

Research Article

Touch Noise Increases Vibrotactile Sensitivity in Old and Young

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ABSTRACT—Stochastic resonance (SR) occurs when the detection of a subthreshold signal is aided by the presence of random energy fluctuations in the signal modality, commonly called noise. SR is counterintuitive because such noise usually worsens performance. Nonetheless, SR has been demonstrated both theoretically and experimentally in human sensory systems. Using a psychophysically sophisticated paradigm, we show that SR aids the detection of vibrating touch stimuli presented to the foot soles of both healthy elderly people with elevated vibrotactile thresholds and healthy young people with normal vibrotactile thresholds. The results also suggest that it is possible to know a priori the amount of noise needed for optimal SR effects given the degree to which the signal is subthreshold. Thus, SR may be practical as a rehabilitative aid for individuals with elevated sensory thresholds.

Stochastic resonance (SR) is a ubiquitous phenomenon, widely studied in physics, in which the detection of a subthreshold signal is enhanced by the presence of noise, that is, ongoing random fluctuations of the same modality as the signal, but informationally unrelated to it (e.g., Gammaitoni, Hänggi, Jung, & Marchesoni, 1998). SR has been experimentally demonstrated to occur in various animal sensory systems, for example, crayfish sensory hairs (Douglass, Wilkens, Pantazelou, & Moss, 1993), cricket cercal receptors (Levin & Miller, 1996), rat cutaneous receptors (Collins, Imhoff, & Grigg, 1996a), and toad sciatic nerve (Morse & Evans, 1996). The study of SR has been extended to human sensory systems, and it has been demonstrated to occur in the human auditory (Ward, Desai, Rootman,

Tata, & Moss, 2001; Zeng, Fu, & Morse, 2000), visual (Kitajo, Nozaki, Ward, & Yamamoto, 2003; Ward et al., 2001), proprioceptive (Cordo et al., 1996), and tactile (Collins, Imhoff, & Grigg, 1996b, 1997; Richardson, Imhoff, Grigg, & Collins, 1998) sensory systems. Because SR can improve the ability of a sensory system to detect weak stimuli, it may be of use to individuals (e.g., the old or people with diseases such as multiple sclerosis or diabetes) who have elevated sensory thresholds.

The present experiment had three goals: first, to improve upon previous demonstrations of human tactile SR in several ways; second, to determine under rigorous psychophysical conditions if SR could lower thresholds in a sensory system in which thresholds had been elevated by age; and third, to quantify the level of noise needed to produce optimum SR effects given the characteristics of the target stimulus. Quantifying noise levels in this way would allow clinicians to know a priori which characteristics of noise would most benefit detection of weak signals, thus making SR more practical as a rehabilitative aid.

How does SR work? In threshold SR (Gingl, Kiss, & Moss, 1995), there are three necessary components: a threshold, a subthreshold stimulus, and noise. In this scenario, noise is randomly fluctuating ambient energy unrelated to the target stimulus (see Fig. 1). An optimal amount of noise, such as that shown in Figure 1b, makes the subthreshold stimulus (Fig. 1a) detectable without swamping the signal (as in Fig. 1c). Consider Braille reading, for example. If the Braille dots are too small, they are subthreshold and cannot be felt. If the paper is too smooth (but not perfectly smooth) or too rough, there is too little or too much tactile noise, respectively, and the dots cannot be distinguished from the paper. If the paper roughness is just right, however, the texture of the paper could actually aid in the detection of the Braille text. In a sensory system where the detection threshold has been elevated because of age, such as the tactile system of the elderly (Kenshalo, 1977, 1986), noise could be used to make subthreshold signals detectable.

