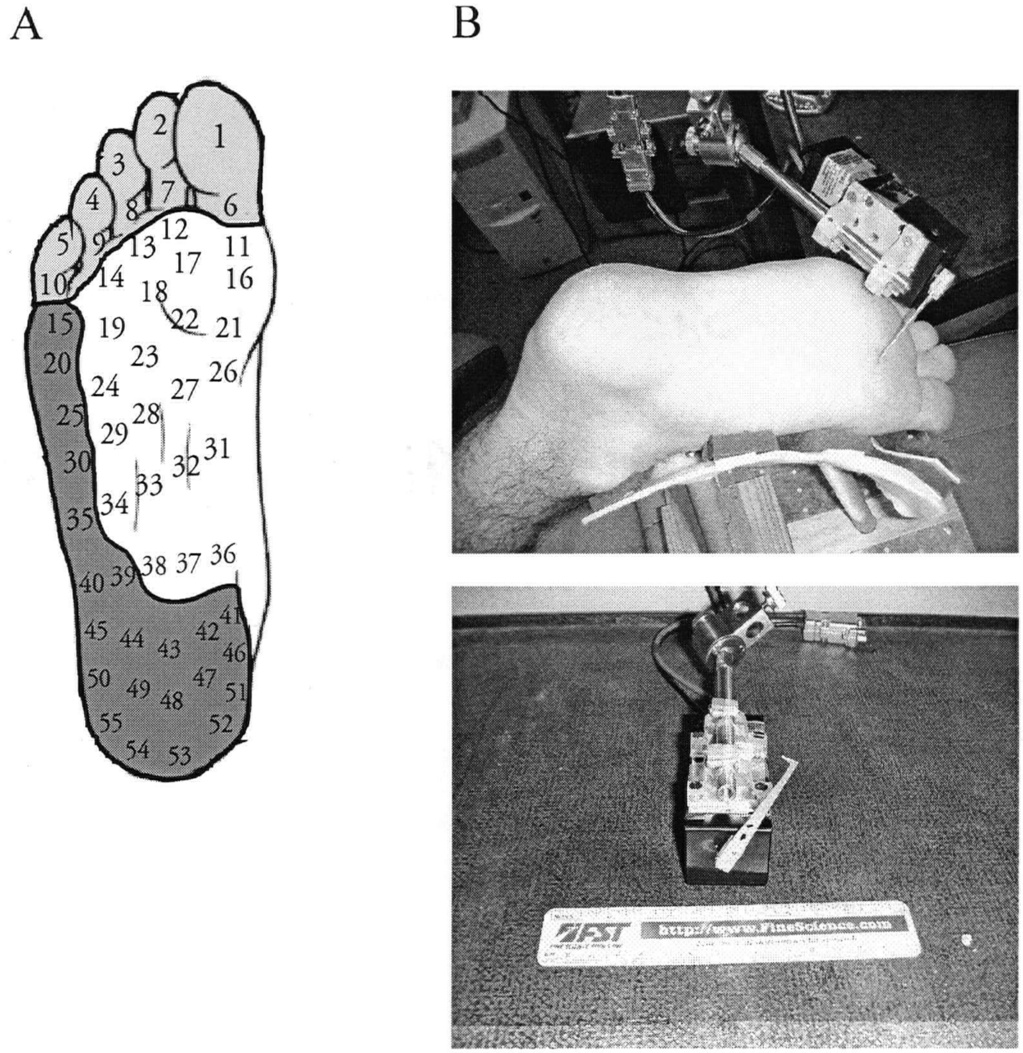


Figure 8: A. Footsole test locations. B. Equipment set-up. The upper panel shows the lever arm applied to footsole. The lower panel shows the motor and lever arm, with 6in./15cm ruler.

Sinusoidal signals were generated using Matlab 5.1 (The Mathworks, Inc., Natick, MA) and LabView 4.2 (National Instruments, Houston, TX), and sent as a voltage value via a PCI-MIO XE-10 multi-input –output board to an NI BNC 2090 BNC output box. The voltage waveform was supplied to an ASI model 300B dual-mode lever arm motor system. The diameter of the lever arm head was 1.5mm. The excursion amplitude, measured in μm, was the dependent variable of interest.

To begin a trial, the head of the lever arm was placed on the footsole perpendicular to the test site. The lever arm head was placed against the foot so that the head was in contact with the footsole, but so that no amplitude offset was produced. This was done to ensure that mechanoreceptors were not activated before stimulus onset. Sinusoidal vibrotactile stimuli were delivered in 1s pulses, with a 1s inter-pulse time. The stimuli were sampled at 10 times the current test frequency.

Thresholds at each location were determined using the up and down staircase method with a step size of .25μm (.05μm for young subjects at frequencies above 25Hz) (Cornsweet, 1962). These steps sizes were chosen to reflect the acuity of the age groups at different frequencies, as determined by Verrillo (1979). On the first iteration of the staircase, the amplitude of the stimulus sinusoid was set at threshold values determined by Kekoni et al (1989) for similar footsole areas for young subjects, and pilot data for older subjects. The stimulus amplitude was increased in 1-step increments, until the subject indicated a "yes" response by closing a finger switch. The amplitude of the sinusoid was then increased above (by 1 or 2 steps) the just determined threshold value, and testing for the down part of the staircase commenced. Before each 1s pulse, the power in the sinusoid was decreased by 1 step until the subject indicated that they could no longer feel the stimulus. At this point, the amplitude of the sinusoid was decreased below the threshold value and testing of the next iteration of the staircase commenced. This was repeated 10 times. The last 8 of 10 up and down flights were averaged to determine the threshold value. The 55 sites were tested in serial order, however order was counterbalanced between subjects (sites 1 to 55, or sites 55 to1) to eliminate serial effects. All 4 frequencies were tested at one sight before moving to a new site. This was done because it was time consuming to move the motor between sites. Testing on each subject took about 3 hours. Trials were blocked by frequency, with the order of presentation of each frequency block randomized across subjects. Two data sets were collected for each trial: a time series representing the force exerted by the motor arm on the participant's foot sole, and a voltage time series representing the excursion of the lever arm against the footsole. The voltage time series was converted to a time series of the displacement of the head of the motor arm using a conversion factor supplied by the equipment manufacturer. The vibratory amplitude time series was time linked to a force data time series, which was used to monitor the force with which the stimulus was applied. Any trial in which the force application was irregular was discarded - for example, trials in which the participant's foot had moved away from the lever arm. The range of unusable trials across subjects was between 0 (minimum) and 4 (maximum).

2.3.4 Data Analysis

Thresholds from the 55 locations were grouped into 7 anatomical regions that were similar to those used by Kekoni et al. (1989): toes, medial-, mid-, and lateral-ball, medial-, and lateral-mid-foot, and heel). This was done in order to compare the results of this study with those of Kekoni et al. (1989). Next, the thresholds from the 55 data points were clustered in 2 ways. Clustering is a data analysis technique in which objects are grouped together based on similar characteristics (Hartigan, 1975). First, threshold values from the 55 data points were clustered within each frequency and age group. This was done using a hierarchical tree cluster algorithm, where the data points were assigned to distinct groups in successive steps, based on similarity of threshold values. This preliminary clustering showed a trend toward 3 clusters: toes, arch/ball and lateral border of the foot/heel. Secondly, k-means clustering was run on all subjects at each frequency. In k-means clustering, the number of clusters is set *a priori* (in this case, 3, as determined by the tree analysis). The algorithm then allocates the data points into three clusters so that inter-cluster variability is maximized, and intra-cluster variability is minimized, like a reverse analysis of variance (ANOVA). The distinction of the clusters was confirmed by running a 2 Age x 4 Frequency x 3 Region ANOVA (with repeated measures on all factors except age) on the clusters generated by 3-means clustering. The main effect of cluster was significant at $F(2,20)=94.371$, $p<.01$. To ensure that the clusters were not an artifact of the analysis technique, ANOVAs were run on the results of the 4-means clustering. Of the different k-means clustering results, 3-means clustering produced the lowest intra-cluster variability and highest inter-cluster variability(3-means: $F(6,60)=3.00$, 4-means:$F(6,60)=2.37$.

2.4 RESULTS

There were 2 interesting results from the experiment: first, there were 3 anatomical clusters. These clusters had an ordinal pattern of sensitivity that was age and frequency invariant. Second, there was acuity loss in the elderly. This loss varied with vibration frequency.

The 3 clusters generated from the 55 data points are illustrated in Figure 8, and the mean thresholds are presented quantitatively in Table 1 and Table 2. The clusters consisted of the toes, which consistently had the highest threshold; the lateral border of the foot and the heel; and finally the ball of the foot and the medial arch, which had the lowest threshold. Interestingly, this ordinal pattern of regional sensitivity was maintained across age and frequency; however the specific values of thresholds for the clusters changed as a function of these factors. ANOVA revealed a 3-way interaction of frequency, cluster and age on threshold (Greenhouse-Geisser correction: $F(2.917, 29.174)=3.00$, $p=.048$). Tukey *post hoc* analysis showed that at postulated FAI mediated frequencies (young=25Hz; old=25, 50Hz; (Verrillo, 1979)) all three anatomical clusters were significantly different from one another (Tukey HSD; critical difference=9.54μm). At the lowest FAII frequency, however (young=50Hz, old=250Hz; (Verrillo), the sole clusters were not distinct from each other, but were different from the toes. At 250Hz and 400Hz in young participants, all 3 clusters were similar. At 400Hz in old participants, the sole clusters were again not distinct from each other, but distinct from the toes.

Frequency	25Hz	50Hz	250Hz	400Hz
Toes	64.67μm, sd=2.2 low=55 high=71	24.50μm, sd=1.1 low=19 high=29	11.00μm, sd=2.0 low=4 high=9	11.67μm, sd=2.0 low=5 high=15.00
Ball/Arch	44.00μm, sd=1.8 low=34 high=39	10.50μm, sd=1.8 low=4 high=15	5.50μm, sd=2.5 low=1 high=6	6.67μm, sd=1.2 low=1 high=7
Lat./Heel	53.83μm, sd=2.3 low=42 high=62	13.33μm, sd=1.9 low=8 high=19	6.17μm, sd=1.2 low=1 high=8	8.50μm, sd=1.9 low=1 high=9

Table 1 : Means for Threshold, young subjects

Frequency	25Hz	50Hz	250Hz	400Hz
Toes	66.00μm, sd=4.1 low=50 high=73	62.17μm,sd=4.3 low=56 high=70	33.33μm, sd=7.4 low=27 high=44	66.00μm, sd=5.4 low=54 high=73
Ball/Arch	38.67μm, sd=3.8 low=35 high=52	39.17μm, sd=4.2 low=29 high=52	20.50μm, sd=3.8 low=13 high=29	43.00μm, sd=8.0 low=31 high=53
Lat./Heel	55.00μm, sd=6.2 low=40 high=59	50.33μm, sd=6.1 low=35 high=61	25.50μm, sd=3.6 low=20 high=34	59.00μm, sd=5.8 low=40 high=63

Table 2 :Means for Threshold, older subjects

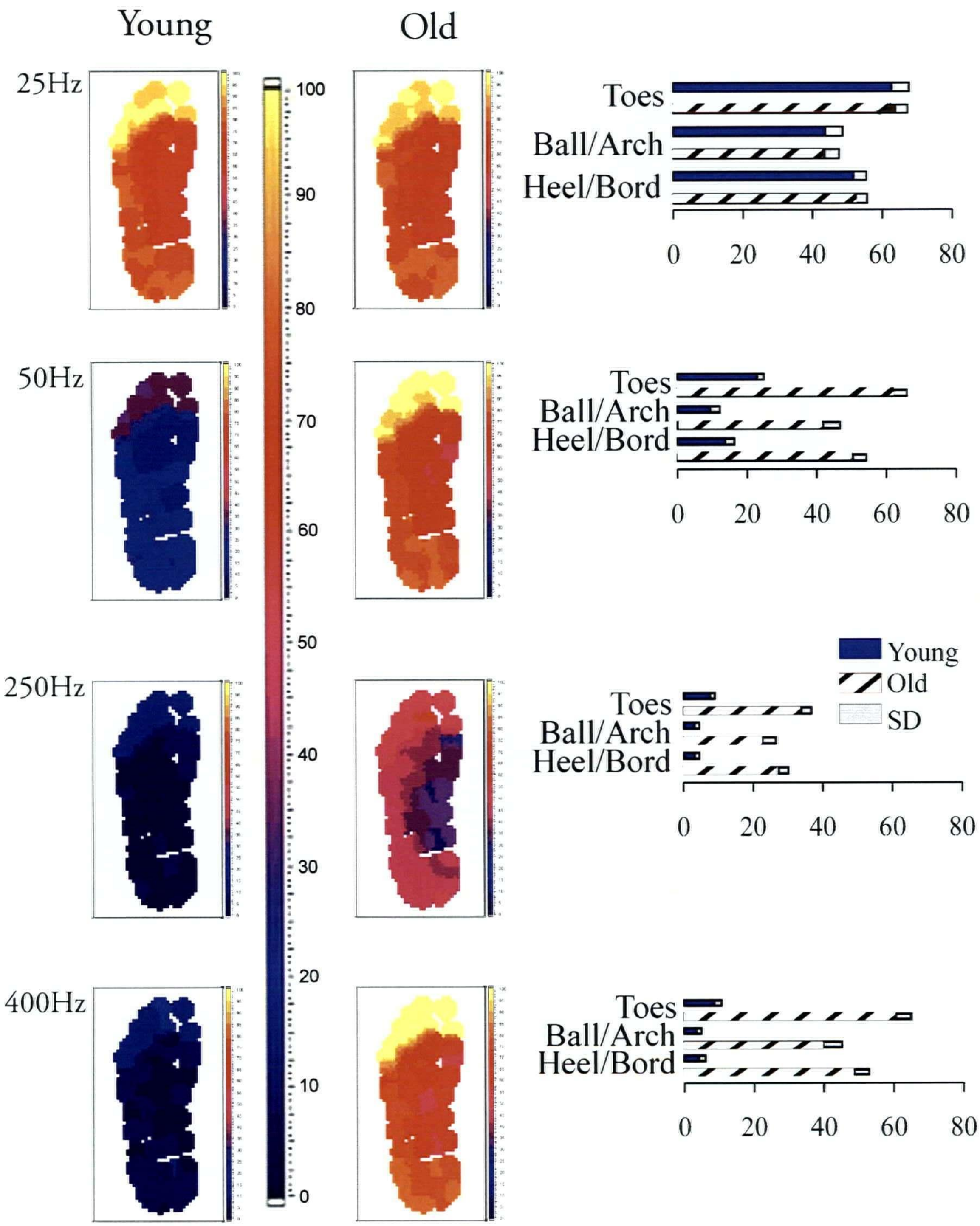


Figure 9: A. The colour gauge indicates threshold level. Light colours represent high thresholds; dark colours represent low thresholds. B. Thresholds for the 3 clusters for each of the age groups at the 4 frequencies are shown. Thresholds are measured in μm.

Acuity loss in the elderly is summarized in Figure 10 and quantified in Table 3. Figure 10 shows threshold levels averaged across the entire 55 data points, and shows the global changes in the vibrotactile sense that occur with age. At 25Hz, both young and old groups have similar thresholds. As the frequency increases, the trace representing the younger group decreases steeply, while the older group's curve is flatter until 50Hz, and then decreases. The distance between the 2 curves represents acuity loss. When expressed as a percent ([older threshold value/young threshold value]*100; see Table 3), loss increased as a function of frequency starting at 50Hz. At frequencies mediated by FAII receptors in both the young and elderly (250Hz and 400Hz), loss of acuity was greatest in the heel/lateral border area, followed by the ball/arch area, and finally the toes. At all frequencies, the variance of thresholds in the old group was greater that that of the young group, consistent with larger individual differences in the elderly.

Frequency	**25Hz**	**50Hz**	**250Hz**	**400Hz**
Toes	N/A	253%	303%	565%
Ball/Arch	N/A	373%	372%	645%
Lat./Heel	N/A	377%	413%	700%

Table 3: Acuity loss in the elderly expressed as a percentage of young thresholds

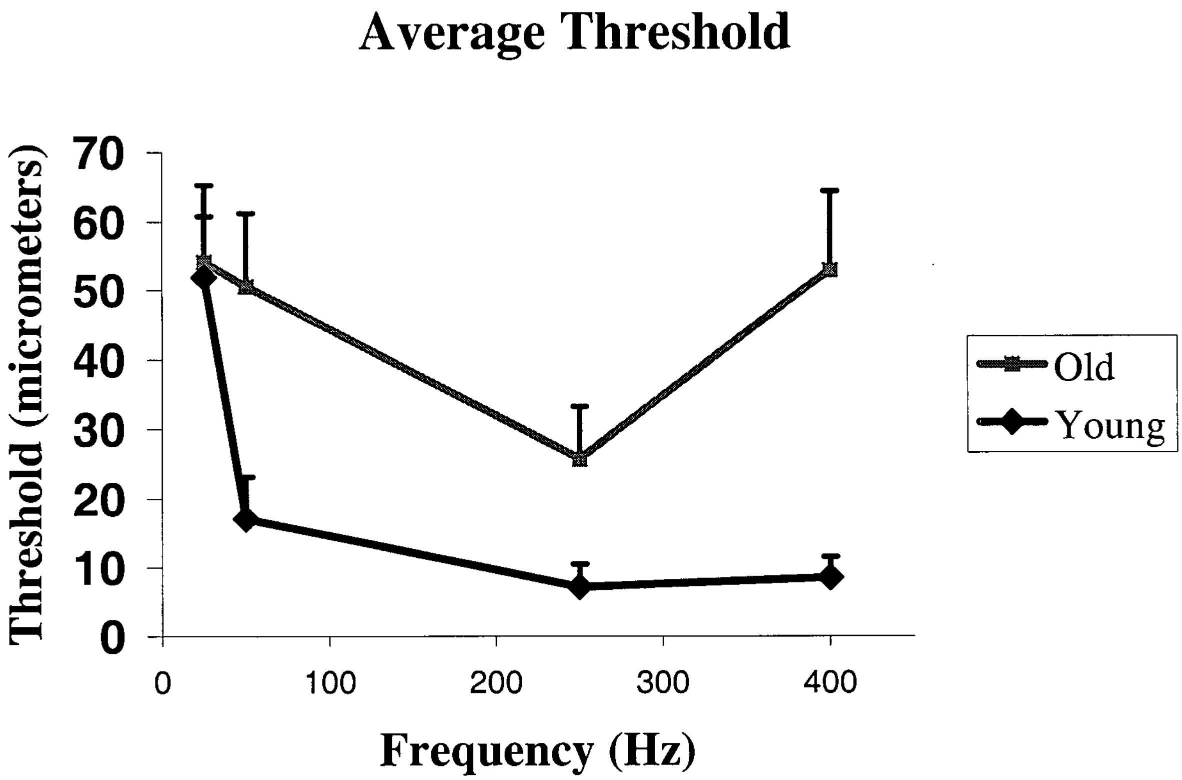


Figure 10: Vibrotactile sensitivity in the footsole plotted as a function of age and frequency. All 55 data points are averaged. Bars represent standard deviations.

2.5 Discussion

The 2 results of the study (3 distinct clusters of different sensitivities, and acuity loss in the elderly) suggest that there may be a gait-related function linked to each of these areas, and that functionality may decline as a result of acuity loss. The implications of these results are discussed, along with a comparison of vibrotactile thresholds in the hand and foot.

2.5.1 Differences in Vibration Sensitivity Between the Hand and the Foot

With the 55 locations grouped into the 7 anatomical regions used by Kekoni et al. (1989), thresholds for young subjects were comparable at similar frequencies (our 25Hz with Kekoni et al. 20 Hz; our 250 Hz with Kekoni et al. 240 Hz). Footsole data from Kenshalo (1986) shows plantar vibrotactile thresholds to be, in general, lower when compared with our results, especially at 40Hz for young subjects (young subjects, 40Hz=4.85μm, 250Hz=0.57μm; older subjects, 40Hz=34.59μm, 250Hz=28.25μm). There are several possible reasons for this. First, the mean age of Kenshalo's subjects is not specified, so it may be that his subjects were younger, producing lower thresholds at 40Hz. Since this is likely an FAII mediated frequency in young people, thresholds will vary depending on age. Second, the data presented in Table 1 and Table 2 show averages for an entire cluster. Since these values are averaged from between 10 data points (toes) and 23 data points (lateral border/heel cluster), and since each data point is in turn averaged from 8 values, it is reasonable to expect that our values will be different from Kenshalo's. For the sake of comparison, Table 1 and Table 2 include the lowest and highest values of data points from each cluster and at each frequency. The values supplied by Kenshalo are within the range of our low and high values. Finally, Kenshalo did not specify where the testing on the plantar surface was done. It could be that his values are from an extremely sensitive area of the foot, for example from the ball or from the medial arch.

In general, thresholds from this study, and those of Kekoni et al. (1989) and Kenshalo (1986), are higher on the foot than on the hand (Kekoni: thresholds on the hallux are approximately 100X that of thenar eminence at 240Hz; Kenshalo: thresholds on the plantar surface are approximately 6.3X that of the thenar eminence at 250Hz in men). One reason for this may be that, while the glabrous skin of the footsole and hand contains similar receptors, footsole receptors have higher force activation thresholds (footsole: FAI: 11.8mN, FAII: 4.0mN (Kennedy and Inglis, 2002); hand: FAI: 0.58mN, FAII: 0.54mN Johansson and Vallbo, 1980)). Further, it has been speculated that age related changes in myelination may cause decreased nerve conduction velocity (Kenshalo, 1986). Thus, the longer conduction distances to the feet would induce greater vibrotactile sense dysfunction.

2.5.2 THE RELATIONSHIP BETWEEN FOOT REGION SENSITIVITY AND FOOT REGION FUNCTION

Our study and others (Kekoni et al., 1989; Kenshalo, 1986; Nurse and Nigg 1999) have found regional difference in foot sole sensitivity. Since there are no differences in mechanoreceptor density in the footsole (Kennedy and Inglis, 2002) as there are in the hand (Johansson and Vallbo, 1983), sensitivity differences in the footsole may be due changes in mechanoreceptor function and morphology, and changes in skin mechanics. Bolton et al. (1966) investigated the mechanoreceptor network associated with touch in human glabrous skin and correlated changes in the network with age. With increased age, there is a loss in the total number of receptors. The remaining receptors are irregularly distributed, and their receptive fields are varied in size and shape (Cauna, 1965). In addition to receptor changes, the skin itself changes: the epidermis thins and there is a decrease in the amount of collagen and elastin in the skin (Kenshalo, 1977; Kenshalo, 1978). In addition there can be a build up of callused skin.

It has been shown that thicker skin impedes the transmission of high-frequency vibrations (Pubols, 1987). In our experiment, those areas that were less callused, like the arch/ball cluster, had lower thresholds than the areas that were more calloused, like the heel/lateral border of the foot. While not particularly callused, the toes may have high thresholds because the hinge joint allows them a greater proprioceptive sense, so vibrotactile sensation is not as critical as vibration sensation in this area (Perry et al., 2000).

Nurse and Nigg (1999) found that regional differences in sensitivity are correlated with peak forces and pressures during walking and running: the higher the sensitivity, the higher the peak force or pressure (pressure correlation with 125Hz sensitivity, walking: $p=0.02$, running: $p=0.01$; force correlation with 125Hz sensitivity, running: $p=0.038$). These correlations of sensitivity and pressure, and sensitivity and force, along with the fact that different footsole regions have different sensitivities, suggest that whole *areas* play different roles during the gait cycle. For example, the ball of the foot and the FA receptors located there would play a significant role in detecting vibrations during foot-off, while the heel and the FAs located there would mean that the heel would play a significant role in sensing vibration at foot contact.

Nurse and Nigg (1999) have also suggested that the correlation of higher acuity and thresholds during running indicates that sensory feedback from the feet during locomotion could modify locomotion. From this, one could make the argument that if sensory feedback can modify walking, then degraded sensitivity may cause pathological locomotion (Murray et al., 1969). For example, elevated thresholds in the FAs in the heel of the foot would mean that degraded sensory feedback at foot contact would cause dysfunction in the aspects of gait reliant on foot contact sensation (Perry et al., 2000). In support of the hypothesis that degraded sensory input from the footsoles causes pathological gait in the elderly, Murray et al. noted that walking in the elderly does not resemble that of someone with a nervous system pathology, but more closely resembles the gait of someone walking over ice or in the dark who thus has a reduced ability to use sensory information.