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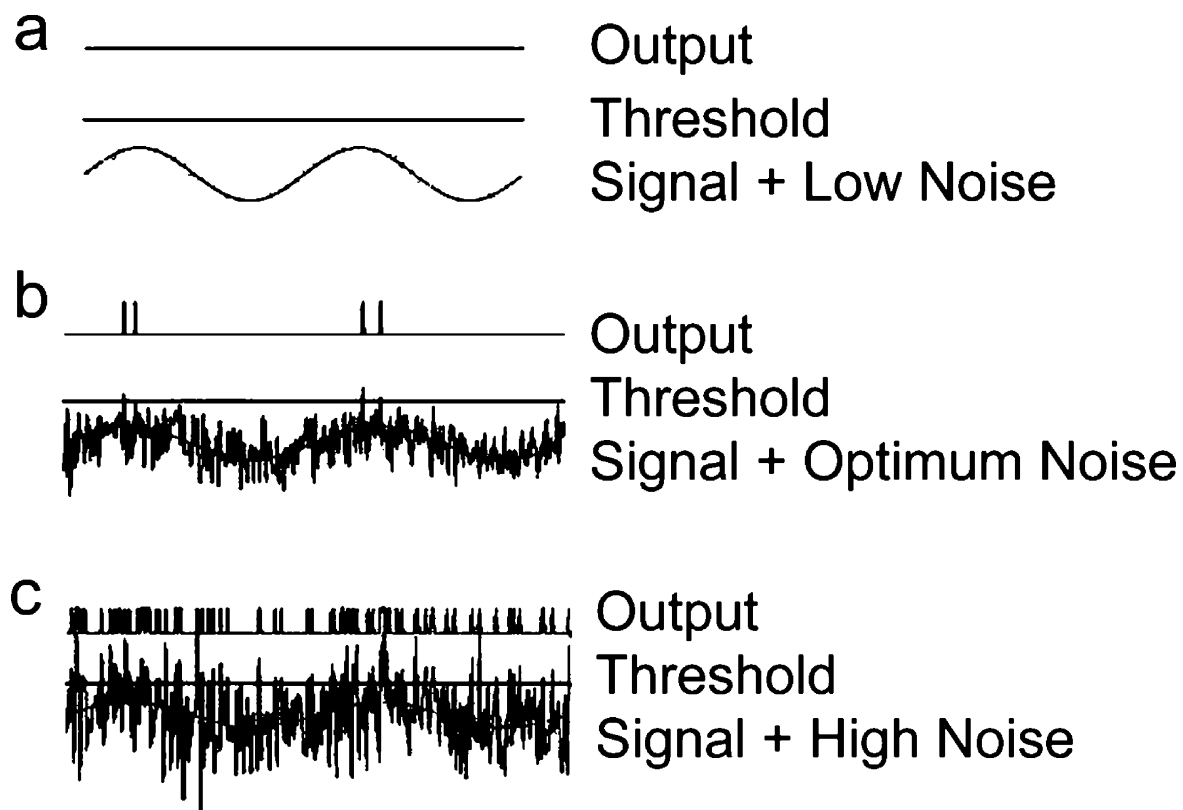


Fig. 1. Illustration of threshold stochastic resonance. (a) In the case of a subthreshold signal with little noise added, the signal does not attain threshold, and thus does not produce any output (spikes representing threshold crossings). (b) When adequate noise is added to the signal, the signal and noise cross the threshold, but generally only when the signal is high. (c) If excessive noise is added to the signal, the threshold crossings do not reflect the phase of the signal, which is swamped by the noise.

SR is a distinct phenomenon from previously reported “negative masking,” in which adding a masker in phase with a signal improves performance for near-threshold signals (reviewed by Laming, 1986). In negative masking, the stimulus and the masker must be of the same type, either noise or sinusoid, and must be added in phase, whereas in SR, rapidly changing, usually Gaussian, noise is added out of phase, or randomly, to the more slowly changing signal, which can be either periodic or aperiodic.

In the present study, we focused on SR in the human tactile system. The tactile system is ideal for studying SR in humans because both negative masking (e.g., Gescheider, Verrillo, & Pelli, 1992; Hamer, Verrillo, & Zwislocki, 1983; Verrillo, Gescheider, Calman, & Van Doren, 1983) and SR have been demonstrated in this system. Absolute detection thresholds in vibrotactile touch are among the sharpest found in any human sensory system; a sharp threshold makes SR easier to study. In humans, vibrotactile sensation in glabrous (nonhairy) skin is encoded by mechanoreceptors that are associated with four different types of afferent nerve fibers (Johansson, Landstrom, & Lundstrom, 1982). Slowly adapting Type II afferents (SAIIs) preferentially encode frequencies below 8 Hz; slowly adapting Type I afferents (SAIs) encode 2 Hz to 32 Hz; fast-adapting Type I afferents (FAIs) encode 8 Hz to 64 Hz; and fast-adapting Type

II afferents (FAIIs) mediate frequencies above 64 Hz. All four types of skin afferent behavior have recently been documented for the human foot sole (Kennedy & Inglis, 2002). It is possible that age-related degradation of vibrotactile sensitivity in the foot sole, particularly at frequencies mediated by the FAI and FAII afferents (Wells, Ward, Chua, & Inglis, 2003) and perhaps arising from the decline in function or number of the relevant mediating receptors (Bolton, Winkelman, & Dyck, 1966), contributes to gait pathology, falls, and injury in the aged (Azar & Lawton, 1964).

In their demonstrations of SR in the human tactile system, Collins and his colleagues used percentage correct responses in a one-interval forced-choice (1IFC) paradigm (Collins et al., 1996a, 1997; Richardson et al., 1998) or a brief yes/no method of limits (Liu et al., 2002) to measure performance. In these studies, participants distinguished between a stimulus that contained vibrotactile noise and a stimulus consisting of the same noise plus a weak square-wave touch stimulus, delivered by a pointed probe touching the skin. Several aspects of these experiments should be refined in order to rigorously demonstrate SR in the human tactile system.

First, in all of these previous experiments, the signal-plus-noise stimulus contained more energy than did the noise-alone

stimulus. Thus, it is possible that participants were detecting the greater energy in the more energetic signal-plus-noise stimulus rather than responding to or detecting the signal per se. As in negative masking, classical psychophysics would predict that when the noise level is very low, both noise-alone and signal-plus-noise stimuli would be subthreshold and detected infrequently, so they would not be reliably discriminated. When the noise level is very high, the noise would mask the weak signal and again noise-alone and signal-plus-noise stimuli would not be reliably discriminated. When the noise level is just below threshold, however, the signal-plus-noise stimulus would be above threshold and frequently detected, whereas the noise-alone stimulus would be beneath threshold and seldom detected. This difference in detection rates for the signal-plus-noise stimulus and the noise-alone stimulus would appear as increased discriminability of the two stimuli at an intermediate noise level, as in SR. Under these conditions, however, it is not possible to ascertain whether participants, who detect the more energetic stimulus containing the signal, are actually perceiving the signal and thus are better able to detect any information contained in it, for example, its vibration frequency.

Second, the percentage correct measure in the IIFC paradigm is not free of criterion effects. In this paradigm, participants are asked to say whether or not a signal is present on each trial, and their answer is affected by where they set their criterion for this decision. For example, for any particular noise-alone and signal-plus-noise stimuli, as the criterion changes from very liberal (many more “yes” answers than “no” answers) to very conservative (many more “no” answers than “yes” answers), the percentage correct measure increases to a maximum, and then decreases again. This peak in percentage correct at the optimal criterion setting will occur whether or not the noise level is optimal for SR, and does not necessarily reflect the sensory threshold. Thus, better performance at a particular noise level could arise in the absence of SR if the average decision criterion were optimal for some nonzero noise level and nonoptimal for other noise levels, including the zero noise level. In a study designed to determine whether noise can improve detection of subthreshold stimuli, it is critical that the measure of performance not be potentially confounded by the possibility that participants could set their decision criteria differently in different noise conditions.

Finally, the brief yes/no method-of-limits paradigm employed in the single study of older people and neuropathy patients (Liu et al., 2002), although widely used in clinical studies, is also subject to bias and thus less useful than more rigorous methods when precise results are required. In this method, participants simply indicate whether or not they detect a sensation as the stimulus intensity is increased or decreased in steps of decreasing size, over a series of 20 presentations. Five null presentations are interspersed among the stimulus trials, to detect a bias to respond positively, and the series is stopped and redone if more than one “yes” response is given to a null

stimulus. Although this method usually yields vibration thresholds near those of forced-choice paradigms (Dyck, O’Brien, Kosanke, Gillen, & Karnes, 1993), it can be fooled by people deliberately manipulating their thresholds (e.g., Dyck et al., 1998; Freeman, Chase, & Risk, 2003), in much the same way that changes in criterion location can influence detection in a IIFC paradigm.

Modern psychophysical practice relies more on the framework of signal detection theory than on the classical threshold concept. Although signal detection theory raises problems for the interpretation of SR (e.g., Tougaard, 2000), these problems can be resolved (Ward, Neiman, & Moss, 2002). Signal detection theory shows that the percentage correct measure is more likely to produce bias-free performance in a two-interval forced-choice (2IFC) paradigm than in a IIFC or yes/no paradigm. Thus, in the present experiment, we used a 2IFC paradigm to avoid criterion effects. Moreover, we also equated the energy levels in the noise-alone and signal-plus-noise stimuli in order to determine whether added noise would enhance detection of the information in a subthreshold vibrating stimulus in addition to simply increasing its energy (Ward, 2003).