2.5.3 *THE ROLE OF VIBRATION SENSATION IN GAIT*

Our results support Verrillo's (1979) conjecture that, as people age, progressively higher frequencies are mediated by FAI receptors, and that for frequencies that remain mediated by FAII receptors, the vibrotactile system becomes less sensitive (Figure 10). Since people become less sensitive to FAII mediated frequencies with age, one would expect to see age related difficulties with gait components like toe-off and heel strike. This effect has been shown in 2 complementary studies: the first by Perry et al., 2000, and the second by Maki et al., 1999. In the first study, Perry et al. simulated the sensory loss of the aged by cooling participants's feet, (vibrotactile threshold on the 1^{st} metatarsal-phalangeal joint at 100Hz increased to 6.9+\-4.0 from 4.1+\-1.1μm). As a result, when participants were given a signal to terminate gait abruptly, the investigators observed an increased loading rate after initial contact of the first and second steps subsequent to the signal. This increased loading indicated that the CoM had not been slowed adequately prior to foot contact. The authors hypothesized that, under normal conditions, cutaneous information from the heel at heel contact would initiate a short-latency reflex loop to extend the leg and slow the forward progress of the CoM. Because of cooling however, cutaneous sensation from the heel was impoverished, and this reflex loop was not adequately engaged.

While the effect of cooling on heel strike related gait function is temporary, it is possible that an analogous failure of the reflex loop may happen in older adults with plantar sensory loss. This hypothesis complements the data from our protocol that show that FAII mediated vibration sensation loss is greatest in the elderly heel/lateral foot area, making heel contact and weight transfer the aspects of gait most likely to be affected by age (see Table 3). Since vibration sensation is not as impoverished in the arch/ball area, the aspects of gait relying on vibration sensation in this area likely would not be affected to the same extent.

In the second study, Maki et al. (1999) diminished sensation in the elderly footsole was facilitated. Here, the researchers used 3mmd plastic tubing to trace the outline of the footsole 1cm interior to the border of the foot. The investigators hypothesized that facilitating the sensation of the footsole boundary would facilitate determining the proximity of the CoM to the boundaries of the BoS. The position of the CoM with respect to the BoS is thought to be critical in maintaining uprightness during gait (Perry et al., 2000). Boundary facilitation reduced the number of steps and arm reactions used to recover from unpredictable perturbations. During continuous perturbations, older subjects were able to reduce the extent to which the center of pressure (CoP) approached the posterior limit of the BoS. Opposite to the cooled condition of the first experiment, there was a reduction in the loading rate after foot contact, indicating an improved ability to sense foot contact and engage the reflex loop to extend the leg and slow the forward progress of the CoM. This suggests that aides can alleviate some dysfunctional aspects of gait, so it is possible that an aide like SR that could facilitate footsole sensation and improve gait dysfunction.

2.6 BRIDGING SUMMARY

Experiment 1 showed that vibration sensitivity varied as a function of the anatomical area of the footsole to which the vibration was applied. Further, while the relative sensitivity of the 3 footsole clusters was the same for both age groups, the actual threshold values changed as a function of frequency.

It has been hypothesized that when vibrotactile acuity is lost due to age, that cutaneous reflexes, an integral part of gait, are not adequately engaged due to lack of sensation. This results in gait dysfunction. This suggested that if SR were to be able to improve acuity, gait might also be improved. This was the justification for the second study.

3 EXPERIMENT 2

3.1 INTRODUCTION

Stochastic resonance (SR) occurs when the detection of a sub-threshold signal is made possible by the presence of noise. While counter-intuitive, this phenomenon has been shown both theoretically, and practically in the human sense of touch.

Given the ability of SR to improve detection of weak signals, it may be possible to parlay SR into functional aides for those individuals with elevated sensory thresholds. This idea motivated the present experiment, in which an SR protocol was tested on the footsoles of elderly people with elevated vibrotactile thresholds. The results showed that SR was effective in helping elderly people detect sub-threshold signals. Further, the results suggested that it is possible to know *a priori* the amount of noise needed for optimal SR effects, based on characteristics of the signal to be detected. This knowledge makes SR more practical as a rehabilitative aid for those with elevated thresholds.

3.2 BACKGROUND

SR is a phenomenon in which the detection of a sub-threshold signal is enhanced by the presence of noise; that is, ongoing spontaneous activity that is unrelated to the signal (Chialvo and Apkarian, 1993; Collins et al., 1996; Douglass et al., 1993; Levin and Miller, 1996; Pei, Wilkins and Moss, 1996; Gammaitoni et al., 1998). The SR phenomenon has been demonstrated experimentally in the auditory system (Ward, Desai, Rootman, Tata and Moss, 2001; Zeng, Fu and Morse, 2000), in the visual system (Simonotto, Riani, Seife, Roberts, Twitty and Moss, 1997; Ward et al., 2001), in the cat tactile system (Manjarrez, Rojas-Piloni et al., 2002), in the young human tactile system (Collins et al., 1997; Richardson et al., 1998, Manjarrez, Diez-Martinez et al., 2002), and in the elderly and diseased tactile systems (Liu et al., 2002; Dhruv et al., 2002). Interestingly, because SR can improve the ability of a sensory system to detect weak signals, it may be of use to those, like the elderly, who have elevated sensory thresholds (Kenshalo, 1977; Kenshalo, 1986; Thornbury and Mistretta, 1981; Study 1). There were two goals to this study: first, to determine if SR could lower tactile thresholds in the elderly, and second, to quantify the level of noise needed to produce optimum SR effects based on the characteristics of the target signal. Quantifying noise levels in this way would allow clinicians to know *a priori* which characteristics of noise would most benefit weak signal detection, thus making SR more practical as a rehabilitative aid for people with sensory deficits.

Biologically, noise has been shown to improve the functional behaviour of both animals (Levin and Miller, 1996; Douglass et al., 1993; Greenwood et al., 2000) and humans (Chialvo and Apkarian, 1993; Garver and Moss, 1995; Cordo, Inglis, Verschueren, Collins, Merfeld, Rosenblum, Buckley and Moss, 1996; Collins et al., 1996). How does SR work? Every signal detection system is made up of 4 fundamental components: (1) the detection threshold, (2) the signal, (3) the record of the detection, and (4) noise. These components, and the effect of different levels of noise on a sub-threshold signal, are illustrated in Figure 6. This figure shows that an optimal amount of noise, such as that shown in panel B, makes the sub-threshold signal detectable without swamping the signal. In terms of people with elevated vibrotactile thresholds, SR may be used to render sub-threshold signals detectable.

In humans, vibrotactile sensation in the glabrous skin of the foot is encoded by mechanoreceptors that are associated with 4 different types of afferent nerve fibers (Kennedy and Inglis, 2002). Slowly adapting type II afferents (SAIIs) preferentially encode frequencies below 8 Hz; slowly adapting type I afferents (SAIs) encode 2-32Hz; fast adapting type I afferents (FAIs) encode 8-64Hz; and fast adapting type II afferents (FAIIs) mediate frequencies above 64Hz (Johansson et al., 1982). It is possible that the degradation of vibrotactile sensitivity in the footsole as a function of age, perhaps due to the decline in function or number of the mediating receptors (Bolton et al., 1966) or due to changes in the quality of the skin, may contribute to vibration detection pathology in the elderly.

The improvement in functional behaviour of the mechanoreceptors due to noise can be quantified by one of several information measures: SNR (Douglass et al., 1993; Levin and Miller 1996; Pei et al., 1996), C1 (Collins et al., 1995; Collins et al., 1996; Heneghan, Chow, Collins, Imhoff, Lowen and Teich, 1996; Ivey et al., 1998) or %Corr (Collins et al, 1997; Richardson et al., 1998). For all of these information measures, the higher the value of the measure, the greater the number of events the system is detecting. When these measures are plotted as a function of the amount of noise in a detection system, SR produces a characteristic effect on the measure's value: with increasing noise, the value rapidly increases to a maximum, and then gradually declines. The maximum value is produced by the optimal amount of noise for the system.

The measure chosen in our experiments was %Corr (Collins et al, 1997; Richardson et al., 1998), for two reasons: ease of calculation, the ability to calculate the measure in real time (as the experiment progressed). Collins et al. and Richardson et al. have used the %Corr (Equation 1) measure to quantify the effects of noise in psychophysical studies. In a one-interval forced choice (1IFC) protocol, participants were presented with a stimulus that contained either vibrotactile noise only, or noise plus signal. Subjects were asked to identify whether or not the stimulus contained a signal.

$$\%Corr = \left(\frac{N_{Correct}}{N_{Total}} \right) \times 100$$

Equation 1

where : $N_{Correct}$ is the number of correct responses

N_{Total} is the number of presentations of stimulus

There are several aspects of these experiments that could be refined in order to determine more clearly the exact mechanism of SR. First, in the 1IFC paradigm, the noise only stimuli and the noise *plus* signal stimuli contained unequal amounts of energy. Thus, it is possible that participants were able to detect greater energy, rather than signal. This produces an SR effect, however it is not possible to ascertain whether participants, while detecting the greater energy, are better able to detect any information contained in the signal, for example, frequency information.

Second, the %Corr measure in a 1IFC protocol is not free of criterion effects. In the 1IFC paradigm in which participants are asked to choose whether or not a signal is present, their answer is affected by where they set their decision criterion. For example, with noise and noise+signal distributions constant, as criterion changes from very liberal to very conservative, the %Corr measure increases to a maximum at the optimal location, between the two distributions, and then decreases. This peak in %Corr will occur whether or not the noise distribution is optimal, and does not necessarily reflect the sensory threshold. This confound does not occur in the 2IFC paradigm where judgement in not made based on a criterion, but rather which epoch contains "more" of the target signal. In a study designed to determine the effects of noise on physical threshold, it is critical that the threshold not be confounded by the participant's criterion.

In addition to criterion and energy effects needing to be addressed, to date there has been little experimentation published showing whether SR is effective in lowering vibrotactile detection thresholds in the elderly (Liu et al., 2002, Dhruv et al., 2002), so this aspect of SR should be investigated further. Since it *has* been shown that the thresholds for higher frequency vibrations increase as a function of age, facilitating sensation through SR may reduce elevated sensation thresholds. This may be important, for example, in the plantar surfaces of the feet, where decreased sensation may lead to gait pathology, falls, and result in injury (Azar and Lawton, 1964). It is also important in the hands, where SR could improve the detection of micro-slips, which aid in proper grasp force generation (Wells, 1998).

These 3 issues were addressed in this experiment. First, age effects were addressed by the inclusion of an older subject group. The issues of unequal energies and of criterion effects in a 1IFC design were addressed by using a 2-interval forced choice (2IFC) protocol, where one epoch contained noise only, and the other epoch signal plus noise. Both epochs were designed to contain the same amount of power, so this protocol avoided the possibility of confounding SR with energy detection.

3.3 METHODS

The goals of the experiment were investigated using a 2 Age (young, older) x 4 Frequency (25Hz, 50Hz, 250Hz, 400Hz) x 6 Noise Level (0, 33, 50, 67, 83, 100% of threshold power) x 2 Signal Level (90, 80% of power at threshold) design, with repeated measures on all factors except age. At each frequency, one of the noise levels was combined with one of the signal levels to form one interval, while the other interval was formed from an equivalent amount of noise only. The noise-only and noise+signal intervals were presented in random order, and the participant was required to identify which of the intervals contained the signal.

3.3.1 Subjects

A total of 12 participants were used: 6 from the younger age group (mean age=26 years, 2 months +5 years 7 months /- 3 years 3 months, 4 men and 2 women) and 6 from the older age group (mean age=88 years 8 months, +5 years 4 months/-15 years 3 months, 2 men and 4 women). The number of participants was similar to that used in 2 previous studies (Verrillo, 1979; Kekoni et al., 1989). Participants were self-reported free of neurological disease, were non-smokers and moderate drinkers. While some participants in both age groups were taking medication regularly, none of the medications have been shown to affect the sense of touch.

3.3.2 Procedures

The protocol was carried out according to the University of British Columbia Office of Research Services and Administration Behavioral Research Ethics Board approval. The test protocol comprised 2 different stages: the threshold determination stage, where each participant's vibrotactile and noise thresholds were determined; and the SR stage, where vibrotactile and noise threshold information from the first stage was used to generate sub-threshold stimuli. The threshold determination stage has been described elsewhere (Study 1), and so will only briefly be discussed here when it is needed to explain the SR protocol.

In the first stage, thresholds for each of 4 sinusoidal vibration frequencies (25Hz, 50Hz, 250Hz, 400Hz) were determined for each individual from Verrillo (1979). Thresholds were determined for the upper arch on the right foot. The foot was chosen as the test location because, with advancing age, age-related neuropathies generally manifest themselves the extremities first and most (Rothwell, 1986). The upper arch was chosen because this location had the lowest aggregate threshold for the 4 test frequencies, and the thick skin of the heel and ball of the foot impedes the transmission of high-frequency vibration (Pubols, 1987). In general, the arch was the least callused area of the foot.

3.3.3 Apparatus

The equipment set-up was the same for both the threshold determination stage and the SR stage. Sinusoidal signals and noise were generated in LabView 4.2 and sent as a voltage value via a PCI-MIO XE-10 multi-input –output board to an NI BNC 2090 BNC output box. The voltage waveform was supplied to an ASI model 300B dual-mode lever arm motor system. The power spectrum of the waveform was calculated, and the power in the waveform determined by integrating a +/-10% band of the power spectrum around the target frequency. The lever arm of the motor supplied the tactile stimulus.

Using the vibrotactile detection thresholds from Study 1, sub-threshold power signals and noise were used to test the SR hypothesis. This stage of the experiment used a 2IFC paradigm. One of the epochs contained one of 2 sub-threshold levels of signal at one of the 4 frequencies, plus one of 6 sub-threshold levels of noise. The other epoch contained noise only. The power in the noise only epoch was set equal to the noise *plus* signal epoch. Subjects were asked to identify which of the epochs contained the target signal.

The 2IFC paradigm was implemented in a 2 Age (young, old) x 4 Frequency (25Hz, 50Hz, 250Hz, 400Hz) x 2 Signal Level (90% of signal threshold power, 80% of signal threshold power) x 6 Filtered Noise Level (0%, 33%, 50%, 67%, 83% and 100% of signal threshold power) design. Repeated measures were on frequency, signal level and noise level. The dependent variable of interest, %Corr, was a measure of the number of trials where the participant correctly identified the epoch containing the target signal.

Each signal level plus noise level combination was presented 60 times, for a total of 720 trials (60 Trials x 2 Signal Levels x 6 Noise Levels) at each of the 4 frequencies. The trials were presented in 12 pseudo-random blocks, where each block contained 5 trials of each frequency/signal level/noise level combination. The testing time for each block was approximately 20 minutes. Testing took about 4 hours. Participants rested between blocks on an as needed basis. The rest periods gave the double benefit of letting the participants relax, and negating any habituation effects, however there were not likely any habituation effects to vibration, since these effects have been shown at very suprathreshold levels only (Goble and Hollins, (1994): 20dB above threshold; Gescheider, Frisina and Verrillo (1979): 24dB above threshold).

3.3.4 Stimuli

The sub-threshold signal levels were set to 90% and 80% of the power of that individual's threshold at the frequency of interest. Noise levels contained 0%, 33%, 50%, 67%, 83% or 100% of the power in the threshold signal for that individual at the frequency being tested.

Noise was 0-mean Gaussian noise and Butterworth band-pass filtered so that when testing FAI mediated frequencies (as hypothesized by Verrillo (1979): young subjects: 25Hz; older subjects: 25 and 50Hz,), only non-FAII mechanoreceptors would be activated by the noise (young pass-band: 0.125Hz to 25Hz; older subjects pass-band: 0.125Hz to 50Hz). While testing FAII mediated signal frequencies (young subjects: 50, 250 and 400Hz; older subjects: 250 and 400Hz), noise was Butterworth band-pass filtered to contain only FAII mediated noise (young pass-band: 25Hz to 500Hz; older pass-band: 50Hz to 500Hz). Filtering of noise was done because, while FAII-mediated noise added to an FAI-mediated frequency signal would not detract from the FAI afferent's ability to detect signal, it would activate FAII afferents in the vicinity and possibly confound threshold levels or have a sub-threshold "priming" effect on FAI receptors. A similar filtering scheme was used by Collins et al. (1997) to constrain excitation to SA receptors only. Frequency mediation was hypothesized from the results of Study 1. Signals were sampled at 1KHz. Noise was sampled at 10KHz.

3.3.5 Data Analysis

Two data sets were collected for each 2IFC trial: a time series representing the force exerted by the motor arm on the participant's footsole, and the participant's choice of which time epoch contained the signal. The force data were collected so as to identify any trials where the force was inconsistent. These trials were re-done so that each participant always completed 60 usable trials. %Corr was calculated using Equation 1, where $N_{Correct}$ was the number of trials where the participant correctly identified the epoch containing the signal, and N_{Total} was 60.

The dependent variable of interest, %Corr, was analyzed using a 2 Age x 4 Frequency x 2

Signal Level x 6 Noise analysis of variance (ANOVA) with repeated measures on all factors except age. Greenhouse-Geisser corrections were used to account for sphericity violations. Statistically significant ANOVA findings were further analyzed using the Tukey HSD *post hoc* method.

3.4 RESULTS

For each signal level, there was an optimal noise level that maximised the %Corr measure. The optimal noise level was dependent on the signal level. Previous research has shown that specific levels of noise produce a maximum in the %Corr measure, however noise levels have not been previously expressed generally, in terms of characteristics of the target signal.

3.4.1 THERE IS AN OPTIMUM LEVEL OF NOISE THAT MAXIMISES %CORR

The results of the experiment are summarized in Figure 11. At the 90% signal level in both young and older subjects, 33% noise produced a maximum in %Corr ($F(5.169, 51.695)=3.087$, $p<.015$). At the 80% signal level, either 50% or 67% noise produced a maximum, however there were no statistical differences between the maxima in %Corr produced by these noise levels. This effect was frequency invariant. For all frequencies, signal levels and age groups, 0% noise and 100% noise produced chance results. All subjects showed the signature of SR, however occasionally the %Corr measure increased from the 83% noise condition to the 100% noise condition. There was no statistical difference in the %Corr measures produced by these 2 noise levels.

That the optimal level of noise was higher for the 80% signal level than the 90% level is reasonable, since one would expect a lower signal level to require a higher noise level for the two to combine to be supra-threshold. Greenwood, Ward and Wefelmeyer (1999) have proved this mathematically using Fisher information as the measure of SR. Their research has shown that as the distance from the signal to the threshold decreases, so does the optimal value of the noise variance, while the value of the information measure increases. There is a theoretical upper limit to the distance between the signal and threshold for which SR can still be achieved. Once the gap between signal and threshold becomes too great, the amount of noise increases to the point where it swamps the signal.

3.5 Discussion and Conclusions

Using a 2IFC design, it was shown that SR is effective in aiding the detection of sub-threshold signals in both young and elderly subjects. While similar in some respects, SR is a distinct phenomenon from negative masking. Both phenomena enhance the detectability of weak signals, however in negative masking, the stimulus and the masker must be sinusoids of the same frequency and phase (Hamer, Verrillo and Zwislocki, 1983; Verrillo, Gescheider Calman and Van Doren, 1983; Gescheider, Verrillo and Pelli, 1991). In SR, the "negative masker" is not a sinusoid, but noise.

The use of the 2IFC design to test the effectiveness of SR improved upon previous 1IFC designs, because it eliminated criterion effects. Further, the 2IFC design showed that the mechanism of SR does not just increase the energy in a stimulus (termed energy SR or type E SR), it increases the information that an organism can derive from a stimulus (termed

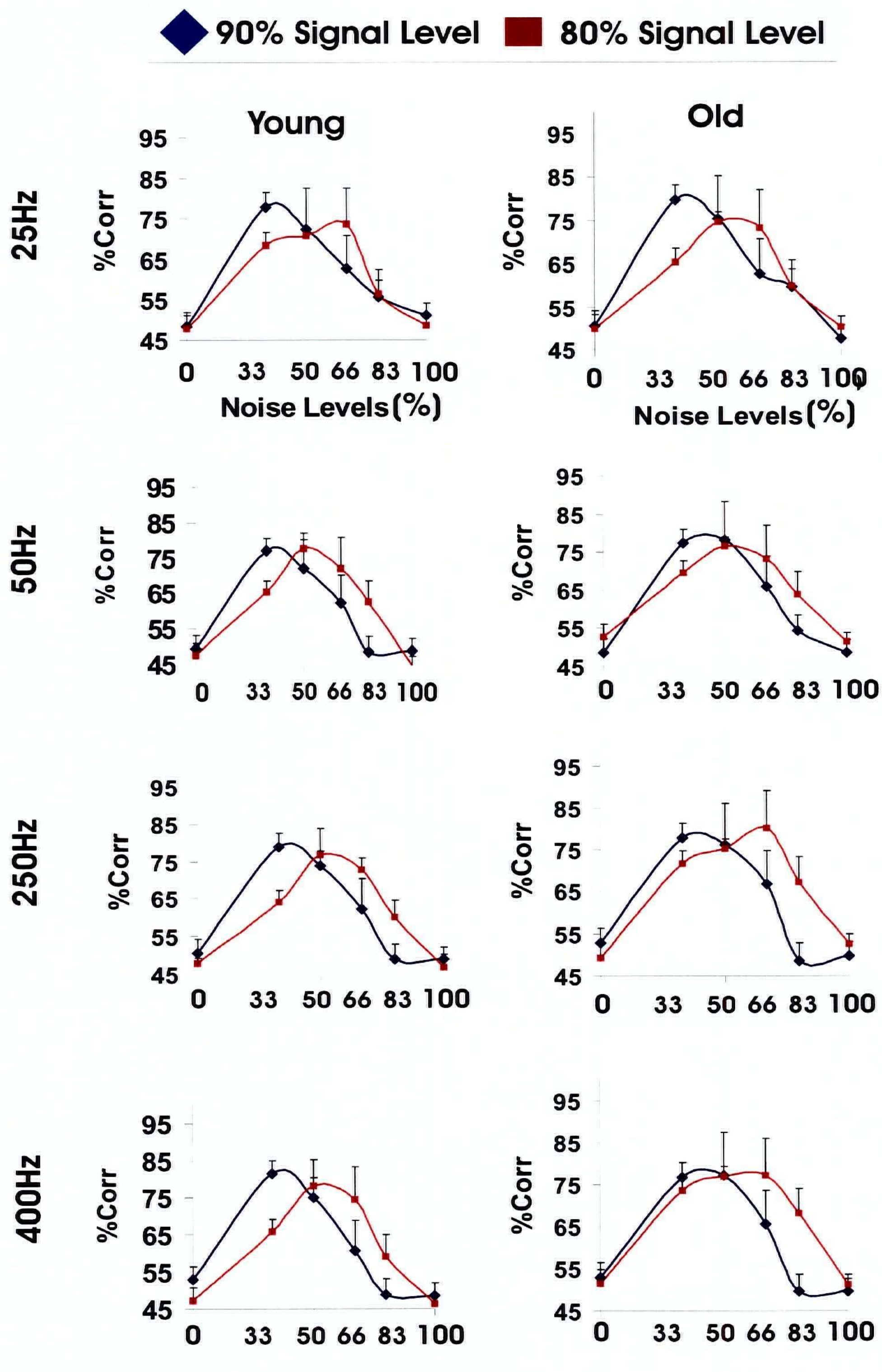


Figure 11: Values of the dependent measure, %Corr, vs. different values of the independent variables Frequency, Signal Level and Noise Level. At each frequency, %Corr shows the signature of SR: the value of %Corr with increasing noise rises quickly to an optimum, and then declines slowly.

information SR or type I SR (Ward, 2002)).

3.5.1 QUANTITATIVE IMPROVEMENT

Based on the results of the experiment, 2 main conclusions can be drawn regarding the use of SR in the elderly. The first is that noise can help the elderly feel what would otherwise be sub-threshold signals (90% and 80% of threshold). Second, because of the experimental design, it is possible to know *a priori* the characteristics of noise that will most improve vibrotaction sensitivity in the feet, based on how sub-threshold the signal is.

First, the use of SR rendered sub-threshold signals detectable to both young and old age groups. This has never before been demonstrated in either the young or the elderly footsole. The degree to which noise can improve sensation in the elderly can be expressed more compellingly in terms of improved performance, expressed in years of age. Assuming a linear increase in thresholds between the mean ages of the young and old groups, and further assuming that 90% and 80% signals are made at least threshold by the use of noise, SR allows the 88-year old (mean) nervous system to react like an 81- and 75-year old system, respectively, for the 2 sub-threshold signal strengths. This suggests that SR could be used as an aid to reclaim functionality in the elderly, and reduce injury resulting from lost functionality.

Second, since results show that the optimal amount of noise is related to the distance of the signal below threshold, it is possible to know *a priori* what level of noise will optimize the transmission of signal through the tactile system. With respect to a functional task (for example, using SR to facilitate the sensation of frequencies commonly felt by the plantar surface of the foot during walking or running) SR may alleviate some of the effects of gait dysfunction caused by diminished sensation in the foot. It has been hypothesized that plantar vibration sensation plays an important role in gait (Diener, Dichgans, Guschlbauer and Mau, 1984), and furthermore, that increased sensation thresholds on the plantar surface of the foot have been shown to cause gait dysfunction (Perry et al., 2000). This age-related plantar vibration sensation decrepitude may lead to pathological gait and falls, the major cause of accidental death in people over age 75 (Azar and Lawton, 1964). Were it possible to determine the vibration frequencies felt in the foot associated with gait, the sensation of these frequencies could be facilitated. It has already been shown that other types of plantar sensation facilitation have been helpful in the elderly by improving the effectiveness of stabilizing reactions evoked in response to unpredictable postural perturbations (Maki et al., 1999). It has been shown that electrical noise is effective in lowering detection thresholds for vibration (Dhruv et al., 2002), thus, it is likely that an SR aide could be developed using electrical noise to facilitate vibration sensation, perhaps via an electrical insole.

These conclusions, along with the fact that noise can help the elderly achieve a performance level (%Corr level) similar to young subjects, suggest that noise could be used as a sensory aid for the elderly.

3.6 Bridging Summary

The second study showed that SR is effective in lowering vibrotactile thresholds, and that it is effective in both young and elderly subjects. The amount of noise that optimizes the %Corr measure was dependent on the degree to which the target signal was below threshold.

The results of the experiment indicate that SR may potentially be developed into an aid for those with elevated thresholds. Similar to other types of plantar sensation facilitation that improve the effectiveness of stabilizing reactions in gait (Maki et al., 1999), an SR-based rehabilitative aid may work by lowering vibrotactile thresholds in the footsole, making it easier to engage the cutaneous reflexes involved in posture and gait that are initiated in the feet. Because the optimal amount of noise for aiding sub-threshold signal detection can be expressed as a characteristic of the signal itself, an SR aid could be implemented based on the how elevated a person's vibrotactile thresholds are, which is based loosely on age.

In the second study, subjects were required to differentiate noise from noise+signal. When both of these epochs are supra-threshold, this is an easier task than differentiating between 2 epochs that each contains a sinusoid of similar frequency. A person's accuracy at discriminating between 2 signals may have a bearing on cutaneous reflexes, since different reflexes may be activated by different frequencies. If a person's ability to discriminate signals can be improved, so too may the activation of reflexes triggered by the perception of those frequencies, which may in turn improve the aspects of gait that rely on perception of these cutaneous signals. This consideration motivated experiment 3.

4 EXPERIMENT 3

4.1 ABSTRACT

Stochastic resonance (SR) is a phenomenon whereby the addition of the right amount of noise to a sub-threshold stimulus can render the stimulus detectable by a sensory system. Recently, SR has been shown to be effective at lowering vibrotactile detection thresholds in the feet of young and old participants. To date, however, no research has been done asking whether SR can improve performance in a more complicated task. The goal of this experiment was to determine whether SR can decrease the differential threshold for cutaneous mechanical vibratory stimulus on the feet.

The effectiveness of SR in decreasing differential threshold detection was determined with a 2IFC paradigm, implemented using a 2 Age (young, old) X 2 SR Condition (SR, no SR) X 2 Frequency Range (around 25Hz, around 250H) X 6 Signal Level (90%, 100%, 110%, 150%, 300% of threshold, and 20dB above threshold) protocol on 6 younger and 6 older subjects. Results revealed that SR was effective in shrinking the differential threshold for young and old subjects in the 25Hz range at the 100% and 110% signal levels. At the 250Hz range, young subjects improved at the 100% and 90% levels, while older subjects improved at the 100% level only. The lack of improvement at the 90% level in older subjects at the 250Hz range does not necessarily refute the existence or benefits of SR at differentiating high frequencies in an older population, since different levels of noise than the levels tested here may prove beneficial.

4.2 INTRODUCTION

With age, many of the human sensory systems become decrepit: sight and hearing become less sharp, while the sense of taste also declines. It has been noted that the sense of touch is also affected by age. Vibrotactile thresholds at higher frequencies increase with age (Verrillo, 1979), a trend that increases proximal to distal in the body (Kenshalo, 1986). Thus, footsole vibrotactile thresholds for higher frequencies are elevated in the elderly, and, it has been hypothesized that these elevated thresholds may contribute to dysfunctional gait (Perry et al., 2000).

In humans, vibrotaction is divided into 2 sub-modalities: flutter sensation and vibration (Talbot, Darian-Smith, Kornhuber and Mountcastle, 1968). Each of these sub-modalities is encoded via a specific type of cutaneous afferent: FAIs encode approximately 8-64Hz; while FAIIs, in general, mediate frequencies between 64Hz and 500Hz. Several studies have shown that vibrotactile detection thresholds in the FAII mediated frequency range increase with age, in both the glabrous skin of the hand (Verrillo, 1979; Kekoni et al., 1986) and foot (Kenshalo, 1986). Further, evidence from psychophysical studies suggests that increasingly higher frequencies become mediated by FAI afferents as a person ages (Verrillo).

The ability to differentiate vibrotactile stimuli of different frequencies, called the differential threshold for frequencies, has been investigated both in animal models (Mountcastle, Talbot et al., 1969; LaMotte and Mountcastle, 1975) and humans (Goff, 1967; Mountcastel, Talbot et al., 1969; LaMotte and Mountcastle, 1975; Goble and Hollins, 1994). On the hand at least, differential thresholds are similar between humans and monkeys, suggesting that the peripheral and central mechanisms used for frequency differentiation are comparable between the species (Mountcastle et al.). While the hands of monkeys and humans have similar acuity,

acuity may vary on the same animal on different body parts. An investigation by Rothenberg, Verrillo, Zahorian, Brachman and Bolanowski (1977) comparing frequency discrimination ability on the fore-arm, the thenar eminence of the hand and the fingertip found that of the 3 areas, the forearm was the least sensitive (had the highest differential threshold) and the finger was the most sensitive. This indicates that different areas of the body have different vibrotactile acuity, presumably based on the function of the body area Rothenberg et al., 1977). We know of no studies showing whether differential thresholds are influenced by age, as are detection thresholds.

One method of alleviating possible age effects on differential thresholds is via SR, a phenomenon in which the detection of a sub-threshold signal is enhanced by the presence of noise (Chialvo et al., 1993, Douglass et al., 1993; Pei et al, 1996; Collins et al., 1996; Gammaitoni et al., 1998). The SR phenomenon has been demonstrated experimentally in the auditory system (Garver and Moss, 1995), in the visual system (Ward, et al., 2001) and in the young human tactile system (Collins et al., 1997; Richardson et al., 1998). Recently, SR has been shown to be effective in lowering vibrotactile thresholds in the feet of the elderly, who in general have elevated sensory thresholds at hypothesized FAI mediated frequencies. Because SR can improve the ability of the elderly to detect weak vibrotactile signals, SR may be useful as a rehabilitative aid for such functions as grasp, where the detection of low amplitude vibration in crucial in the generation of appropriate grasp forces, and gait, since elevated detection and differential thresholds in the feet may lead to pathological gait (Perry et al., 2000).

The purpose of this experiment was to determine if SR can aid people in discriminating between 2 different vibrotactile frequencies - specifically, whether SR can decrease the differential threshold. The foot was chosen as the test location because of the worsening proximal to distal effects of age related neuropathies. Testing on the footsole also allowed us to compare these results with the previous 2 studies. If the elderly have increased differential thresholds that contribute to dysfunctional gait, SR techniques, if proven beneficial in lowering differential thresholds, could be used as an aid to alleviate this dysfunction.

4.3 METHODS

4.3.1 OVERVIEW

The protocol was implemented in 4 different stages: stage 1: absolute threshold determination, stage 2: equal subjective intensity determination, stage 3: un-aided frequency discrimination, and stage 4: SR aided frequency discrimination. The primary goal of this experiment was to determine whether SR could improve a subject's ability to differentiate 2 different frequencies, as measured by their accuracy at identifying the higher of 2 frequencies. To determine this, a 2IFC protocol was used in stages 3 and 4: stage 3 used no SR, while stage 4 did. The protocol was implemented in a 2 Age (young, old) x 2 SR Condition (SR, no SR) x 6 Signal Level (90%, 100%, 110%, 150%, 300% of threshold, and 20dB above threshold) x 2 Frequency Range (around 25Hz, around 250Hz) design. There were repeated measures on all factors except age. If SR *does* aid in frequency differentiation, then participants should be able to correctly identify the epoch with the higher frequency with less of a frequency difference between the 2 epochs in the SR condition, than in the no SR case. The different signal levels were chosen to demonstrate the effect, if any, of noise on different levels of signal. The 20dB level was chosen to compare our results from the un-aided frequency differentiation procedure with those of other investigations (Goff, 1967).

Two procedures were implemented prior to the SR/no SR protocol. In stage 1, detection thresholds were determined at the ranges of 25-35Hz and 250-390Hz Hz. This was done so that the 6 signal levels used in the SR testing procedures of stages 3 and 4 could be calculated. In stage 2, subjective intensity bands were determined for the 25 and 250Hz ranges, so that the signal portions of the epochs were presented at the same subjective intensity (Goff, 1967; Mountcastel et al., 1969, LaMotte and Mountcastle, 1975; Rothenberg et al., 1977).

4.3.2 Subjects

Research was conducted with approval of the UBC Office of Research Services and Administration Behavioral Research Ethics board. Twelve participants were used: 6 from a young age group (mean age=28 years, + 4 years 8 months/-3years, 4 months) and 6 from an older age group (mean age=70 years, +12 years 5 months/-8 years 1 month). Participants were self-reported free of neurological disease. Some participants in both age groups were taking medication, however none of the medications have been shown to affect the sense of touch.

4.3.3 Equipment, Instrumentation and Stimuli

The equipment, vibrotactile stimuli and instrumentation were set up as in studies 1 and 2. The noise portion of the stimuli was Butterworth band-pass filtered white noise, so that when testing FAI mediated frequencies (young subjects: approximately 29Hz and below; older subjects: entire low range), only FAI mechanoreceptors would be activated by the noise (filter band-pass for young subjects: 0.125Hz to 29Hz; filter band-pass for older subjects: 0.125Hz-35Hz). While testing FAII mediated signal frequencies (young subjects: above 30Hz; older subjects: entire high range), noise was band-pass filtered to contain only FAII mediated frequencies (filter band-pass for young subjects: 30Hz to 400Hz; filter band-pass for older subjects: 250Hz to 400Hz). Noise filtering in an SR tactile protocol has been done by Collins et al, (1997). While high-frequency noise would not detract from the FAI receptors ability to detect the signal, it would activate FAII receptors in the vicinity and possibly confound threshold levels or have a sub-threshold priming effect on FAI receptors. Frequency mediation was hypothesized based on the work of Verrillo (1979) and the results of Study 1. Stimuli were sampled at 10KHz.

As in experiments 1 and 2, force data were used to ensure that the stimulus was applied with constant force. Trials in which the force application was irregular (for example, if the footsole moved beneath the lever arm) were discarded and the trials repeated. The number of re-done trials ranged from a minimum of 2 trials to a maximum of 7 trials per condition, per subject. Data were collected using LabView 4.2 at a sampling rate of 10 times the experimental frequency.

4.3.4 PROCEDURES

Procedures were implemented over 2 successive days. On the first day, stages 1 (absolute threshold determination) and 2 (equal subjective intensity determination) were implemented, as well as one of stages 3 and 4. On the second day, the remaining of the last 2 stages was completed. This was done because the entire protocol was too long to implement on one day. The order of presentation of stages 3 and 4 was randomized across subjects. On the second day of testing, an abbreviated version of stage 1 was implemented in order to ensure that the participant's threshold had not changed substantially. Subjects rested whenever they desired during the experiment.

4.3.4.1 Stage 1: Vibrotactile detection threshold determination

Vibrotactile detection thresholds were determined for 2 frequency ranges ([25Hz, 35Hz] and [250Hz, 390Hz]) at 1 location on the footsole (see Figure 8) in young and old age groups. The frequencies were chosen to fit the range of physiological response in human cutaneous receptors (Johansson et al., 1982), and to show the mediation changes suggested by the literature (Verrillo, 1979; Kekoni et al., 1989). The location was chosen to compare results with experiment 2.

Detection thresholds were calculated at 0.5Hz increments above the 25Hz range, and 5 Hz increments above the 250Hz range using the method discussed in study 1. This iterative procedure was repeated 5 times. The last 4 of 5 up and down pairs were averaged to determine the threshold value.

Thresholds for each frequency range were determined starting at the standard frequency (25Hz and 250Hz). Once the threshold was determined at the standard, the threshold was determined for the new frequency by increasing the frequency by .5Hz for the range starting at 25Hz, and 5 Hz for the range starting 250Hz. These procedures were repeated for each new frequency until the upper limit of the frequency range was reached.

4.3.4.2 Stage 2: Equal subjective intensity determination

Using the method of limits with equal judgements allowed, frequencies at 2Hz intervals within the 25-35Hz frequency range were compared randomly with the 25Hz standard, and frequencies at 20Hz intervals within the 250-390Hz frequency range were compared randomly with the 250Hz standard. At each interval, the participant was presented with 2 stimuli: a standard (25Hz or 250Hz), and a comparison. The standard and comparison stimuli initially contained the same power; the amplitude of the comparison was either increased or decreased by the experimenter in 10% increments until the participant indicated that the 2 stimuli felt equal. Each interval was tested twice, and the 2 values for the intervals were averaged. This procedure was followed for 5 different power settings relative to the standards: 100%, 110%, 150%, and 300% of threshold power and 20dB.

4.3.4.3 Stage 3: Upward differential frequency threshold determination

Upward differential frequency threshold determination was done with the standards 25Hz and 250Hz at 6 signal levels of the standard frequency: 90%, 100%, 110%, 150% and 300% of threshold power, and 20dB above threshold. Similar to Goff (1967), thresholds were determined only above the standard frequencies due to time constraints (hence the term "upward" differential frequency threshold). In each trial, 2 epochs were presented, one containing the standard frequency, and one containing a comparison frequency. The task of the participant was to identify which of the 2 epochs contained the higher frequency. The participant's accuracy at correctly identifying the higher interval at each standard-comparison pairing was quantified using %Corr (Collins et al., 1997; Richardson et al., 1998). The frequency of the comparison epoch was randomly changed for each trial to one of the 24 increments in the low range, or one of the 33 increments in the high range. For the threshold and supra-threshold signal levels, the amplitude of the signal in the comparison epoch was adjusted to keep the intensity of the signal within the center of the subject's variable intensity band. For the 90% condition, both signal levels were 90% of threshold. The standard and variable epochs were presented in random order. Each stimulus was 1-second long, with a 1-second inter-epoch time.

An adaptive algorithm was used to present the standard-comparison pairings. Trials were presented in blocks, with each block containing 5 trials of each standard-comparison pairing (120 trials per block for the 25Hz range, 165 trials per block in the 250Hz range). To begin, 2 blocks were presented with as much of a rest interval between the blocks as needed. The participant's %Corr at each standard-comparison interval was monitored as the experiment progressed so that for subsequent blocks, only those intervals where the subject did not score perfect (10 out of 10) or chance (5 out of 10) were repeated. The minimum number of trials for any given pairing was 10, and the maximum number was 30. Completion times for each signal level ranged from 20 minutes to 1 hour.

4.3.4.4 Stage 4: SR aided frequency discrimination

In this stage, noise was added to sub-threshold and supra-threshold signals to determine how the addition of noise would affect the ability of subjects to differentiate frequencies. In this procedure, the signal portions of the stimuli were determined by selecting the signal level of the standard frequency, and selecting the level of the corresponding comparison frequency so that this level was in the middle of the participant's subjective intensity band as in stage 3. The optimal amount of noise for the 90% threshold signal (33% noise, as determined in Study 2) was added to whichever epoch contained higher power. Enough noise was added to the other epoch so that both epochs contained the same power. In the case of the 90% level signal, the signal portions of both epochs were determined as 90% of power at threshold, since both signals, being below threshold, were presumably equally subjective. Completion times for each signal level ranged from 20 minutes to 1 hour.

4.3.5 Data Analysis

4.3.5.1 Stages 1 and 2: Detection threshold determination and equal subjective intensity determination

Detection thresholds for each subject at each of the frequencies in the test ranges were recorded and used in subsequent stages of the experiment. Representative results are shown from one subject in each age group in Figure 12. A one-way ANOVA was performed to determine if the means at 25Hz and 250Hz from this experiment were statistically different from those from Study 1. Next, subjective intensity bands were plotted for each participant at each signal level. Results from single subjects are shown in and Figure 13 and Figure 14.

4.3.5.2 Stage 3: Frequency Discrimination

In order to compare our data with those of previous studies by other researchers, the Weber fraction for differential discrimination was calculated at the differential threshold (Weber fraction = frequency difference/frequency).

4.3.5.3 Stages 3 and 4: Frequency Discrimination vs. SR aided frequency discrimination

Statistica (StatSoft Inc.) was used to fit each participant's %Corr data points to a logistic curve. The model for the curve, based on a model from Macmillan and Creelman (1991) was corrected for the range of %Corr (from 50% to 100%). The model was:

$$y = .5\left[\frac{1}{\left(1+e^{\frac{(-(x-\alpha))}{\beta}}\right)}+1\right]$$

where: x represents the frequency difference

y represents the %Corr

α represents the frequency difference at which the participant could correctly identify the higher frequency 75% of the time. This value was taken as the upward differential threshold (Macmillan and Creelman, 1991)

β represents the inverse of the slope of the linear portion of the curve (range of x values in linear portion)

Both parameters α and β were calculated numerically, using either the Quasi-Newton method or the Hooke-Jeeves pattern moves method. The parameter α was the dependent variable of interest used in subsequent ANOVAs. Psychometric functions for each signal level and frequency range are shown for the young and old average (see Figure 15 and Figure 16).

In certain cases the value of the parameter α was outside the range of intervals that were tested. In these situations, the value for α was extrapolated from the %Corr values. Occasionally, as occurred in the 90% signal condition with no SR, α was infinite, and the logistic function was not a good fit for the psychometric curves. In order to compare the results of the different conditions however, the logistic fit was used, and to accommodate this for the purposes of running ANOVAs, a value slightly larger than the largest naturally occurring value was chosen to replace infinity. These replacement values were calculated by adding 10% to the largest naturally occurring value, and then rounding to the nearest whole number. Whole numbers were used so that the replacement values could be easily distinguished from the natural values. For the 25Hz range, this value was set at 16Hz; for the 250Hz range, 200Hz was used. ANOVA conditions and the values used are presented Table 4 and Table 5. The entry "Nat" for "natural" in the tables indicates that the values were either within the range tested, or were extrapolated to a non-infinite value. In cases where the α parameter was infinite, the value used in the ANOVA is entered in the table.

	25Hz											
	No SR						SR					
	20dB	300%	150%	110%	100%	90%	20dB	300%	150%	110%	100%	90%
Young	Nat	Nat	Nat	Nat	16	16	Nat	Nat	Nat	Nat	Nat	Nat
Old	Nat	Nat	Nat	Nat	16	16	Nat	Nat	Nat	Nat	Nat	16

Table 4 :Calculable ANOVA conditions for the 25Hz range

	250Hz											
	No SR						SR					
	20dB	300%	150%	110%	100%	90%	20dB	300%	150%	110%	100%	90%
Young	Nat	Nat	Nat	Nat	200	200	Nat	Nat	Nat	Nat	Nat	Nat
Old	Nat	Nat	Nat	Nat	200	200	Nat	Nat	Nat	Nat	Nat	Nat

Table 5: Calculable ANOVA conditions for the 250Hz range

Since we can expect larger differential thresholds at 250Hz than at 25Hz due to the Weber's law, ANOVAs for each range were run separately. This produced an ANOVA for the low range and an ANOVA for the high range with the following factors: 2 SR Condition (No SR; SR) X 6 Signal Level (20dB, 300%, 150%, 110%, 100%, 90% of threshold) X 2 Age (young, old). Interactions were considered significant at $p<.01$. Greenhouse-Geisser corrections were used to account for sphericity violations. Tukey HSD *post hoc* analysis was performed on the interactions. Because there was a k value of 24 and tables of the Studentized range statistic only go up to 15, q was extrapolated using a logarithmic curve fit from values 2 through 15 ($q=1.030\ln(x)+3.2223$; $R^2=.9945$).

4.4 RESULTS

4.4.1 STAGES 1 AND 2: DETECTION THRESHOLD DETERMINATION AND SUBJECTIVE INTENSITY BANDS

Typical thresholds for young and old subjects at the 2 frequency ranges are presented in Figure 12. A 1-way between experiment ANOVA revealed that thresholds at 25Hz (young: 0.805nJ; old: 0.875nJ) and 250Hz (young: 0.0208nJ; old: 0.1333nJ) were not significantly different from values at the same frequencies from Study 1 ($F(1,10)=.897$, $p=.3659$). This confirmed the stability of using 4 out of 5 pairs to determine absolute thresholds.

In the 25Hz range, plots of threshold values and subjective intensity bands showed traces for both young and old groups were relatively horizontal, however there was a slight negative slope to the portion of the young subjects thresholds and bands in the frequencies above 29Hz. In the 250Hz range, the thresholds and bands for the young subjects were flat, while the bands for the older subjects had a positive monotonic slope.

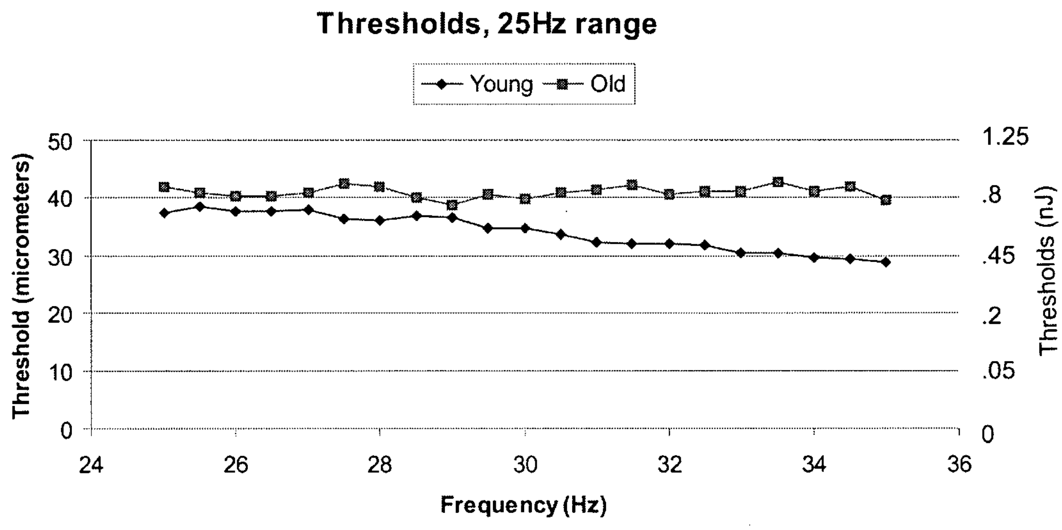
To our knowledge, no equal subjectivity bands other than ours have been generated for vibrotactile sense on the footsole. Once the higher detection thresholds of the footsole had been considered, however (Kekoni et al., 1989: thresholds on the hallux are approximately 100X that of thenar eminence at 240Hz; Kenshalo, 1986: thresholds on the plantar are approximately 6.3X that of the thenar eminence at 250Hz in men), equal subjectivity bands were comparable to results reported in other studies on the hand at similar amplitudes (Goff, 1967; Verrillo, Fraioli and Smith, 1969; Verrillo, 1970; Sinclair and Burton, 1996). Examples of equal subjectivity bands for one young and one old subject are shown in Figure 13 and Figure 14

Since detection thresholds and equal subjective intensity bands were determined only in order to undertake stages 3 and 4, these results will not be discussed further.

4.4.2 Stages 3 and 4: Frequency Discrimination vs. SR Aided Frequency Discrimination

4.4.2.1 Differential thresholds -- 25Hz range

Psychometric functions of averaged data for young subjects and older subjects for each signal level are shown in Figure 12. Each plot shows the psychometric function for the SR and the no SR condition, as well as traces showing the percent of the total possible trials used to determine the value of the corresponding point (percent = sum of the number of points across subjects/ by the total possible trials, 180). The first 2 plots also show a logistic curve fit to the data using Equation 2.