To date, there has been only the single demonstration-in-principle (Liu et al., 2002) that SR is effective in lowering thresholds in old or otherwise compromised sensory systems. That study measured vibration thresholds using the brief yes/no staircase method, at only a single vibration frequency (30 Hz), and only on fingertips of healthy older people (mean age of 74 years) and stroke patients and also on the foot soles of diabetics. The touch thresholds of the older participants were not compared with those of younger people, although it was assumed they would be higher because of age-related sensory loss. It has been shown, however, that tactile thresholds for higher-frequency vibrations increase as a function of age more than do tactile thresholds for lower-frequency vibrations (e.g., Verrillo, 1979; Wells et al., 2003). Indeed, we found that on the foot sole, absolute thresholds for 25-Hz vibrations were roughly the same for older and younger participants (see Procedure section). It is possible that the same was true for the 30-Hz vibrations on the fingertip used by Liu et al. Thus, it is important to establish whether facilitating sensation through SR may reduce thresholds that are demonstrated to be elevated relative to thresholds in a sample of normal participants, for a larger range of functionally relevant vibration frequencies, and on a skin region that might be important for the health and independence of the elderly.

Thus, we compared a sample of healthy elderly adults with a sample of college-age adults in our experiment, and we measured SR effects on the foot sole at vibration frequencies from 25 Hz to 400 Hz. The foot was chosen as the test location because age-related neuropathies generally affect the extremities first and most (Rothwell, 1986), and because neuropathies of the foot are relevant to one of the worst problems facing elderly adults, that of falls causing broken bones and a significantly

increased probability of death following the hospitalization engendered by such falls.

METHOD

Participants

The 12 participants were evenly divided between the young age group (mean age = 26 years 2 months, $SD = 3$ years 3 months; 4 men and 2 women) and the old age group (mean age = 88 years 8 months, $SD = 5$ years 4 months; 4 women and 2 men). Participants reported themselves to be free of neurological disease, were nonsmokers, and were moderate drinkers. Although some participants in both age groups were taking medication regularly, none of the medications have been shown to affect sense of touch.

Apparatus and Stimuli

Sinusoidal vibratory signals and noise were generated digitally on a microcomputer using LabView 4.2 and sent as a voltage value via a National Instruments PCI-MIO XE-10 multi-input-output board to a National Instruments BNC 2090 BNC D-A output box. The voltage waveform was supplied to an ASI Model 300B dual-mode lever-arm motor system. The lever arm of the motor supplied the tactile stimulus. The diameter of the head of the lever arm was 1.5 mm. The shaft of the motor was attached to the lever arm that delivered the stimulus to the subject (Fig. 2).

The subthreshold sinusoidal signal levels were set to 90% and 80% of the energy of each individual's threshold at each frequency. Noise levels were set at 0%, 33%, 50%, 67%, 83%,

or 100% of the relevant noise-threshold energy for that individual. On each trial, the noise comprised two new samples (one for signal plus noise and one for noise alone) from a zero-mean, Gaussian (normal) distribution. When FAI-mediated signal frequencies were tested, noise was band-pass filtered so that only FAI mechanoreceptors would be activated by the noise (0.125–25 Hz for the young age group, 0.125–50 Hz for the old age group; see Verrillo, 1979). When FAII-mediated signal frequencies were tested, noise was band-pass filtered to contain only FAII-mediated noise (25–500 Hz for the young age group, 50–500 Hz for the old age group). Noise was filtered because, although FAII-mediated noise added to an FAI-mediated frequency would not detract from the FAI afferent's ability to detect the signal, it would activate FAII receptors in the vicinity and possibly confound threshold levels or have a subthreshold priming effect on FAI receptors. Signals were sampled at 1 kHz. Noise was sampled at 10 kHz. The power spectrum of the waveform was calculated, and the energy in the waveform was determined by integrating a 10% band of the power spectrum around the target frequency.

Procedure

The two-stage protocol was approved by the Office of Research Services and Administration Behavioural Research Ethics Board at the University of British Columbia. Data from the two stages, absolute-threshold determination and SR measurement, were collected at the same time, but the SR data are reported here, whereas the absolute-threshold data for the sinusoidal stimuli are reported in Wells et al. (2003).