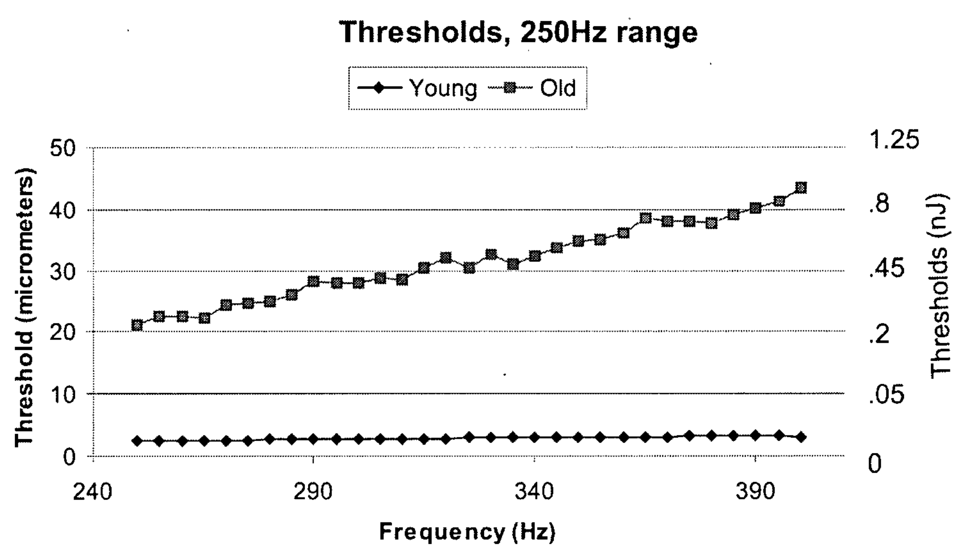
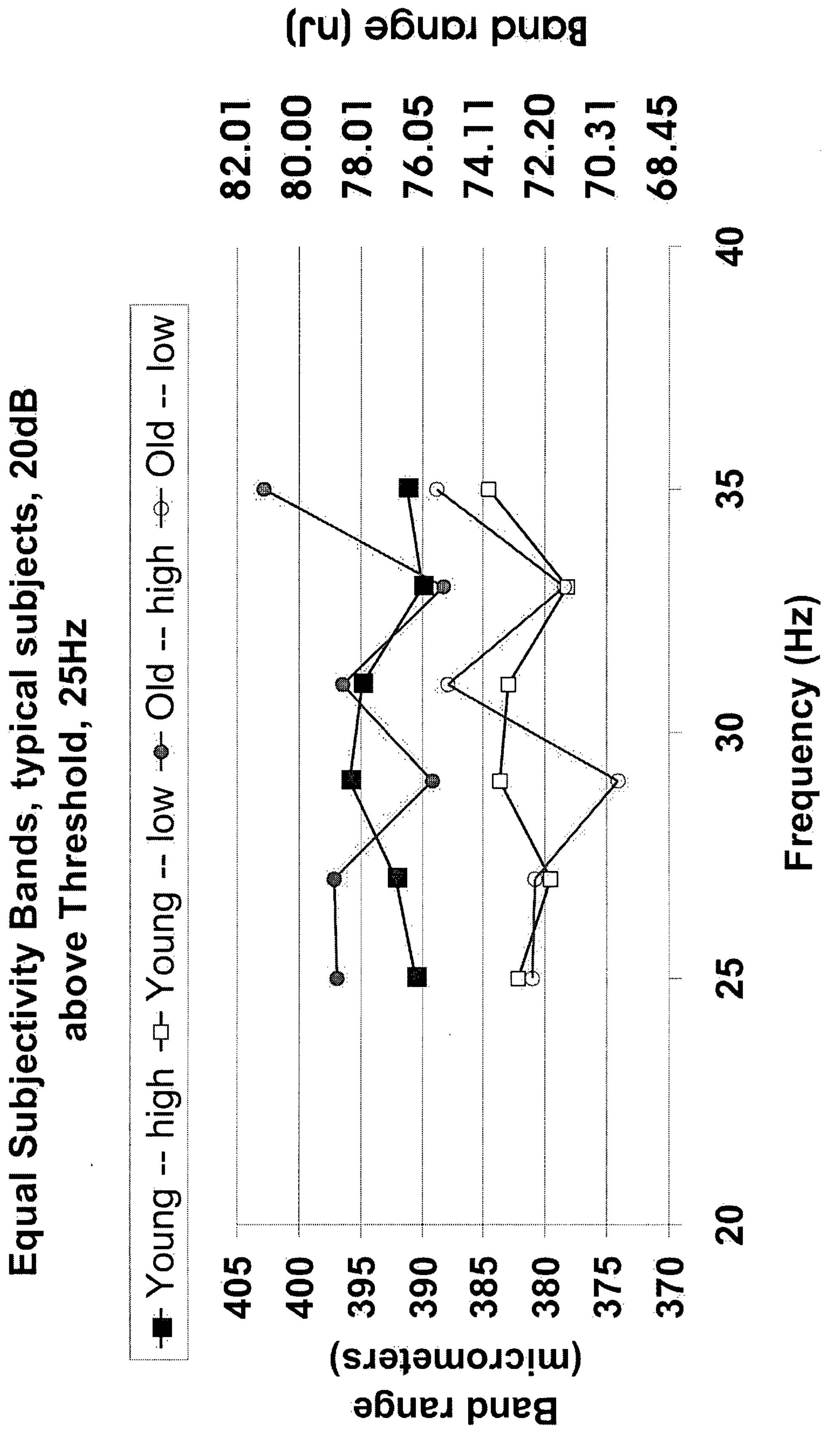


Figure 12: Thresholds from the 25Hz (top panel) and 250Hz (bottom panel) frequency ranges for 1 young and 1 older subject.


Equal Subjectivity Bands, typical subjects, 20dB above Threshold, 25Hz
Young -- high
Young -- low
Old -- high
Old -- low
Band range (micrometers)
405
400
395
390
385
380
375
370
20
25
30
35
40
Frequency (Hz)
Band range (nJ)
82.01
80.00
78.01
76.05
74.11
72.20
70.31
68.45

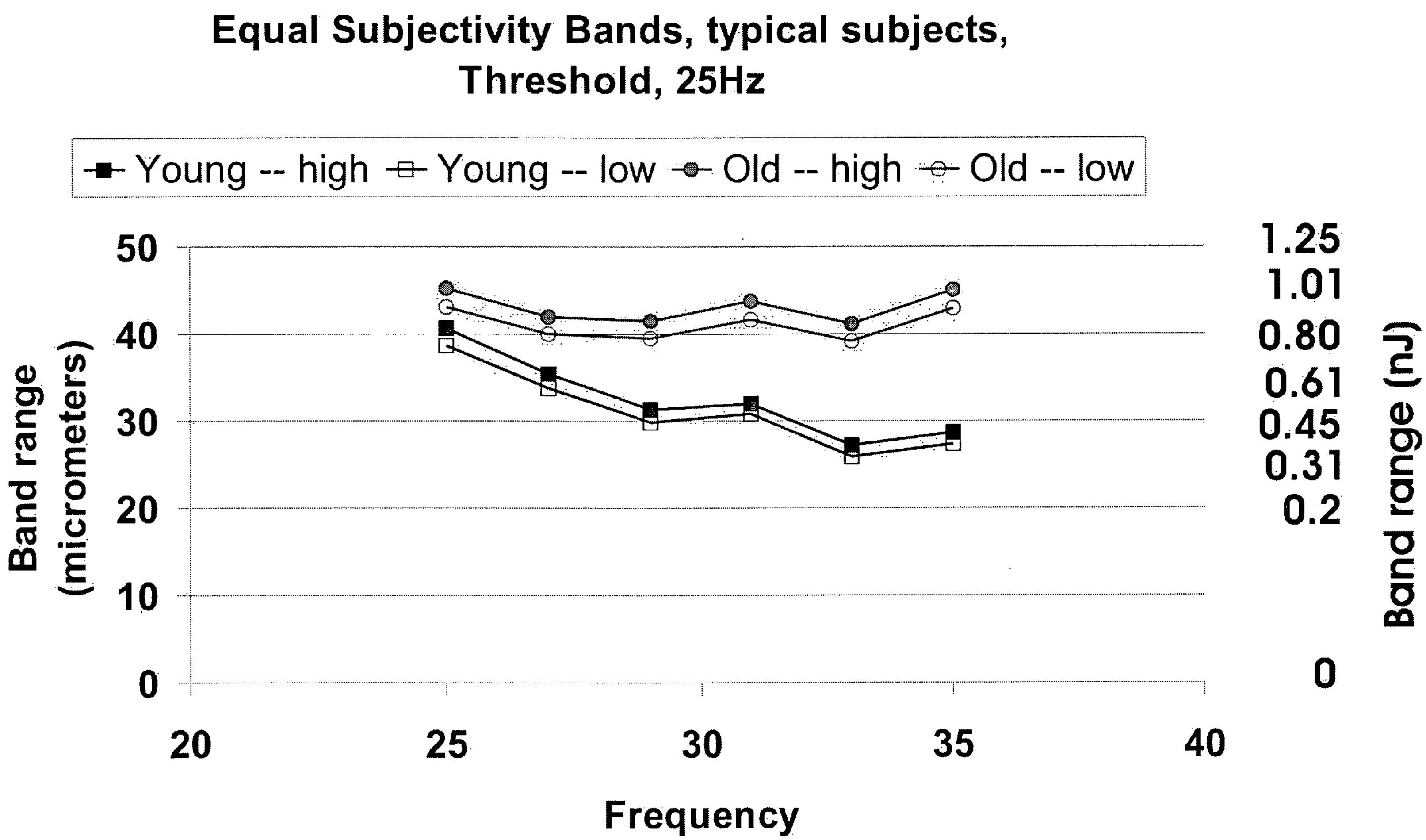
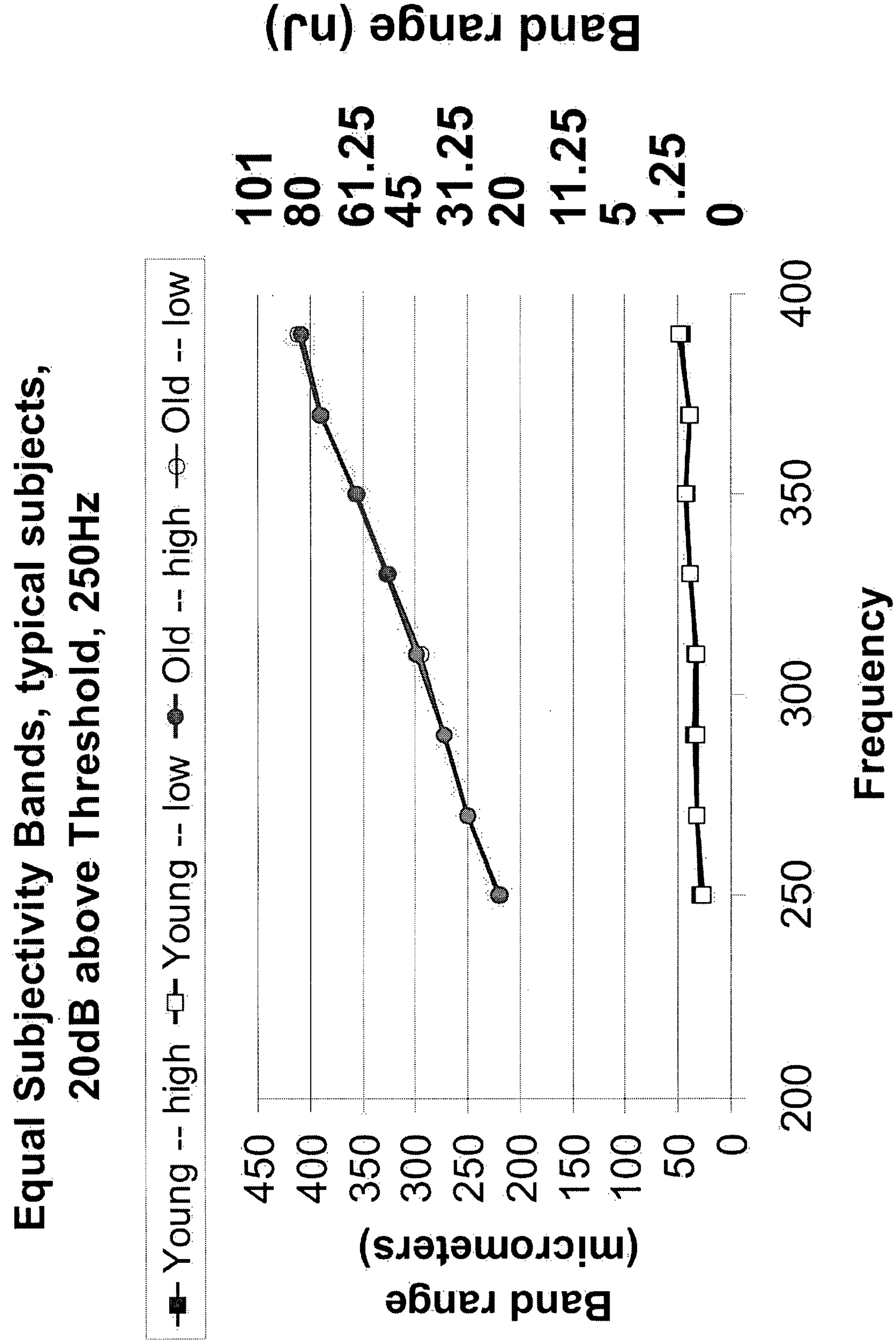


Figure 13: Subjective intensity bands for the 25Hz range. Bands for 1 young and 1 older subject are shown for the 20dB (first panel) and threshold (second panel) power levels.



Equal Subjectivity Bands, typical subjects,
20dB above Threshold, 250Hz
Young -- high
Young -- low
Old -- high
Old -- low
Band range (micrometers)
450
400
350
300
250
200
150
100
50
0
200
250
300
350
400
Frequency
101
80
61.25
45
31.25
20
11.25
5
1.25
0
Band range (nJ)

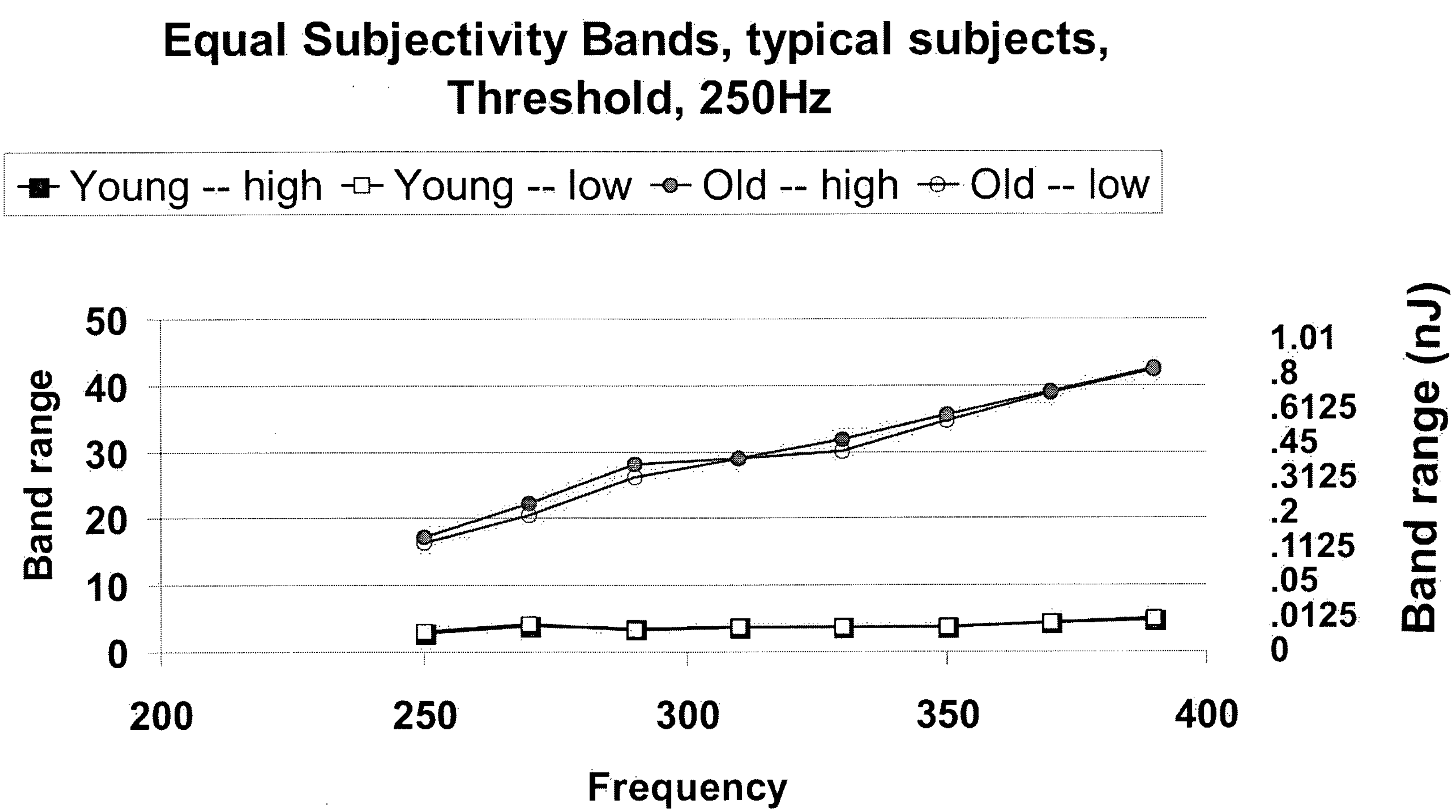
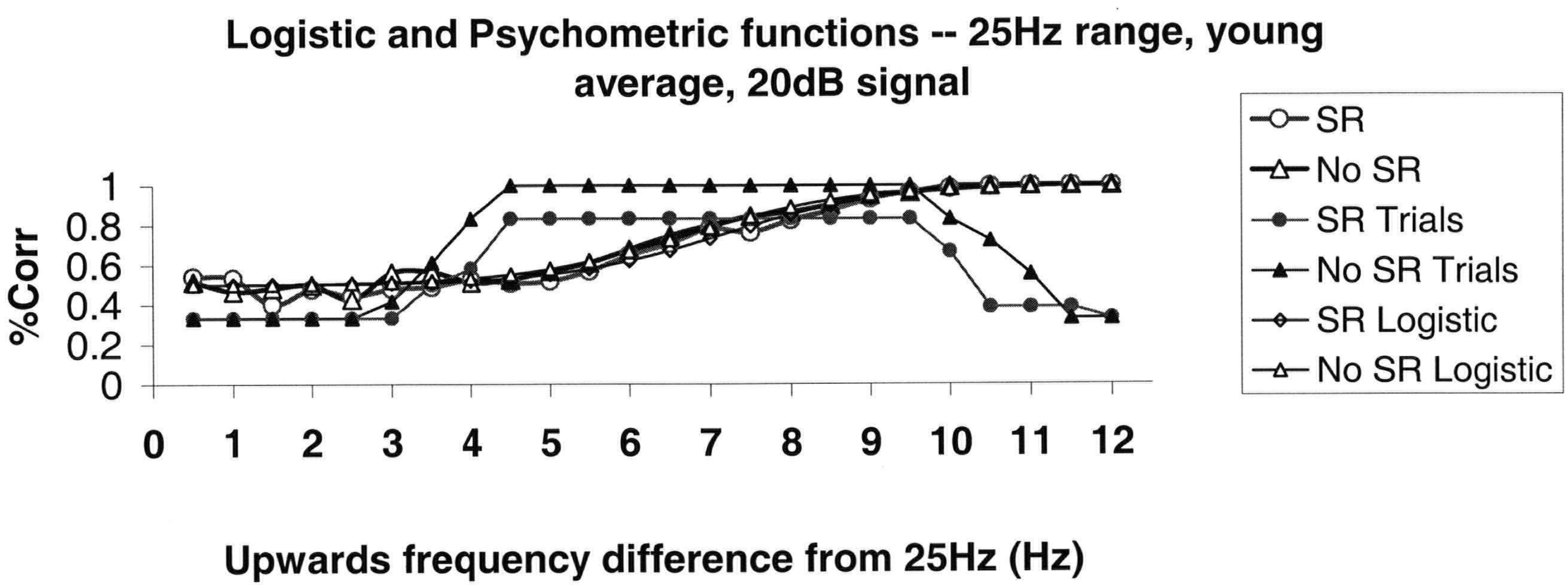


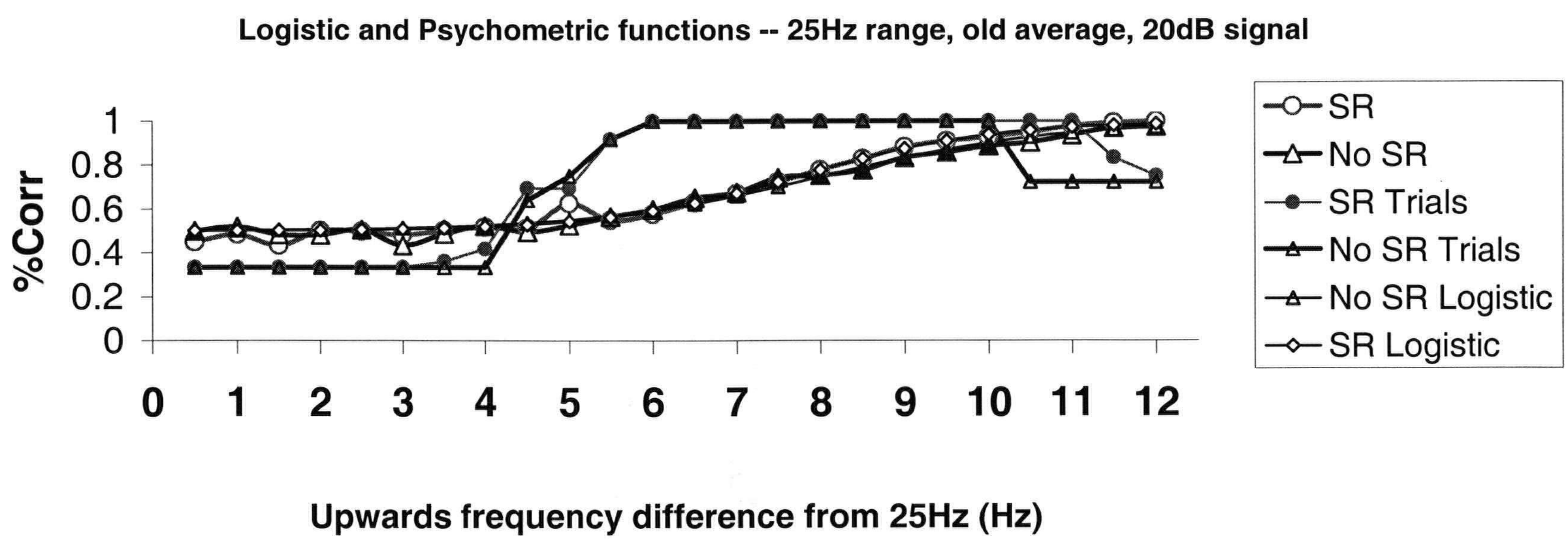
Figure 14: Subjective intensity bands for the 250Hz range. Bands for 1 young and 1 older subject are shown for the 20dB(first panel) and threshold (second panel) power levels.

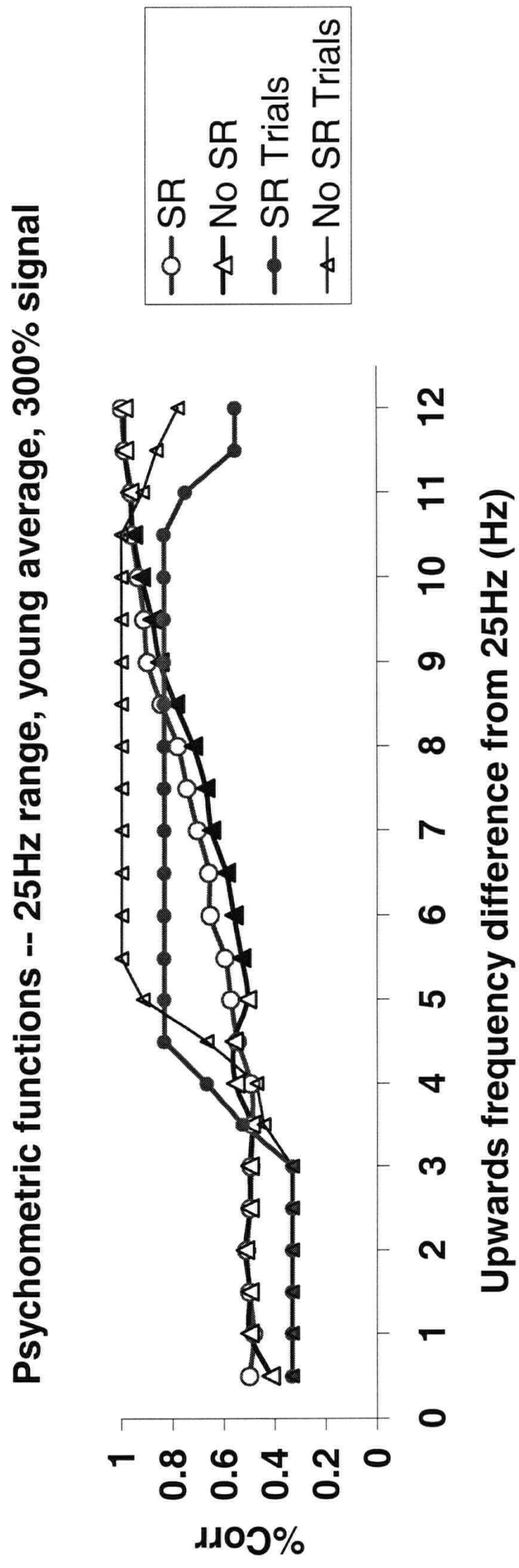
Figure 17 shows the average upward differential threshold for each condition and age group. At the 25Hz range, ANOVA revealed an SR Condition X Signal Level interaction (Greenhouse-Geisser correction: $F(2.355, 23.552)=11.693$, $p<.01$, Tukey HSD critical difference=2.62Hz). For both young and old, SR significantly changed the upward differential threshold for 2 signal levels: 110% and 100%. The improvement at each of the signal levels was as follows: for the 110%, young subjects improved from 13.73Hz to 10.39Hz, while older subjects improved from 14.17Hz to 10.83Hz. At the 100% level, young subjects improved from 16.00Hz to 11.28Hz, while older subjects improved from 16.00Hz to 13.32Hz. For younger subjects, there was improvement at the 90% signal level as well (from 16.00 in the no SR condition to 13.438Hz in the SR condition), however the improvement was not enough to be considered significant (i.e.: was not greater than 2.62 Hz). For older subjects, the upward differential threshold could not be determined at the 90% signal level (i.e.: the psychometric function was flat).

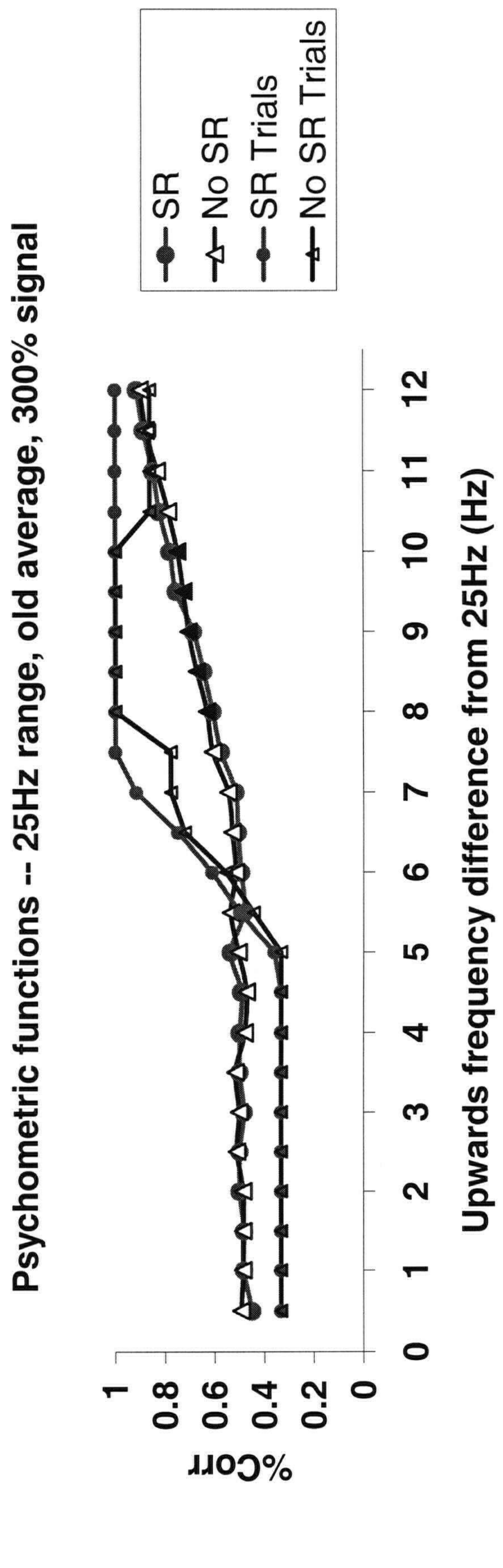
4.4.2.2 Differential thresholds -- 250Hz range

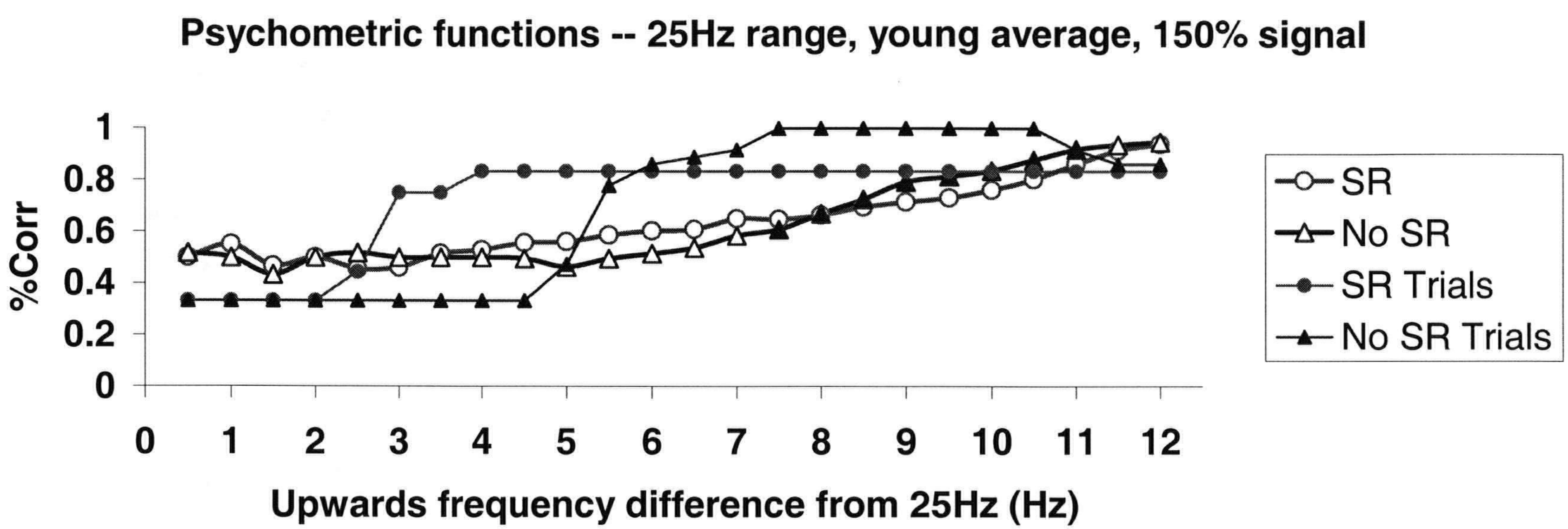
At the 250Hz range, there was an SR condition x Signal Level x Age interaction: detection improved at the 100 and 90% levels in young participants, but only at the 100% level in older participants (Greenhouse-Geisser correction: $F(3.331,33.312)=8.60$, $p<.01$; Tukey HSD *post hoc* analysis critical difference=20.12Hz). Young participants improved their upward differential threshold from 200.00Hz to 153.16Hz at the 100% signal level, and from 200.00Hz to 157.09Hz at the 90% signal level. Older participants improved from 200.00Hz to 160.23Hz at the 100% level. SR produced improvement in only one older subject at the 90% signal level.

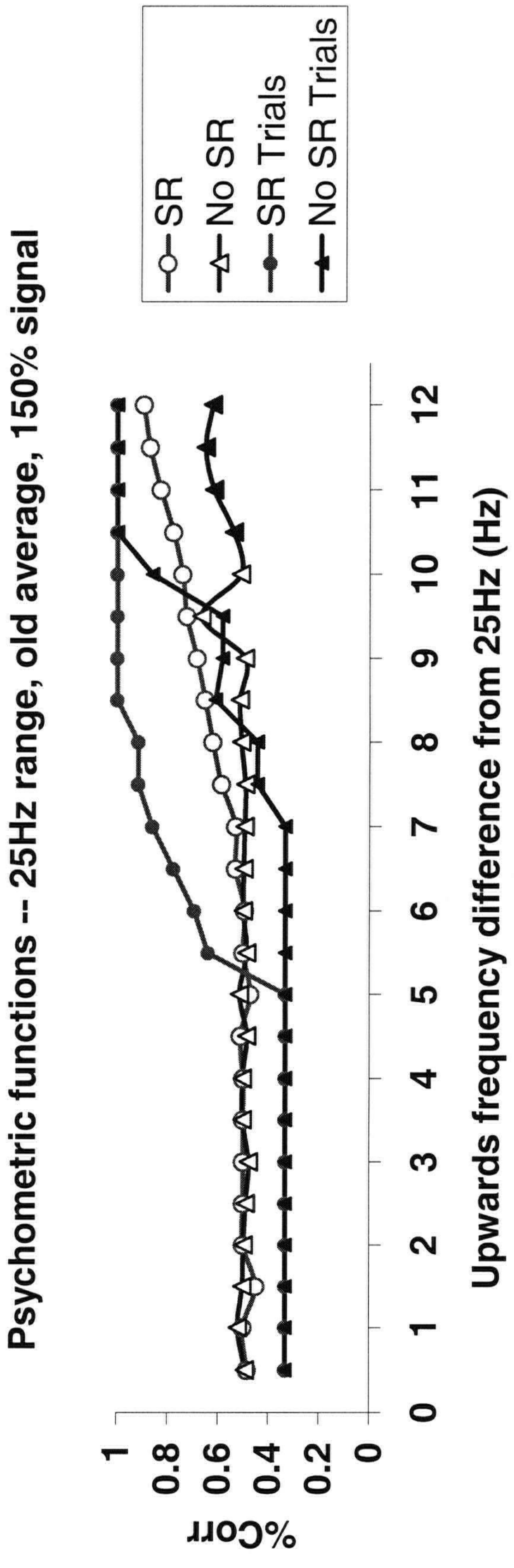

Logistic and Psychometric functions -- 25Hz range, young average, 20dB signal
%Corr
0
0.2
0.4
0.6
0.8
1
0 1 2 3 4 5 6 7 8 9 10 11 12
Upwards frequency difference from 25Hz (Hz)
SR
No SR
SR Trials
No SR Trials
SR Logistic
No SR Logistic

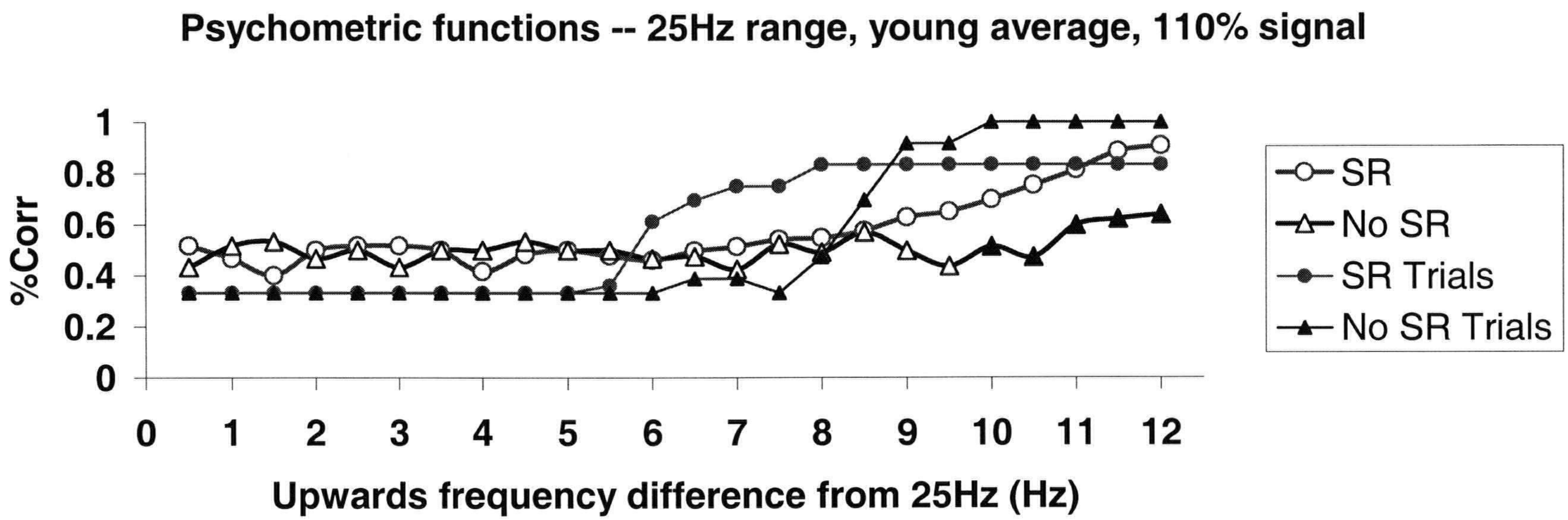

Logistic and Psychometric functions -- 25Hz range, old average, 20dB signal
%Corr
1
0.8
0.6
0.4
0.2
0
0 1 2 3 4 5 6 7 8 9 10 11 12
Upwards frequency difference from 25Hz (Hz)
SR
No SR
SR Trials
No SR Trials
No SR Logistic
SR Logistic

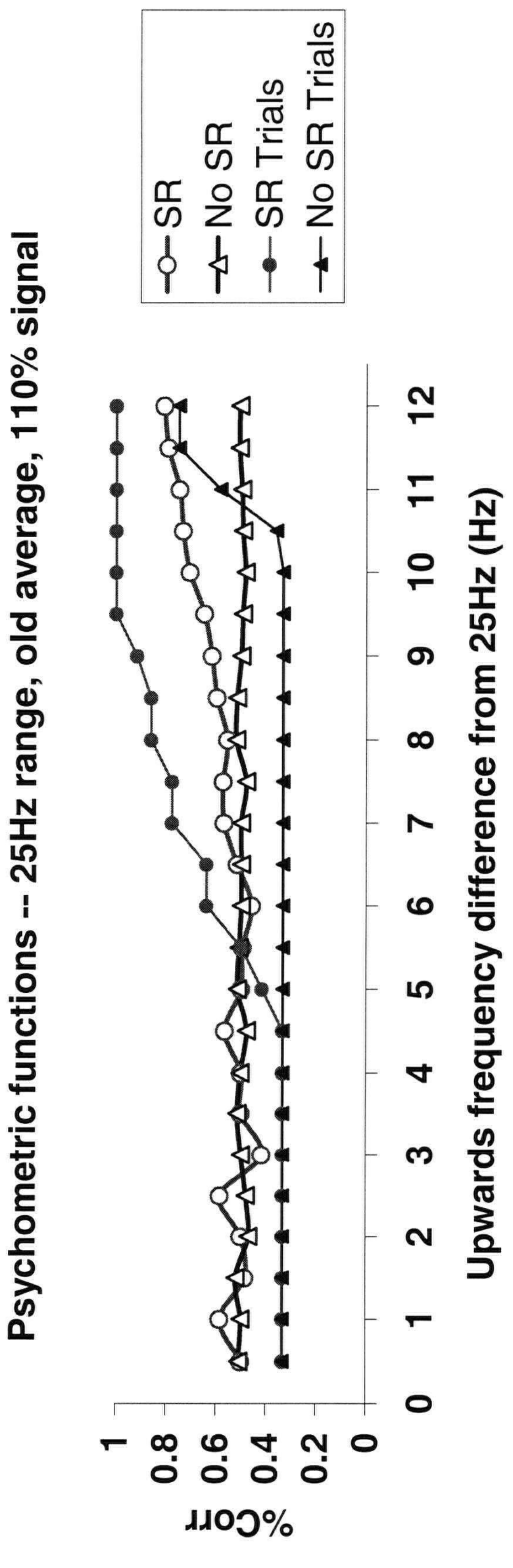

Psychometric functions -- 25Hz range, young average, 300% signal
%Corr
0
0.2
0.4
0.6
0.8
1
0
1
2
3
4
5
6
7
8
9
10
11
12
Upwards frequency difference from 25Hz (Hz)
SR
No SR
SR Trials
No SR Trials


Psychometric functions -- 25Hz range, old average, 300% signal
%Corr
1
0.8
0.6
0.4
0.2
0
0
1
2
3
4
5
6
7
8
9
10
11
12
Upwards frequency difference from 25Hz (Hz)
SR
No SR
SR Trials
No SR Trials

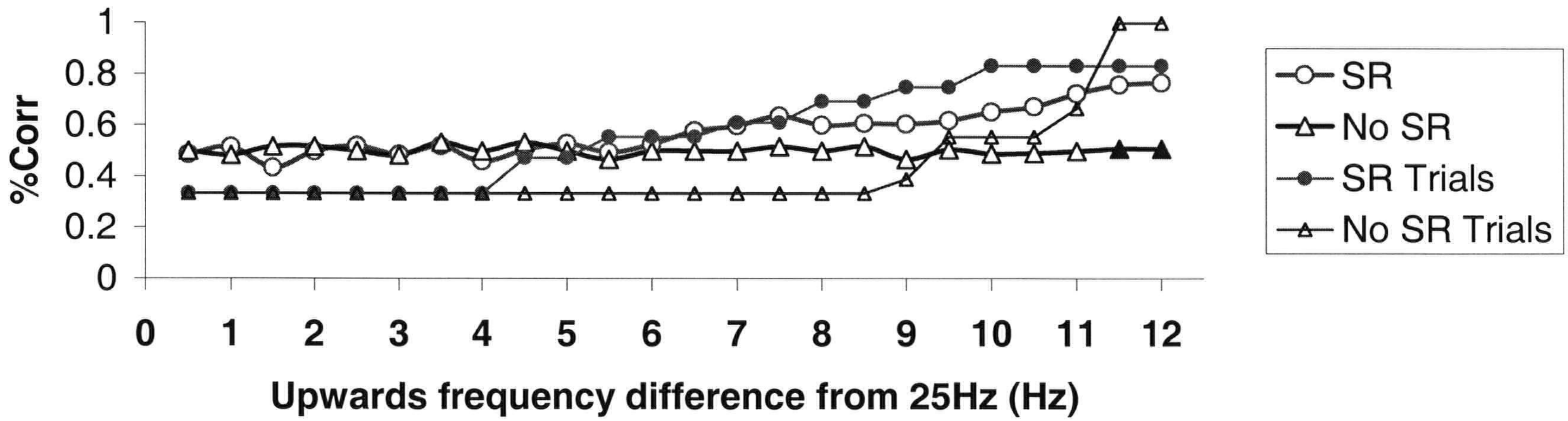

Psychometric functions -- 25Hz range, young average, 150% signal
%Corr
1
0.8
0.6
0.4
0.2
0
0 1 2 3 4 5 6 7 8 9 10 11 12
Upwards frequency difference from 25Hz (Hz)
SR
No SR
SR Trials
No SR Trials

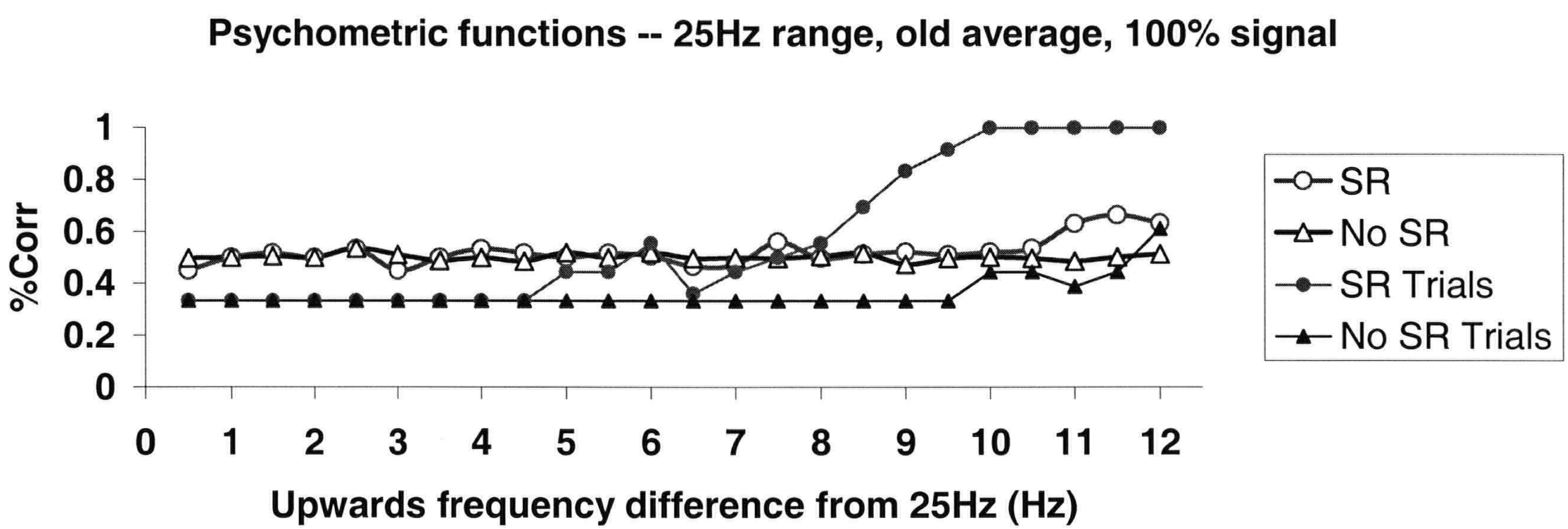

Psychometric functions -- 25Hz range, old average, 150% signal
%Corr
1
0.8
0.6
0.4
0.2
0
0
1
2
3
4
5
6
7
8
9
10
11
12
Upwards frequency difference from 25Hz (Hz)
SR
No SR
SR Trials
No SR Trials

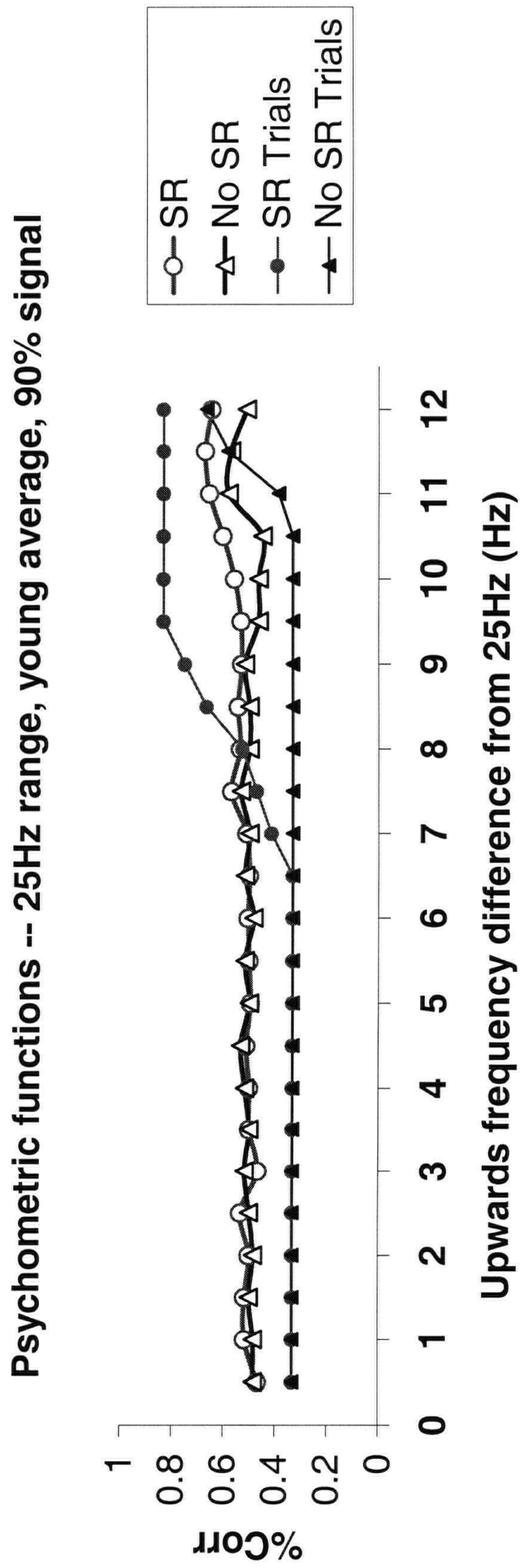

Psychometric functions -- 25Hz range, young average, 110% signal
%Corr
1
0.8
0.6
0.4
0.2
0
0 1 2 3 4 5 6 7 8 9 10 11 12
Upwards frequency difference from 25Hz (Hz)
SR
No SR
SR Trials
No SR Trials


Psychometric functions -- 25Hz range, old average, 110% signal
%Corr
1
0.8
0.6
0.4
0.2
0
0
1
2
3
4
5
6
7
8
9
10
11
12
Upwards frequency difference from 25Hz (Hz)
SR
No SR
SR Trials
No SR Trials

Psychometric functions -- 25Hz range, young average, 100% signal




Psychometric functions -- 25Hz range, old average, 100% signal
%Corr
1
0.8
0.6
0.4
0.2
0
0 1 2 3 4 5 6 7 8 9 10 11 12
Upwards frequency difference from 25Hz (Hz)
SR
No SR
SR Trials
No SR Trials



Psychometric functions -- 25Hz range, young average, 90% signal
%Corr
0
0.2
0.4
0.6
0.8
1
0
1
2
3
4
5
6
7
8
9
10
11
12
Upwards frequency difference from 25Hz (Hz)
SR
No SR
SR Trials
No SR Trials

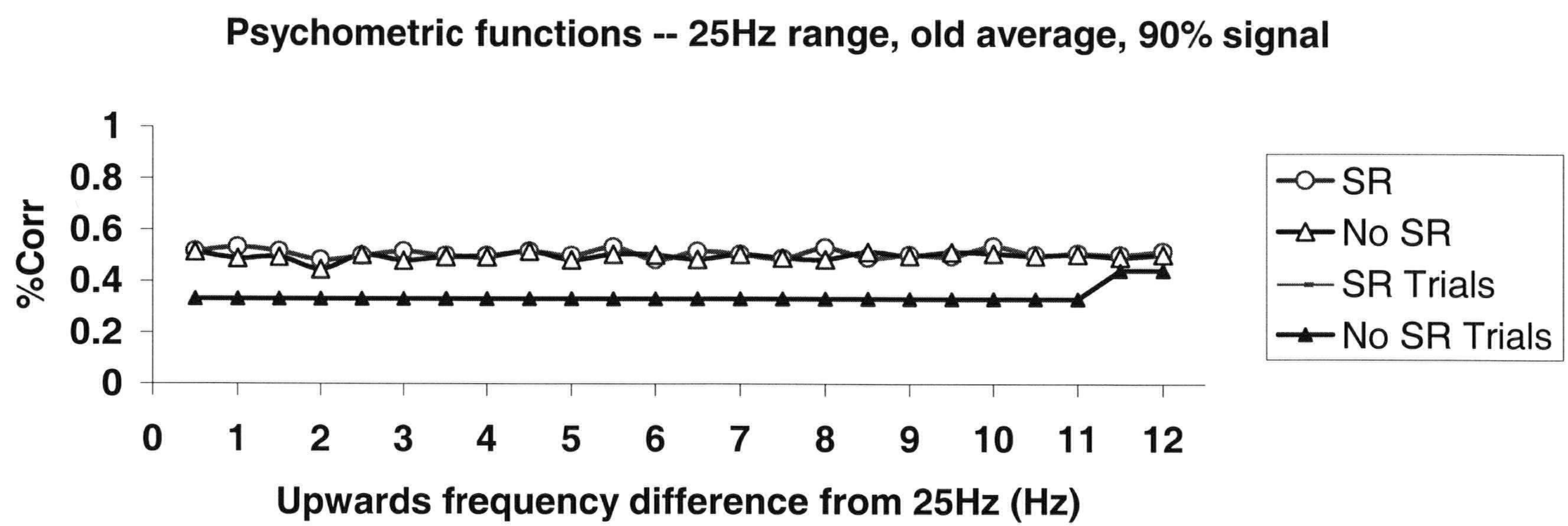
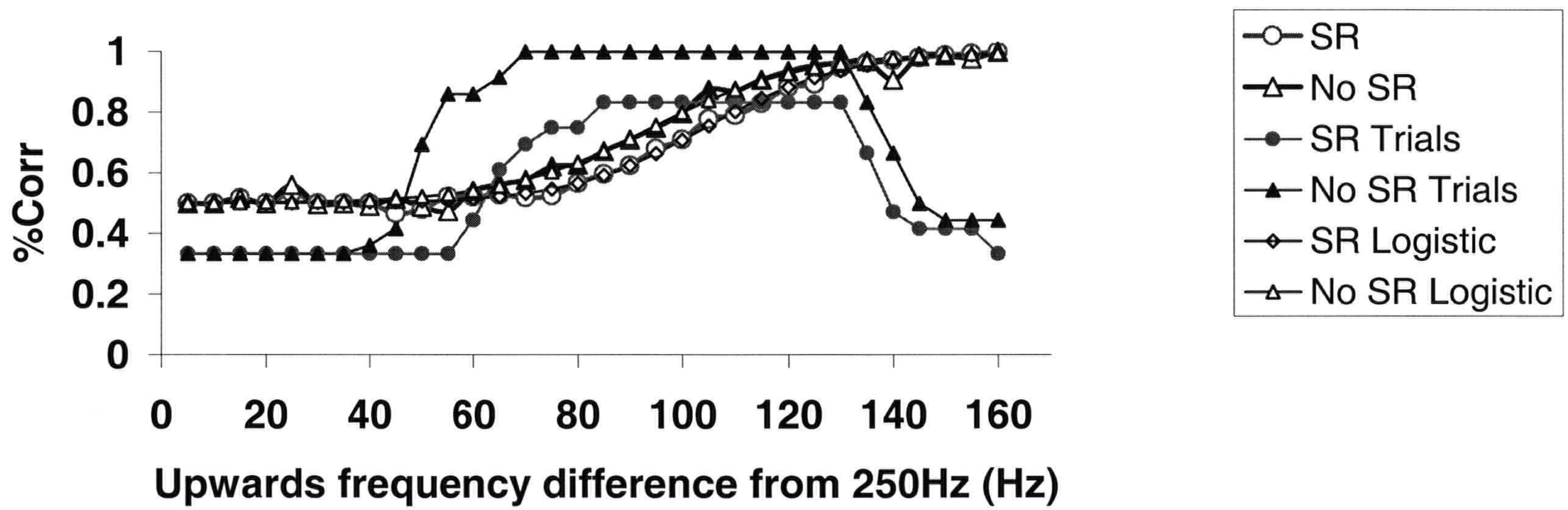
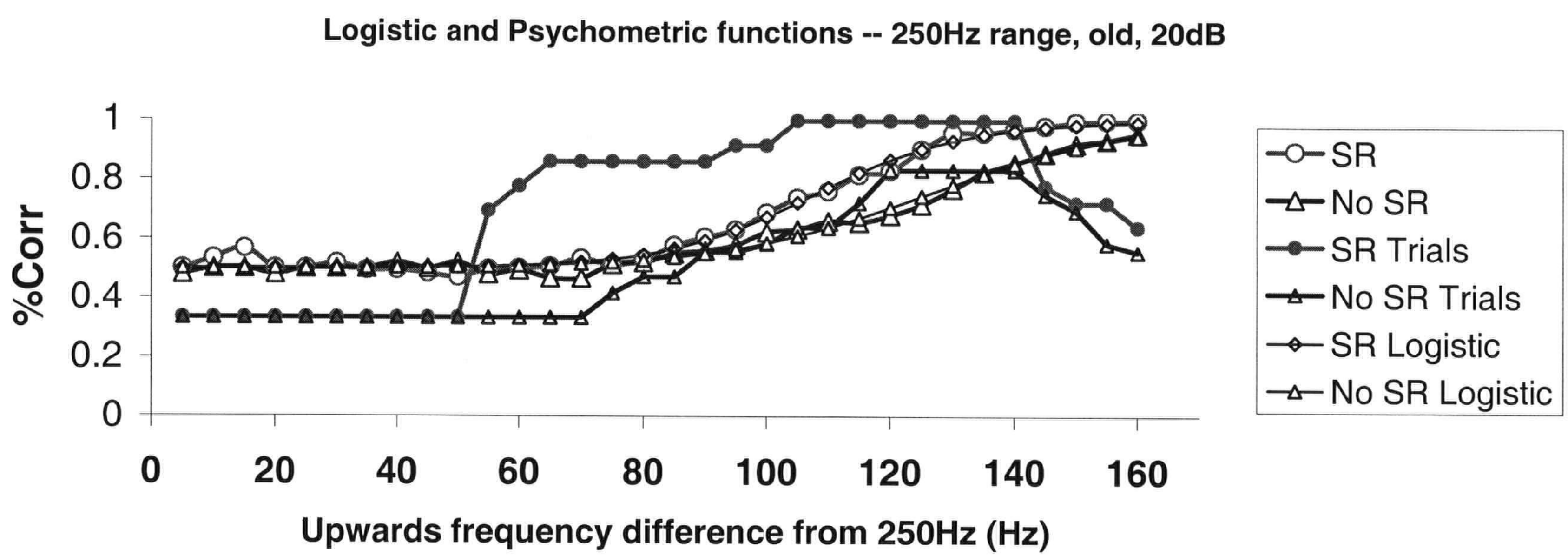


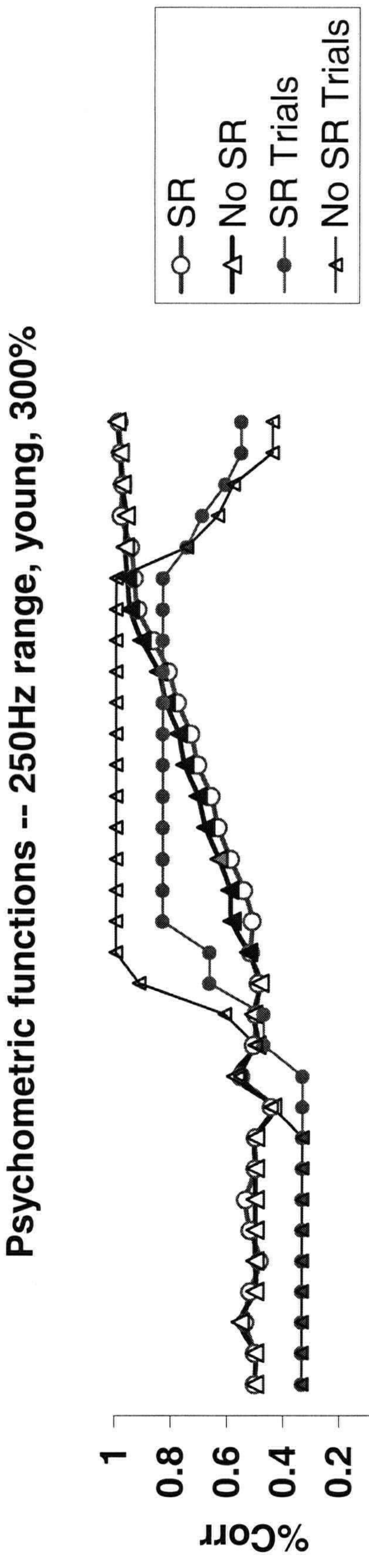
Figure 1: Logistic curves of average %Corr values, young and old subjects, 25Hz. Traces with no markers represent the percent of the maximum number of trials (maximum: 30 trials per subject X 6 subjects = 180 points) that contribute to each point. Note that the largest number of trials was used in determining the %Corr values of the sloped parts of the logistic curves.

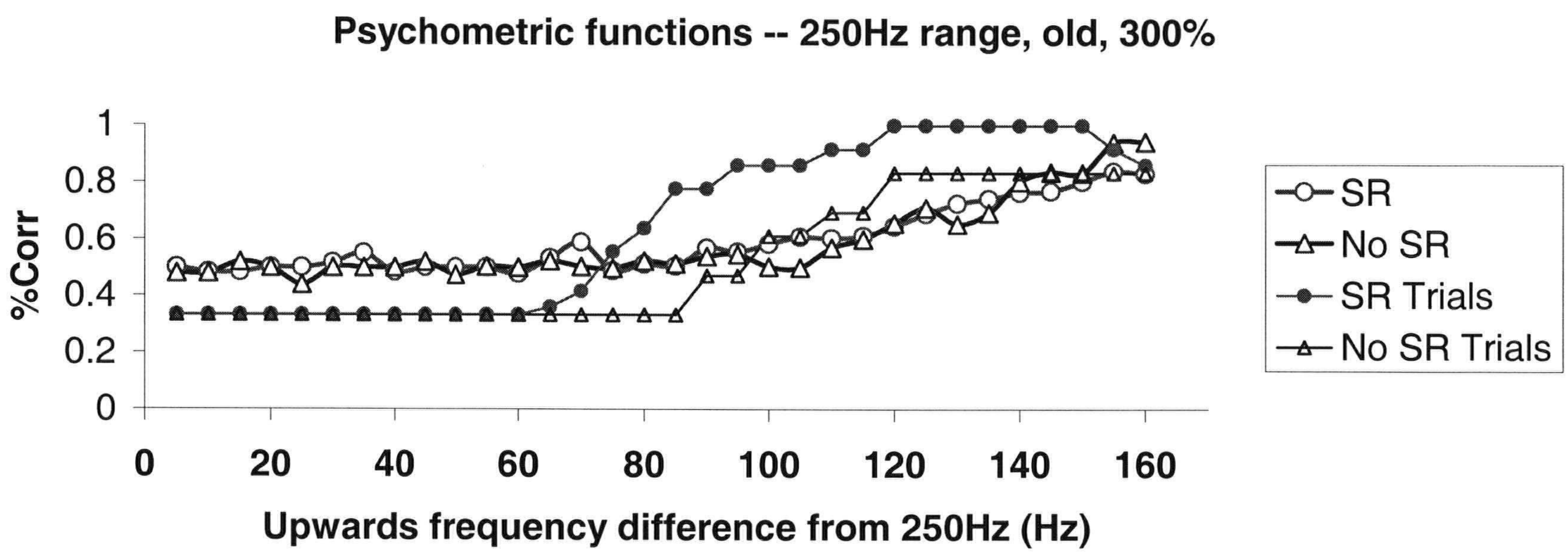
Logistic and Psychometric functions -- 250Hz range, young, 20dB



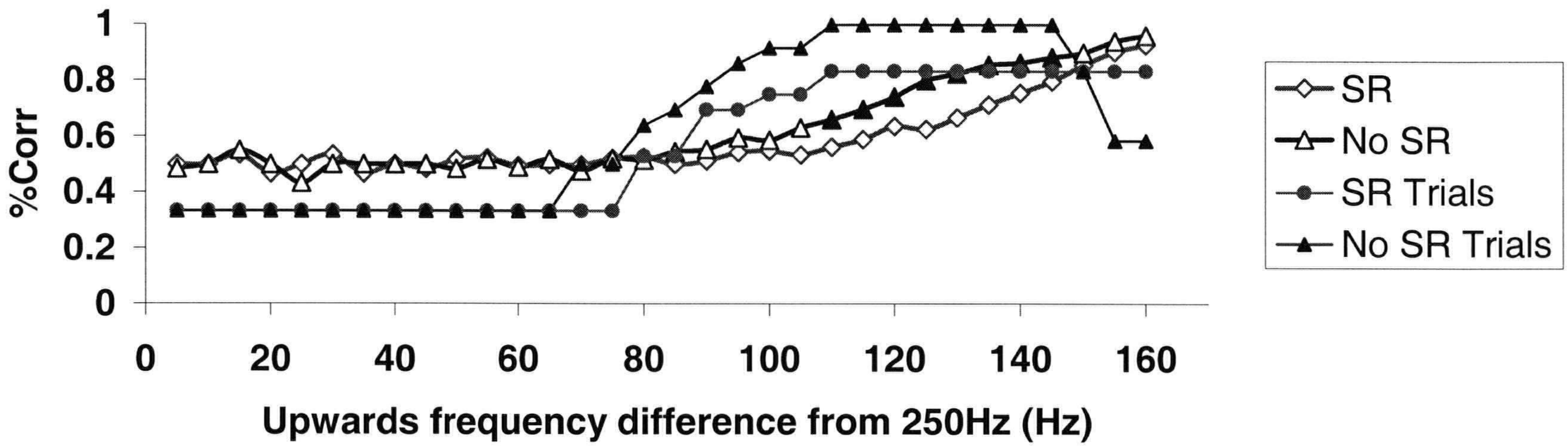


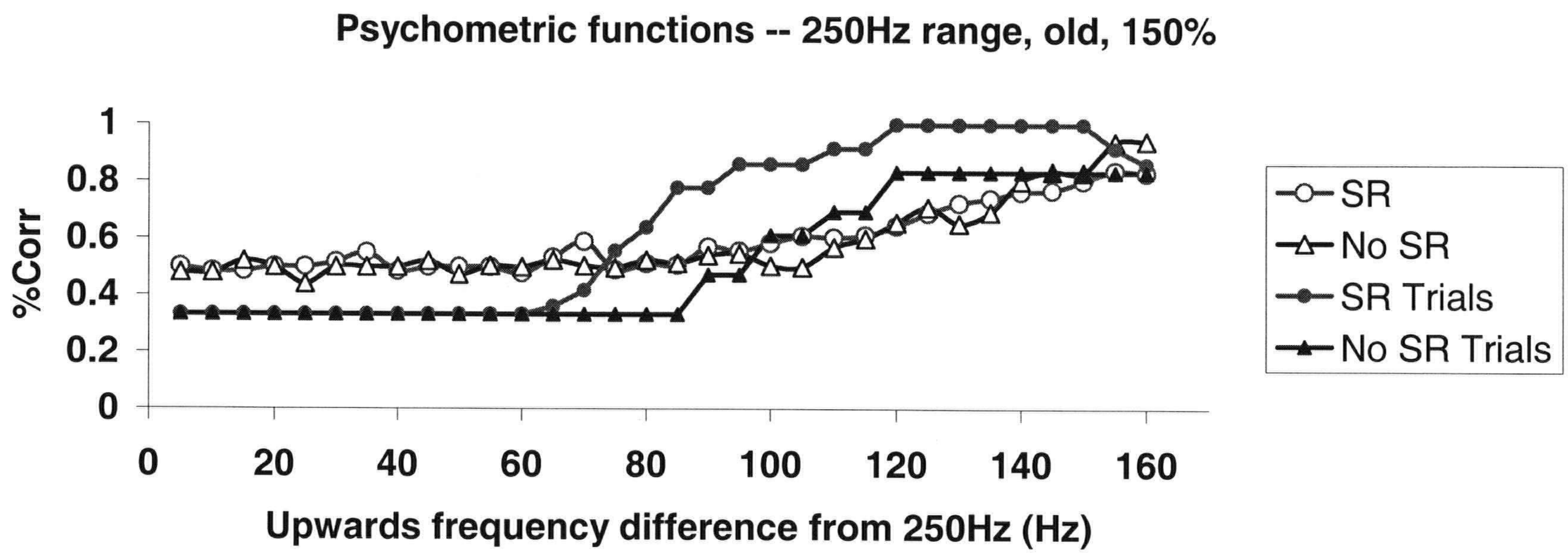
Logistic and Psychometric functions -- 250Hz range, old, 20dB
%Corr
1
0.8
0.6
0.4
0.2
0
0
20
40
60
80
100
120
140
160
Upwards frequency difference from 250Hz (Hz)
SR
No SR
SR Trials
No SR Trials
SR Logistic
No SR Logistic


Psychometric functions -- 250Hz range, young, 300%
%Corr
1
0.8
0.6
0.4
0.2
0
0
20
40
60
80
100
120
140
160
Upwards frequency difference from 250Hz (Hz)
SR
No SR
SR Trials
No SR Trials

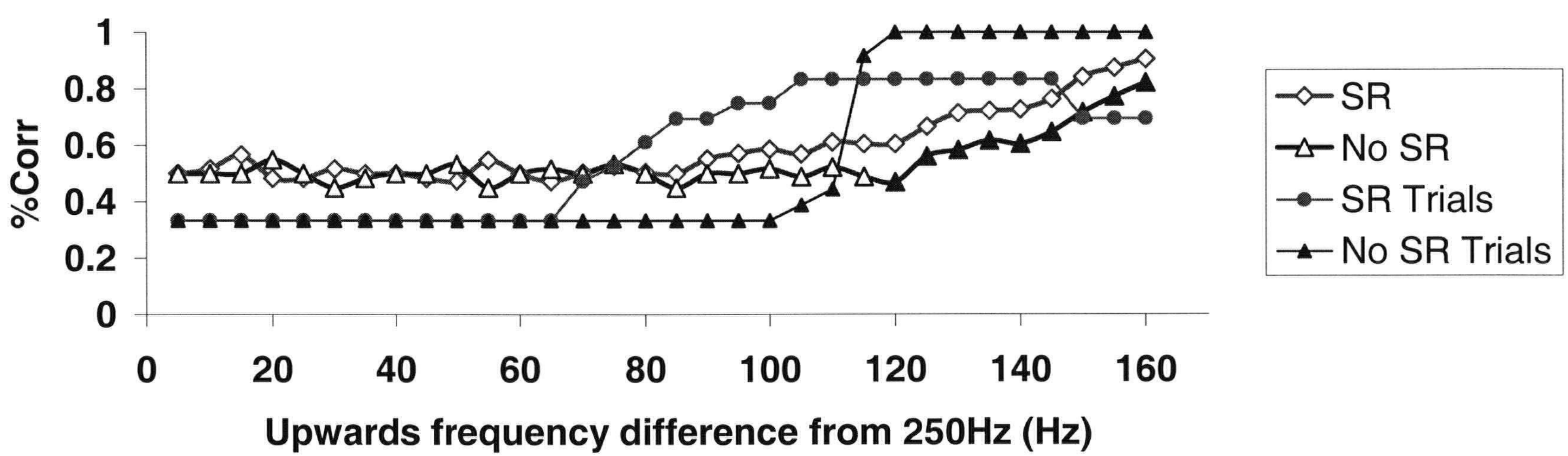

Psychometric functions -- 250Hz range, old, 300%
%Corr
1
0.8
0.6
0.4
0.2
0
0
20
40
60
80
100
120
140
160
Upwards frequency difference from 250Hz (Hz)
SR
No SR
SR Trials
No SR Trials

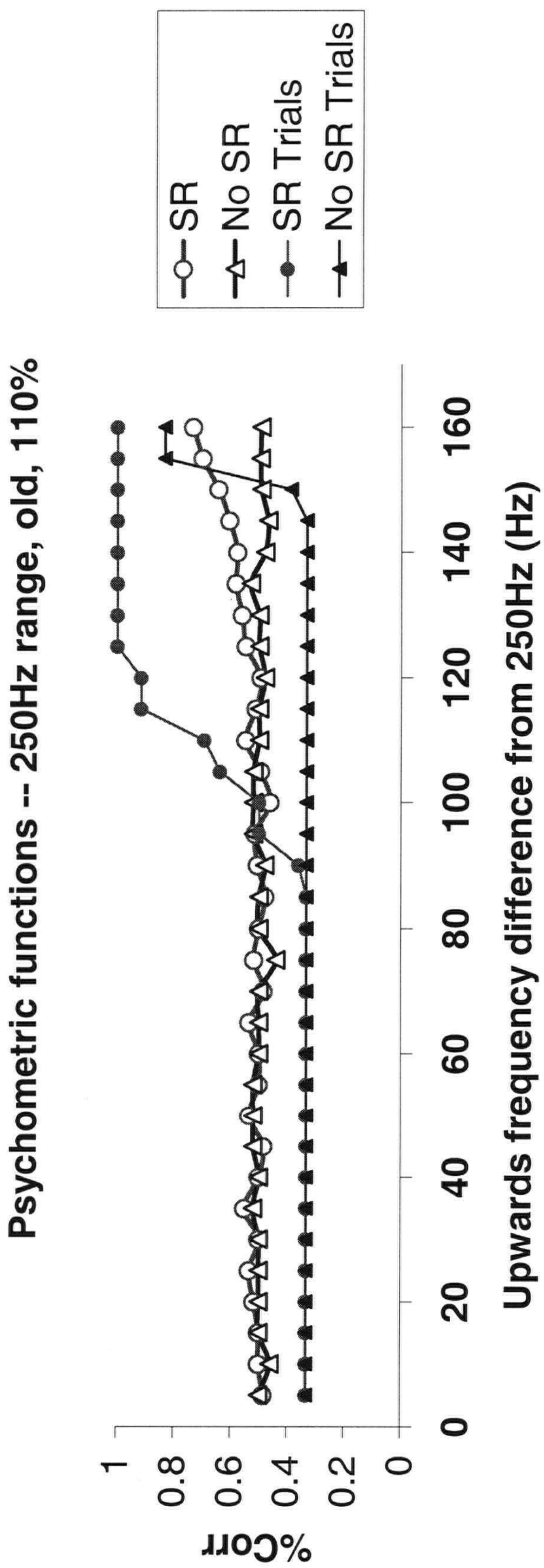
Psychometric functions -- 250Hz range, young, 150%



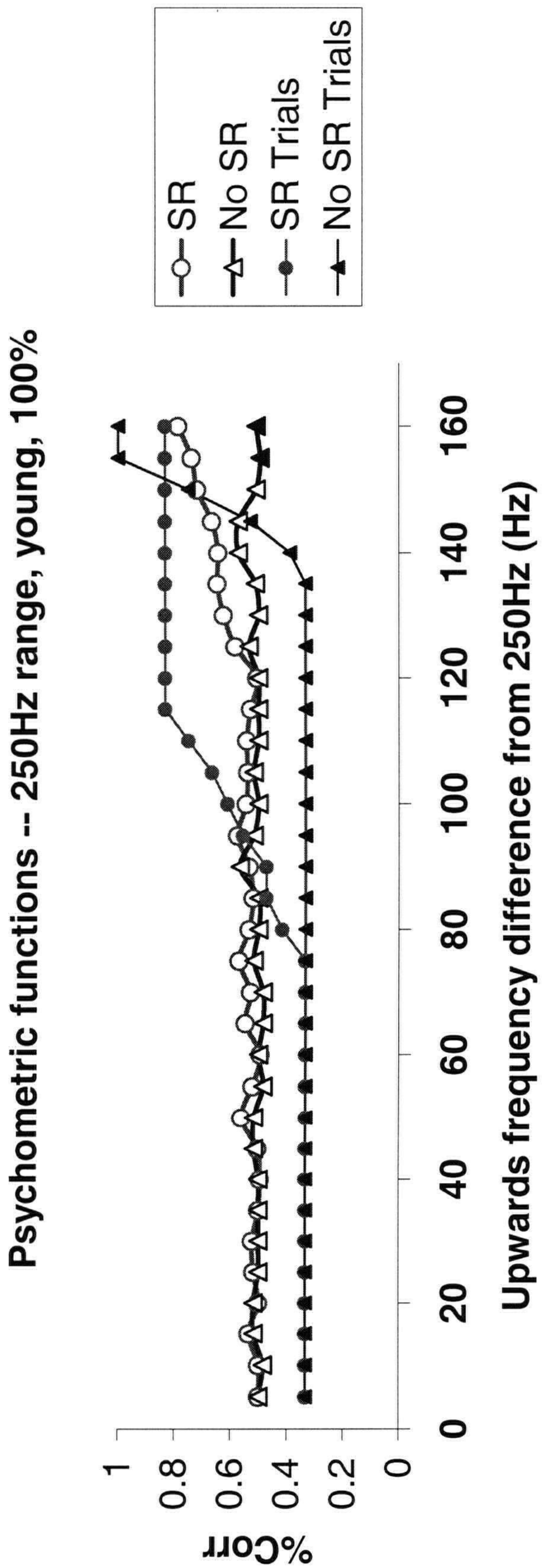

Psychometric functions -- 250Hz range, old, 150%
%Corr
1
0.8
0.6
0.4
0.2
0
0
20
40
60
80
100
120
140
160
Upwards frequency difference from 250Hz (Hz)
SR
No SR
SR Trials
No SR Trials

Psychometric functions -- 250Hz range, young, 110%

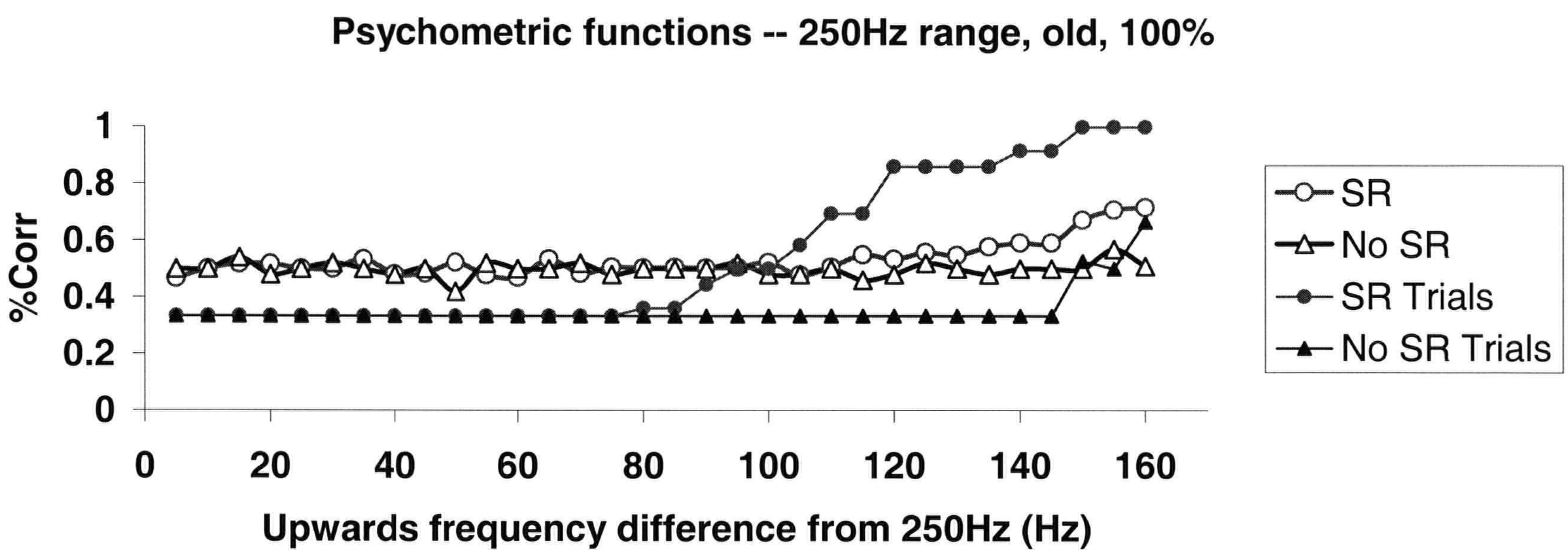


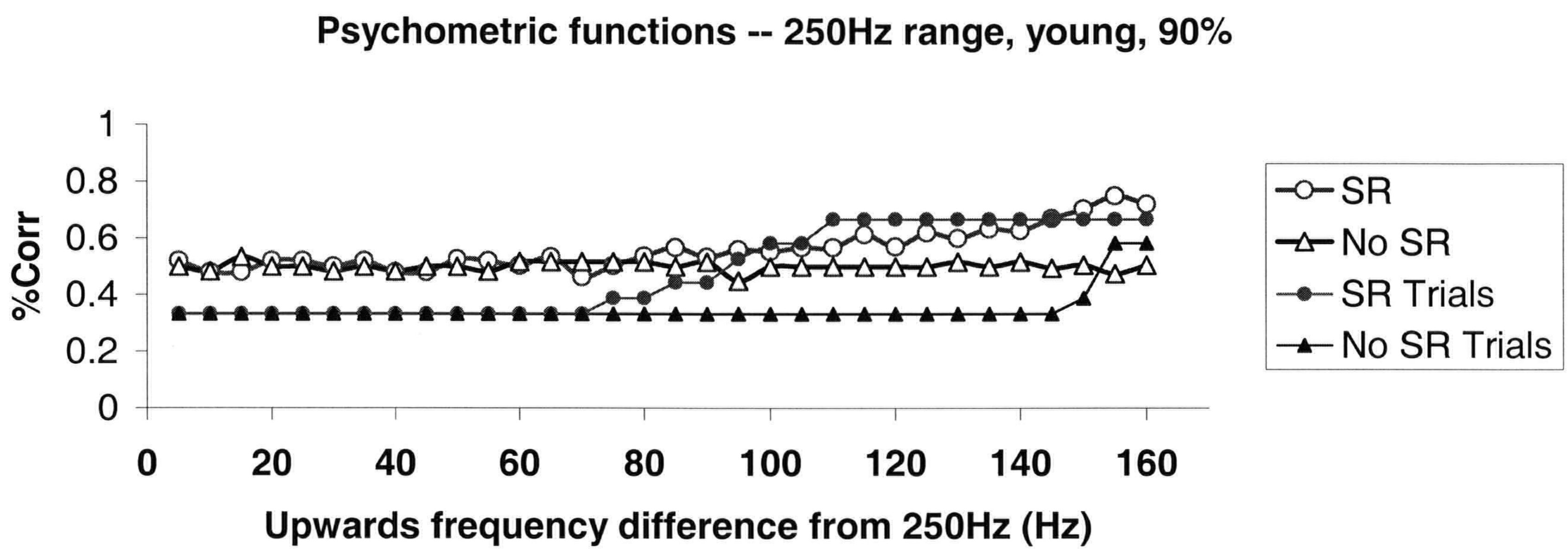


Psychometric functions -- 250Hz range, old, 110%
%Corr
1
0.8
0.6
0.4
0.2
0
0
20
40
60
80
100
120
140
160
Upwards frequency difference from 250Hz (Hz)
SR
No SR
SR Trials
No SR Trials



Psychometric functions -- 250Hz range, young, 100%
SR
No SR
SR Trials
No SR Trials
%Corr
1
0.8
0.6
0.4
0.2
0
0
20
40
60
80
100
120
140
160
Upwards frequency difference from 250Hz (Hz)


Psychometric functions -- 250Hz range, old, 100%
%Corr
1
0.8
0.6
0.4
0.2
0
0
20
40
60
80
100
120
140
160
Upwards frequency difference from 250Hz (Hz)
SR
No SR
SR Trials
No SR Trials


Psychometric functions -- 250Hz range, young, 90%
%Corr
1
0.8
0.6
0.4
0.2
0
0
20
40
60
80
100
120
140
160
Upwards frequency difference from 250Hz (Hz)
SR
No SR
SR Trials
No SR Trials

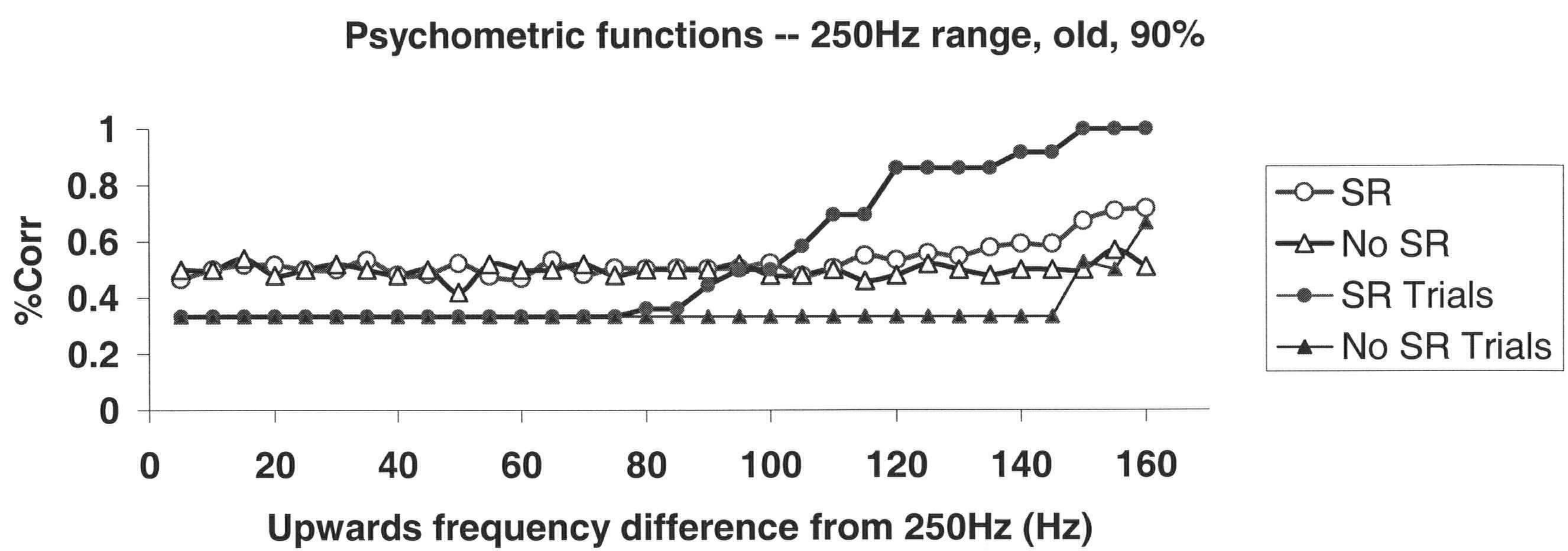
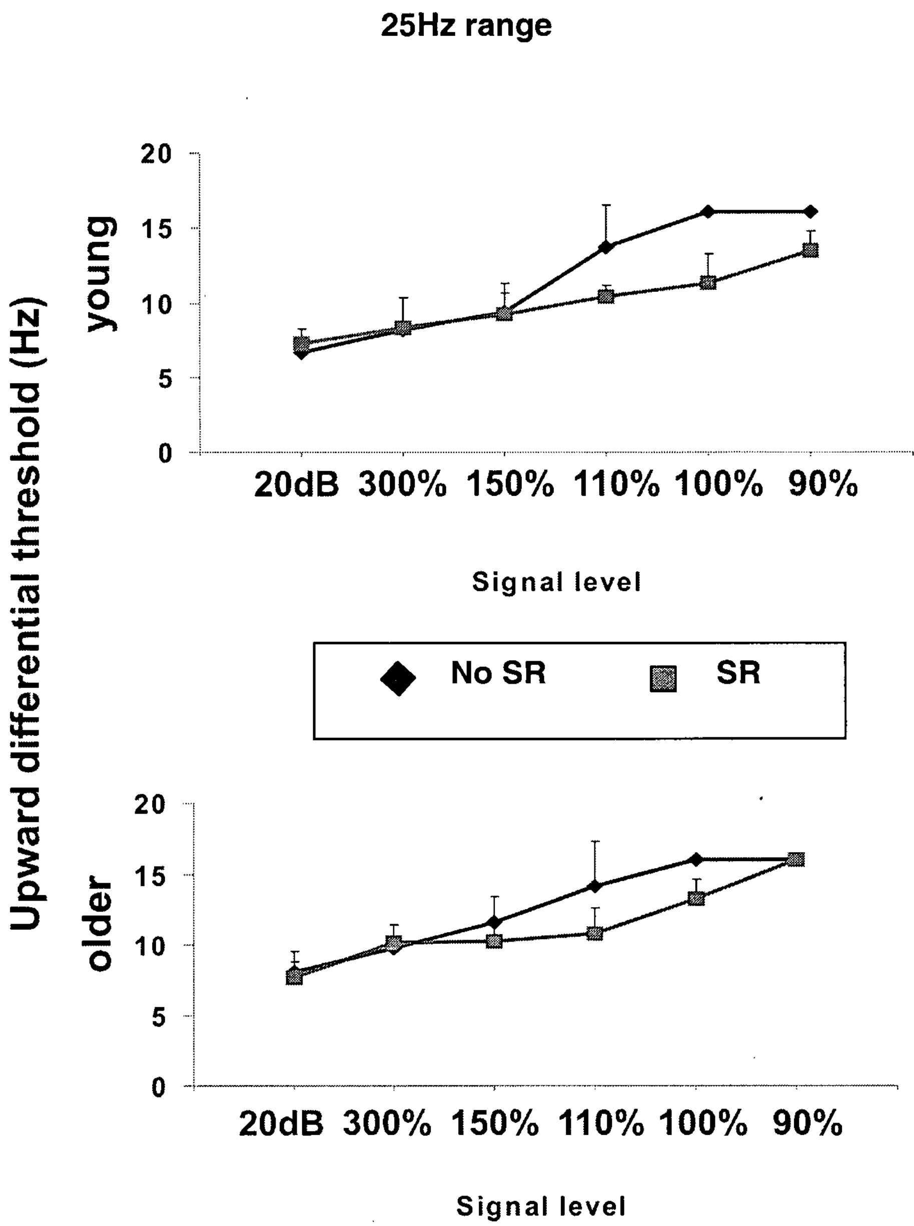


Figure 16: Logistic curves of average %Corr values, young and old subjects, 250Hz. Traces with no markers represent the percent of the maximum number of trials (maximum: 30 trials per subject X 6 subjects = 180 points) that contribute to each point.



25Hz range
Upward differential threshold (Hz)
young
20
15
10
5
0
20dB 300% 150% 110% 100% 90%
Signal level
No SR
SR
older
20
15
10
5
0
20dB 300% 150% 110% 100% 90%
Signal level

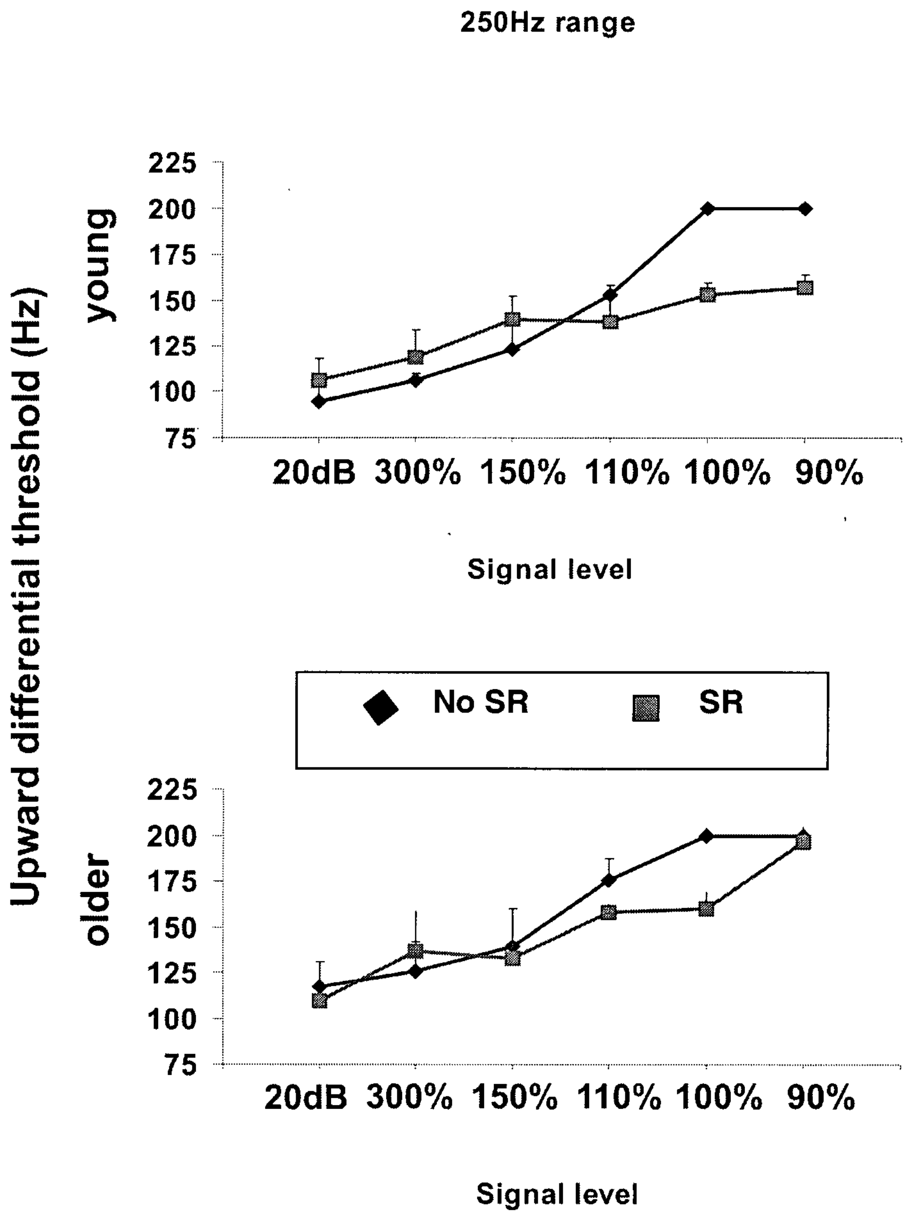


Figure 17: Scatter plots from ANOVAs for the 25Hz (first panel) and 250Hz (second panel) test ranges. Blue traces represent the No SR condition, red traces represent the SR condition. Error bars show 1 standard deviation.

4.4.2.3 Weber Fractions

Weber fractions were calculated in order to compare our data with those of previous studies. Weber fractions are reported in Table 6 and Table 7. At 25Hz, our data are close to those of Goff (1967) for young subjects; however they are higher for older subjects (Goff: 25Hz, 20dB above threshold: 0.32, Wells et al.:25Hz, 20dB above threshold, young subjects: 0.37, older subjects: 0.42). Mountcastle et al. (1969) determined a Weber fraction of 0.11 at 20dB above threshold, 40Hz. This is quite different from our values; however their protocol was also quite different: they used a confidence rating procedure with 6 confidence intervals rather than having subjects simply identify the higher frequency. The 6 intervals may have generated a lower threshold than a 2 choice procedure. In addition, we looked at only upward frequency thresholds, which are typically higher than "downward" frequency thresholds.

	25Hz											
	No SR						SR					
	20dB	300%	150%	110%	100%	90%	20dB	300%	150%	110%	100%	90%
Young	.27	.32	.37	.54	--	--	.29	.33	.37	.41	.45	.53
Old	.32	.39	.46	.56	--	--	.31	.40	.40	.43	.53	--

Table 6: Weber fractions for 25Hz, calculated at the upward frequency threshold that produced 75% correct. No value is entered in the table for signal levels where the discrimination threshold was infinite. Results in bold represent significant improvement.

	250Hz											
	No SR						SR					
	20dB	300%	150%	110%	100%	90%	20dB	300%	150%	110%	100%	90%
Young	.37	.42	.49	.61	--	--	.42	.48	.55	.55	.61	.62
Old	.46	.50	.55	.70	--	--	.43	.54	.53	.63	.64	.78

Table 7: Weber fractions for 250Hz, calculated at the upward frequency threshold that produced 75% correct. No value is entered in the table for signal levels where the discrimination threshold was infinite. Results in bold represent significant improvement.

4.5 Discussion

4.5.1 Weber Fractions

Our Weber fractions were, in general, a bit higher than those of other studies. There are two possible reasons for this. First, our Weber functions were calculated on data from the foot, while other studies were performed on the hand (Goff, 1967; Mountcastle et al., 1969; LaMotte and Mountcastle, 1975; Mountcastle et al., 1990), and the foot is, in general less sensitive than the hand (Kenshalo, 1986, Kekoni et al., 1989). Second, our Weber fractions were based on an upward differential frequency threshold, which is, in general, higher than a "lower" differential frequency threshold. In the 25Hz range, Weber fractions of young and old subjects were similar, reflecting similar vibrotactile thresholds in that range. In the 250Hz range, both young and old subjects had higher Weber fractions. Goff (1967) also found an increase in the Weber fraction as a function of frequency.

Similar to our data, Mountcastle et al. (1969) found that frequency discrimination (40Hz) on the finger was poor when stimulus amplitudes were close to threshold. Weber fractions gradually declined (i.e. discrimination improved as amplitude increased) to a value of about 0.11 at 20dB above threshold. Unlike our data and that of Goff (1967), Mountcastle et al. (1969, 1990) did not find any appreciable change in Weber fraction as a function of frequency.

4.5.2 *UPWARD DIFFERENTIAL THRESHOLDS*

SR is effective in improving upward differential thresholds in both young and older subjects, as evidenced by both groups being able to discriminate at smaller frequency differences in the SR condition in both frequency ranges. At the 25Hz range, it was to be expected that both age groups would experience similar improvements in upward differential threshold. This is indicated by the fact that subjective intensity bands were relatively flat, which resulted in both the standard and comparison frequencies having the same subjective intensity *and* the same power.

One way in which the SR mechanism may work for differential thresholds is by making both sub-threshold signals "feel-able", that is, simply by boosting both signals to a supra-threshold level. In young subjects, results indicate that this is true for the 90% signal level (where there was improvement from an infinite upward differential threshold), but also for the 100 and 110% signal levels. That 33% noise also benefits the 110% signal level is likely because the 110% level falls within the subject's atonal zone, that is, there is enough power in the signal for a subject to distinguish that a mechanical event has occurred, but not enough power for the subject to distinguish the characteristics of the mechanical event, for example, frequency characteristics (LaMotte and Mountcastle, 1975). In monkeys, the atonal zone has been reported to be approximately 7 to 8 dB (with respect to detection threshold, LaMotte and Mountcastle, 1975).

For the elderly, the lack of improvement at the 90% signal level could be due to SR boosting the signal into the elderly group's atonal zone, but not out of it. A corollary of this hypothesis is that, at least in elderly, levels of noise that are optimal for signal detection (at the 90% level) were not adequate for signal differentiation.

In the 250Hz range, thresholds improved for young subjects at the 90% and 100% signal levels, and for older subjects at the 100% level only. For young subjects, these results suggest that 33% noise was adequate to boost the sub-threshold and threshold signals out of the atonal zone. For older subjects, 33% noise may have been enough to boost signals at the 90% level into the atonal zone, but not out of it. The lack of improvement in older subjects does not refute a possible benefit of SR in the higher range, since there was one older subject whose threshold did improve in the SR condition. For the majority of the older subjects, it may have been that, similar to the 25Hz range, the amount of noise used may not have been the correct quantity to realize differentiation. A lack of SR improvement in the FAII mediated range (250Hz) is not attributable to the age related decline in the number of these receptors as hypothesized by Bolton et al. (1966), since study 1 showed that SR facilitates a simple detection task in this frequency range.

Another reason for the lack of universal improvement at the 90% signal level in older subjects could be due to the failure of some central mechanism that facilitates frequency differentiation, but which does not participate to the same extent in vibration detection. Specifically, this mechanism and its age related decline could be a function of the basal ganglia, which play a crucial role in sensory motor integration (Schneider, 1987), and thus may be critical in the functional gating of cutaneous reflexes during walking (Goodwin, John, Sathain and Darian-Smith, 1989).

The evidence for a reflex modulation role of the basal ganglia comes from research showing that Parkinson's patients are two times worse at tactile grating differentiation than age matched controls, and that both elderly groups perform worse than young controls (age-matched elderly by a factor of 1.25) (Sathian et al., 1989). Monkey research has shown that neuronal responses to the tactile grating discrimination task are comparable to responses to vibrating probes (Goodwin et al., 1989), which would presumably be true in humans as well, since vibration sensation is mediated equivalently in both species (LaMotte and Mountcastle, 1975). Because tactile grating differentiation is adversely affected by age and Parkinson's, it is likely that vibration frequency differentiation would be affected similarly. Thus, any role that vibration differentiation plays in cutaneous reflex modulation during gait could be influenced by age-related changes in the functioning of the basal ganglia.

4.5.3 FREQUENCY DISCRIMINATION AND CUTANEOUS REFLEXES

Work by many researchers has shown that skin-initiated reflexes from the footsole may be an important component of functional gait. A typical investigation protocol involves stimulating the sural nerve or one of the branches of the tibial nerve that innervate the footsole. The stimulation is done during different phases of walking and at different frequencies (Yang and Stein (1990): 97Hz; Van Wezel, Ottenhoff and Duysens (1997): 200Hz; Zehr, Komiyama and Stein (1997): 200Hz; Pijnapples, Van Wezel, Colombo, Dietz and Duysens. (1998): 200Hz; Christensen, Morita, Petersen and Nielsen (1999): 250Hz, Van Wezel, Van Engelen, Gabreëls, Gabreëls-Festen and Duysens (2000): 200Hz). Using different frequencies of stimulation may engage particular reflexes to different degrees. For example, Christensen et al. (1999) stimulated at 250Hz (1ms pulse, 3ms interpulse time) at a level of stimulation of two times perception threshold, at approximately 10% of the gait cycle after the start of swing phase. Pijnapples et al.

(1998) stimulate at 200Hz, at the same level and at approximately the same point in the gait cycle. In the Pijnapples et al. study, the level of electromyogram (EMG) produced in the early swing phase tibialis anterior (TA) burst is approximately 44% of maximum voluntary effort (MVE), based on a representative subject. In the Christensen et al. study, the level of EMG produced in early swing phase TA burst was approximately 28% of MVE based on averaged data. Thus, the reflex TA burst to clear the foot over the ground during early swing phase may be preferentially activated by 200Hz, as evidenced by increased magnitude EMG for 200Hz. 200Hz is a frequency that may be generated during push-off. Extending this to natural stimulation of the footsole during walking, it may be important for the nervous system to be able to differentiate between different frequencies, so that the associated reflexes are activated at the correct times during gait. Thus, an inability to differentiate between frequencies may cause a dysfunction in the activation of the reflexes necessary for gait, and thus gait dysfunction.

It has been shown that age has a detrimental effect on vibrotactile differential thresholds, and that SR may be effective in lowering these thresholds. This may, in turn, have a beneficial effect on cutaneous reflexes that are not engaged adequately due to age-related threshold elevation, and thus improve dysfunctional gait.

5 GENERAL SUMMARY

This research had 3goals. The first aim was to determine the effects of age, frequency and location on vibrotactile sensitivity of the footsole. The second aim was to determine whether SR could be effective in lowering vibrotactile detection thresholds in the footsoles of the elderly. The third aim was to determine whether SR could lower vibrotactile differential thresholds in young and elderly. Except for this work, we know of no SR studies of the elderly, and no studies that have shown, in either young or old populations, that SR can improve the performance on a complex perceptual behaviour like frequency discrimination. Showing that SR is effective in lowering both detection and discrimination thresholds in the elderly indicates that SR may be parlayed into an aide for improving these functions, both for the elderly and other populations with elevated thresholds. Because elevated vibration thresholds may cause dysfunction in those aspects of gait and grasp that rely on vibration sensation, an aide that improves vibrotaction may improve gait, and therefore alleviate dangerous falls in the elderly.

The purpose of Study 1 was to determine if there was a difference in acuity in vibration detection between young and old subjects, and if so, to determine whether these differences were a function of frequency and location on the footsole. Clearly, if no difference in vibrotaction were found between young and old subjects, then any age-related gait dysfunction would have to be a result of another mechanism, and thus improved vibration sensation through SR would not be of benefit to gait.

There were 2 important results from Study 1. First, vibration detection acuity could be grouped into 3 anatomical clusters on the footsole. In order of acuity they were: (1) the ball and arch of the foot, (2) the heel and lateral border of the foot, and (3) the toes. This ordinal pattern of sensitivity was age and frequency invariant. Second, there was dramatic acuity loss in the elderly, however this loss was only present in those frequencies mediated by FAII afferents. When loss was expressed relative to young thresholds, loss was greatest in the heel, followed by the arch/ball cluster, and the toes. Acuity loss increased with increasing frequency (Table 3).

It has been hypothesized that when vibrotactile acuity is lost due to age, cutaneous reflexes, an integral part of gait, are not adequately engaged due to lack of sensation. This results in gait dysfunction. This suggested if SR were to be able to improve acuity, gait might also be improved. This was the motivation for the second study.

The purpose of Study 2 was to determine if SR could lower the elevated vibrotactile thresholds in the elderly footsole found in Study 1. This effect of SR on sub-threshold signals was measured by the ability of subjects to correctly identify which of two equally powered epochs contained a signal plus noise, as opposed to noise only. While SR had been shown to be effective at lowering vibrotactile thresholds in the fingertips of young subjects, no studies had been done on the footsole. If an improvement were found in vibrotactile acuity in the elderly, this would indicate that an SR rehabilitative aide may be possible for gait.

The results of the second study showed that SR could reduce vibrotactile thresholds. 33% noise was found to be optimal for the 90% signal condition, for both young and old participants, and for frequencies mediated by both FAI and FAII afferents. The 80% signal condition was optimized by higher levels of noise, which changed as a function of age and frequency mediation, but not in any systematic way.

These results confirmed previous findings that SR could lower thresholds in young people. It also showed that SR was effective in the elderly, a first step in the development of SR as a rehabilitative aide. Similar to other types of plantar sensation facilitation that improve the effectiveness of stabilizing reactions in gait (Maki, et al., 1999), an SR based rehabilitative aide may work by lowering vibrotactile thresholds in the footsole, causing the cutaneous reflexes involved in posture and gait that are initiated in the feet to engage more strongly.

Differentiating between noise and signal+noise is relatively easier than the task of differentiating between two signals where the information content is similar. Putting a bound on a person's accuracy at differentiating different signals also gives us an idea of how accurate they are at identifying signal.

The purpose of the third study was to determine if SR could be used to lower differential thresholds. To our knowledge, an SR study of this sort has never been done on either young or old subjects. Similar to lowering detection thresholds, lowering elevated differential thresholds could improve the degree to which different cutaneous reflexes are engaged during the gait cycle, and, in the hand, the degree to which cutaneous reflexes are engaged to produce grasp forces in response to micro-slips. The results of the study showed that noise was effective in lowering differential thresholds. At lower frequencies (25Hz) noise was effective in lowering differential thresholds for sub-threshold signals in both young and older subjects at the 110% and 100% levels. It also was effective at supra-threshold levels in boosting signals out of the atonal zone so that they could be differentiated. At higher frequencies, noise was effective in young subject at the 100% and 90% levels, but at the 100% level only in older subjects. In older subjects at the 90% level, the amount of noise used may not have been sufficient to boost signals out of the atonal zone.

The accuracy at discriminating between two signals may have a bearing on cutaneous reflexes, since certain reflexes may be preferentially activated by specific frequencies. If a person's ability to discriminate signals can be improved, so to may the activation of reflexes triggered by the perception of those frequencies. This may in turn improve the aspects of gait that rely on perception of these cutaneous signals.

5.1 FUTURE DIRECTIONS

Having completed this research, there are 2 possible interesting extensions. First, SR may be a used to reduce increased sway due to age in standing balance, and second, SR may be used in the hand to reduce vibrotactile thresholds.

5.1.1 STANDING BALANCE

Results of experiments in standing balance show that, compared to a young population, older people with cutaneous deficits exhibit increased sway during standing balance (Colledge, Cantley, Peaston, Brash, Lewis and Wilson, 1994). Furthermore, sway increases linearly with age and has been related to an increased tendency to fall (Colledge et al.).

The effects of increased sway have been quantified by research that has shown a significant correlation between decreased vibration sensitivity at 20Hz and sway ($p<.05$) (Hämäläinen et al., 1992). Decreased sensitivity in the FAI range suggests FAI afferents and possibly SAI afferents (afferents that encode pressure) play a role in postural stabilization.

Research into the effects of cutaneous deficits on standing balance in the elderly is supported by research where cutaneous sensation has been temporarily reduced or ablated in young people. One result of reduced somatosensory input on postural control is increased sway that may be caused by the delay in onset of skin-triggered postural reflexes (Wu and Chiang, 1997). This implies that cutaneous information is important for effective postural stabilization during low frequency displacements. It has been hypothesized that SAI afferents participate in the postural regulation of movements below 5 Hz. (Perry et al., 2000).

These studies show that footsole input is important to maintaining balance, and that deficient footsole input can lead to increased sway, which is associated with increased falls. Showing that SR can work to decrease vibrotactile thresholds in low frequencies (those frequencies present in standing balance), suggests that SR could be effective in reducing sway. The results of this thesis show that SR is effective in FAI mediated frequencies, which likely play a role in postural stabilization, thus SR is a candidate method for increasing footsole sensitivity in the hypothesized FAI-mediated range, and thus could decrease postural sway and falls. Further, it is likely that SR would also be effective in lower (SAI) frequency ranges, and may decrease sway by increasing sensitivity of pressure detection. SR has been shown at 3Hz in rat SA receptors and in humans (Ivey et al., 1998).

5.1.2 SR and Grasp

A second possible application of SR may be to improve sensation in the glabrous skin of the fingertips. There may be increased detection thresholds in the glabrous skin of the hand of older people, similar to that shown in this work in the footsole. An increase in vibration detection thresholds in the hand may result in inadequate engagement of slip-reflexes, that is, reflexes that initiate an increase in grip force when an object slips (Wells, 1998). An inadequate engagement of slip-initiated reflexes may result in the dropping of items, an increased incidence of which has been noted in the elderly (Rothwell, 1986). This situation in the hand is analogous to the investigation of inadequate engagement of cutaneous reflexes initiated in the footsole by Perry et al. (2000), where hypothermic anesthesia was used to mimic the effects of age on the skin of the footsole.

The effects of anesthesia in the hand on grip were investigated by Johansson, Häger and Bäckström (1993) during unpredictable load changes of the gripped object. The result of the anesthesia was that participants produced inadequate grip to compensate for the load changes (i.e.: dropped the object) and that the compensatory grip forces were produced at longer latencies. If the effects of anesthesia are similar to the effects of ageing, then SR in the hand may alleviate the problems in grip associated with ageing in the same ways it has been proposed to alleviate inadequate reflex engagement in the footsole.

6 References

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7 APPENDIX I: STATISTICAL TABLES

Source	DF	Sum of Squares	Mean Squares	F-value	P-value	Power
Age	1	19928	19928	1924	<.0001	1
Subject(Grp)	10	103	10			
Frequency	3	24397	8132	676.237	<.0001	1
Frequency*Age	3	11017	3672	305.384	<.0001	1
Frequency*Subject(Grp)	30	360	12			
Cluster	2	6130	3065	94.731	<.0001	1
Cluster*Age	2	459	229	7.099	<.0047	.898
Cluster*Subject(Grp)	20	647	32			
Frequency*Cluster	6	707	117	8.146	<.0001	1
Frequency*Cluster*Age	6	260	43	3.000	.0125	.898
Frequency*Cluster*Subject(Grp)	60	868	14			

7.1 EXPERIMENT 1: ANOVA RESULTS

Table 8: Experiment 1 effects table

Age	Frequency	CLuster	Count	Mean	SD
Y	25Hz	Toes	6	64.667	2.16
		Ball	6	44.00	1.79
		Heel	6	53.83	2.32
	50Hz	Toes	6	24.50	1.05
		Ball	6	10.50	1.76
		Heel	6	16.33	1.86
	250Hz	Toes	6	11.00	2.00
		Ball	6	5.50	2.51
		Heel	6	6.17	1.17
	400Hz	Toes	6	11.67	1.97
		Ball	6	6.67	1.21
		Heel	6	8.50	1.88
O	25Hz	Toes	6	66.00	4.10
		Ball	6	38.67	4.23
		Heel	6	55.00	6.20
	50Hz	Toes	6	62.17	4.36
		Ball	6	39.17	4.17
		Heel	6	50.33	6.12
	250Hz	Toes	6	33.33	7.42
		Ball	6	20.50	3.78
		Heel	6	25.50	3.56

	400Hz	Toes	6	66.00	5.40
		Ball	6	43.00	7.95
		Heel	6	49.00	5.76

Table 9:Means Table for Threshold, Effect: Frequency*Cluster*Age

7.2 EXPERIMENT 2: ANOVA RESULTS

Source	**DF**	**Mean Square**	**F-Value**	**P-Value**	**Power**
Age	1	826	17.519	.0019	.973
Subject(Group)	10	47			
Freq	3	27	1.251	.3088	.292
Freq*Age	3	24	1.138	.3497	.268
Freq*Subject(Group)	30	21			
SigLev	1	422	42.916	<.0001	1.00
SigLev*Age	1	129	13.174	.0046	.916
SigLev*Subject(Group)	10	9			
Noise	5	13356	512.863	<.0001	1.00
Noise*Age	5	19	.733	.6019	.238
Noise*Subject(Group)	50	26			
Freq*SigLev	3	68	5.293	.0048	.903
Frequency*SigLev*Age	3	35	2.701	.0633	.592
Freq*SigLev*Subject(Group)	30	13			
Freq*Noise	15	22	1.087	.3726	.677
Freq*Noise*Age	15	14	.711	.7707	.448

Freq*Noise*Subject(Group)	150	20			
SigLev*Noise	5	1536	35.327	<.0001	1.0
SigLev*Noise*Age	5	65	1.514	.2022	.480
SigLev*Noise*Subject(Group)	50	43			
Freq*SigLev*Noise	15	53	3.087	.0002	.998
Freq*SigLev*Noise*Age	15	31	1.789	.0410	.920
Freq*SigLev*Noise*Subject(Group)	150	17			

Table 10: Experiment 2 effects table

Effect: Age*Frequency * Signal level * Noise Level	**Count**	**Mean**	**Std. Dev.**	**Std. Err.**
y, Hz25, %90, %0	6	48.333	4.714	1.924
y, Hz25, %90, %33	6	78.056	1.948	0.795
y, Hz25, %90, %50	6	72.5	3.456	1.411
y, Hz25, %90, %67	6	62.778	1.361	0.556
y, Hz25, %90, %83	6	55.833	5.137	2.097
y, Hz25, %90, %100	6	51.111	3.277	1.338
y, Hz25, %80, %0	6	47.778	7.577	3.093
y, Hz25, %80, %33	6	68.611	1.255	0.512
y, Hz25, %80, %50	6	70.833	9.818	4.008
y, Hz25, %80, %67	6	73.889	3.6	1.47
y, Hz25, %80, %83	6	56.667	9.603	3.921

y, Hz25, %80, %100	6	48.611	7.258	2.963
y, Hz50, %90, %0	6	49.444	3.6	1.47
y, Hz50, %90, %33	6	76.944	3.562	1.454
y, Hz50, %90, %50	6	71.944	10.078	4.114
y, Hz50, %90, %67	6	62.222	8.074	3.296
y, Hz50, %90, %83	6	48.611	4.139	1.69
y, Hz50, %90, %100	6	48.889	3.277	1.338
y, Hz50, %80, %0	6	47.5	3.456	1.411
y, Hz50, %80, %33	6	65.556	3.103	1.267
y, Hz50, %80, %50	6	77.778	2.277	0.93
y, Hz50, %80, %67	6	71.944	8.782	3.585
y, Hz50, %80, %83	6	62.5	6.032	2.463
y, Hz50, %80, %100	6	44.722	2.453	1.002
y, Hz250, %90, %0	6	50.556	3.6	1.47
y, Hz250, %90, %33	6	78.889	1.361	0.556
y, Hz250, %90, %50	6	73.889	2.018	0.824
y, Hz250, %90, %67	6	62.222	2.018	0.824
y, Hz250, %90, %83	6	48.889	2.919	1.192
y, Hz250, %90, %100	6	48.889	3.277	1.338
y, Hz250, %80, %0	6	47.778	1.361	0.556
y, Hz250, %80, %33	6	64.167	2.934	1.198

y, Hz250, %80, %50	6	76.667	1.054	0.43
y, Hz250, %80, %67	6	72.778	3.277	1.338
y, Hz250, %80, %83	6	60	4.472	1.826
y, Hz250, %80, %100	6	46.944	3.235	1.321
y, Hz400, %90, %0	6	52.778	5.443	2.222
y, Hz400, %90, %33	6	81.389	2.871	1.172
y, Hz400, %90, %50	6	75	1.054	0.43
y, Hz400, %90, %67	6	60.556	2.722	1.111
y, Hz400, %90, %83	6	48.889	3.103	1.267
y, Hz400, %90, %100	6	48.611	1.255	0.512
y, Hz400, %80, %0	6	47.222	3.103	1.267
y, Hz400, %80, %33	6	65.833	5.349	2.184
y, Hz400, %80, %50	6	78.056	1.948	0.795
y, Hz400, %80, %67	6	74.444	4.907	2.003
y, Hz400, %80, %83	6	58.889	4.303	1.757
y, Hz400, %80, %100	6	46.389	3.235	1.321
o, Hz25, %90, %0	6	50.556	6.116	2.497
o, Hz25, %90, %33	6	79.722	1.255	0.512
o, Hz25, %90, %50	6	75.278	3.402	1.389
o, Hz25, %90, %67	6	62.778	3.103	1.267
o, Hz25, %90, %83	6	59.722	5.908	2.412

o, Hz25, %90, %100	6	47.5	8.216	3.354
o, Hz25, %80, %0	6	49.722	6.865	2.803
o, Hz25, %80, %33	6	65.556	2.018	0.824
o, Hz25, %80, %50	6	74.722	4.878	1.991
o, Hz25, %80, %67	6	73.333	4.944	2.018
o, Hz25, %80, %83	6	60	5.27	2.152
o, Hz25, %80, %100	6	50.278	7.025	2.868
o, Hz50, %90, %0	6	48.611	5.519	2.253
o, Hz50, %90, %33	6	77.5	5.028	2.053
o, Hz50, %90, %50	6	78.333	3.651	1.491
o, Hz50, %90, %67	6	66.111	7.722	3.152
o, Hz50, %90, %83	6	54.444	6.116	2.497
o, Hz50, %90, %100	6	48.611	7.558	3.086
o, Hz50, %80, %0	6	52.778	6.206	2.534
o, Hz50, %80, %33	6	69.722	6.784	2.769
o, Hz50, %80, %50	6	76.667	4.346	1.774
o, Hz50, %80, %67	6	73.333	4.216	1.721
o, Hz50, %80, %83	6	63.889	5.128	2.093
o, Hz50, %80, %100	6	51.389	3.861	1.576
o, Hz250, %90, %0	6	52.778	2.277	0.93
o, Hz250, %90, %33	6	77.778	7.577	3.093

o, Hz250, %90, %50	6	76.111	3.443	1.405
o, Hz250, %90, %67	6	66.667	2.582	1.054
o, Hz250, %90, %83	6	48.611	3.402	1.389
o, Hz250, %90, %100	6	49.722	4.524	1.847
o, Hz250, %80, %0	6	49.167	5.349	2.184
o, Hz250, %80, %33	6	71.667	6.055	2.472
o, Hz250, %80, %50	6	75.278	2.215	0.904
o, Hz250, %80, %67	6	80.278	5.717	2.334
o, Hz250, %80, %83	6	67.222	1.361	0.556
o, Hz250, %80, %100	6	52.5	2.934	1.198
o, Hz400, %90, %0	6	52.778	3.277	1.338
o, Hz400, %90, %33	6	76.667	7.958	3.249
o, Hz400, %90, %50	6	77.222	3.6	1.47
o, Hz400, %90, %67	6	65.556	4.303	1.757
o, Hz400, %90, %83	6	49.444	3.277	1.338
o, Hz400, %90, %100	6	49.444	3.752	1.532
o, Hz400, %80, %0	6	51.389	3.861	1.576
o, Hz400, %80, %33	6	73.611	4.399	1.796
o, Hz400, %80, %50	6	76.944	3.058	1.248
o, Hz400, %80, %67	6	77.222	5.34	2.18
o, Hz400, %80, %83	6	68.056	0.68	0.278

o, Hz400, %80, %100	6	51.111	0.861	0.351

Table 11: Means Table for %Corr, Effect: Age*Frequency*Signal Level*Noise Level

7.3 EXPERIMENT 3: ANOVA RESULTS

7.3.1 ANOVA TABLE FOR EXPERIMENT 3: LOW FREQUENCY

Source	**DF**	**MeanSquare**	**F-Value**	**P-Value**	**Power**
Age	1	48	6.082	.0333	.603
Subject(Group)	10	8			
SRCond	1	75	31.302	.0002	1
SRCond*Age	1	2	.691	.4252	.114
SRCond*Subject(Group)	10	2			
SigLev	5	224	143.104	<.0001	1
SigLev*Age	5	1	.822	.5398	.266
SigLev*Subject(Group)	50	1			
SRCond*SigLev	5	17	11.693	<.0001	1

SRCond*SigLev*Age	5	4	2.439	.0470	.722
SRCond*SigLev*Subject(Group)	50	1			

Table 12: Experiment 3 effects table, low frequency range

Effect: age*SRCondition*Signal level	**Count**	**Mean**	**Std. Dev.**	**Std. Err.**
y, noSR, dB20	6	6.695	0.726	0.296
y, noSR, %300	6	8.14	0.421	0.172
y, noSR, %150	6	9.357	1.971	0.805
y, noSR, %110	6	13.728	2.752	1.124
y, noSR, %100	6	16	0	0
y, noSR, %90	6	16	0	0
y, SR, dB20	6	7.23	1.022	0.417
y, SR, %300	6	8.347	1.97	0.804
y, SR, %150	6	9.273	1.387	0.566
y, SR, %110	6	10.387	0.79	0.323
y, SR, %100	6	11.287	1.958	0.799
y, SR, %90	6	13.438	1.288	0.526
o, noSR, dB20	6	8.102	1.412	0.576
o, noSR, %300	6	9.763	0.884	0.361
o, noSR, %150	6	11.577	1.887	0.77
o, noSR, %110	6	14.167	3.091	1.262

o, noSR, %100	6	16	0	0
o, noSR, %90	6	16	0	0
o, SR, dB20	6	7.72	1.093	0.446
o, SR, %300	6	10.152	1.319	0.539
o, SR, %150	6	10.202	1.574	0.643
o, SR, %110	6	10.833	1.775	0.725
o, SR, %100	6	13.32	1.345	0.549
o, SR, %90	6	16	0	0

Table 13: Means table for differential thresholds, low range. Effect: Age*SR Condition*Signal Level

7.3.2 ANOVA TABLE FOR EXPERIMENT 3: HIGH FREQUENCY

Souurce	**DF**	**Mean Square**	**F-Value**	**P-Value**	**Power**
Age	1	6702	17.152	.002	.970
Subject(Group)	10	390			
SRCond	1	4022	32.342	.0002	1
SRCond*Age	1	.001	0	.9979	.05
SRCond*Subject(Group)	10	124			
SigLev	5	25145	139.248	<.0001	1
SigLev*Age	5	365	2.022	.0916	.623
SigLev*Subject(Group)	50	180			
SRCond*SigLev	5	2606	29.790	<.0001	1

SRCond*SigLev*Age	5	752	8.600	<.0001	1
SRCond*SigLev*Subject(Group)	50	87.52			

Table 14: Experiment 3 effects table, high frequency range

Effect	Count	Mean	Std. Dev.	Std. Err.
y, noSR, dB20	6	94.063	8.653	3.532
y, noSR, %300	6	105.56	3.918	1.6
y, noSR, %150	6	123.007	17.521	7.153
y, noSR, %110	6	153.078	2.69	1.098
y, noSR, %100	6	200	0	0
y, noSR, %90	6	200	0	0
y, SR, dB20	6	105.45	12.59	5.14
y, SR, %300	6	118.892	15.311	6.251
y, SR, %150	6	139.48	12.821	5.234
y, SR, %110	6	138.247	19.819	8.091
y, SR, %100	6	153.158	6.507	2.657
y, SR, %90	6	157.088	7.179	2.931
o, noSR, dB20	6	117.087	13.927	5.686
o, noSR, %300	6	125.928	16.097	6.571
o, noSR, %150	6	139.195	20.643	8.428

o, noSR, %110	6	175.4	11.917	4.865
o, noSR, %100	6	200	0	0
o, noSR, %90	6	200	0	0
o, SR, dB20	6	109.28	7.951	3.246
o, SR, %300	6	136.808	21.755	8.882
o, SR, %150	6	132.957	23.185	9.465
o, SR, %110	6	158.263	4.659	1.902
o, SR, %100	6	160.228	8.786	3.587
o, SR, %90	6	196.62	8.279	3.38

Table 15: Means table for differential thresholds, high range. Effect: Age*SR Condition*Signal Level