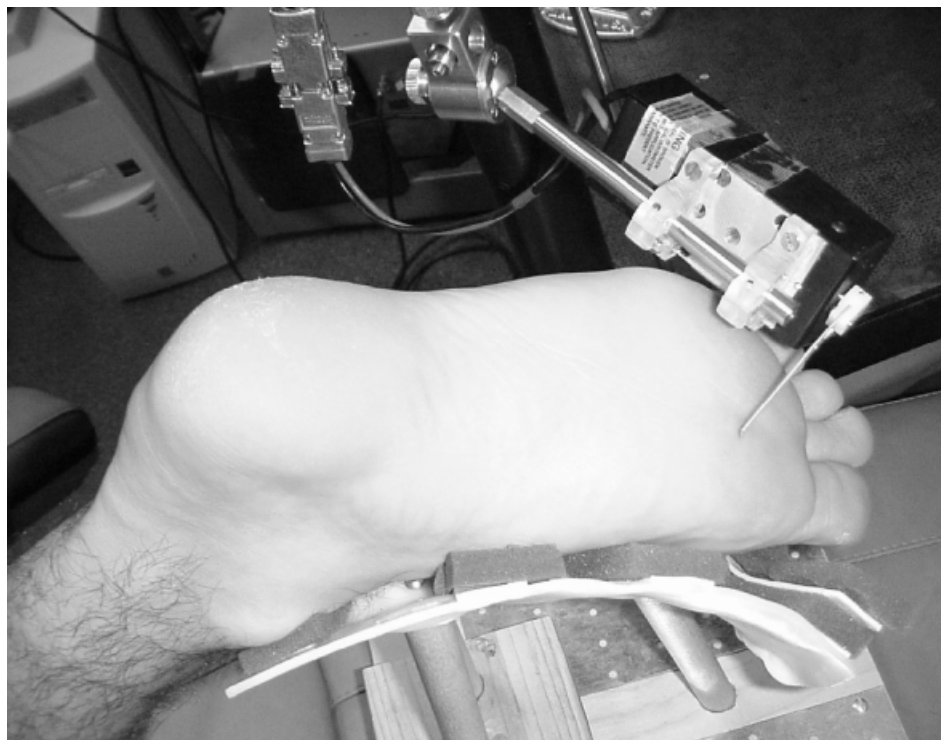


Fig. 2. Equipment setup.

In the first stage of the experiment, absolute thresholds for the upper arch on the right foot for each of four sinusoidal vibration frequencies (25 Hz, 50 Hz, 250 Hz, 400 Hz) and for the two filtered noise sources were determined by a modified method of limits for each individual (see Wells et al., 2003, for details and absolute-threshold data for sinusoidal stimuli). The upper arch was chosen because the thick skin of the heel and ball of the foot impedes the transmission of high-frequency vibration (Pubols, 1987). The arch usually is the least callused area of the foot and showed the lowest threshold of any foot area at all four vibration frequencies (reported in Wells et al., 2003). In general, absolute thresholds were similar for old and young participants at 25 Hz. At 50 Hz and 250 Hz, however, thresholds averaged more than 350% higher for old than for young participants, and at 400 Hz, thresholds averaged more than 600% higher for old than for young participants. At these frequencies, moreover, there was no overlap at all between the two groups' threshold values, indicating substantial loss of sensitivity for all of the older participants at vibration frequencies from 50 to 400 Hz (Wells et al., 2003). Tactile noise thresholds were also uniformly higher for the older participants.

In the second stage of this study, threshold information from the first stage was used to generate subthreshold vibration signals that were then combined with various noise levels (all but the very highest were subthreshold) to measure SR effects. During both stages, the participants lay face down on a massage table with their right foot supported in a padded restraint to expose the foot sole. The foot was strapped to the restraint using soft webbing.

The experiment employed a 2IFC paradigm, in which one of the 1-s epochs contained one of two subthreshold levels of signal at one of the four frequencies plus one of six levels of noise. The other 1-s epoch contained noise only. The energy in the noise-alone epoch was set equal to the energy in the signal-plus-noise epoch. To begin a trial, the head of the lever arm was placed against the foot sole perpendicular to the test site and without producing any force offset. This ensured that mechanoreceptors were not activated before stimulus onset. The appropriate waveforms were applied to the lever arm in 1-s epochs separated by 1 s. Participants were asked to identify which of the epochs contained the target signal.

Each combination of the two signal levels and six noise levels was presented 60 times, for a total of 720 trials, at each of the four frequencies. The trials were presented in 12 pseudorandom blocks, with each block containing 5 trials of each combination of frequency, signal level, and noise level. The testing time for each block was approximately 20 min. Participants rested between blocks on an as-needed basis.

Data Analysis

Two data sets were collected for each 2IFC trial: a time series representing the force exerted by the motor arm on the partic-

ipant's foot sole and the participant's choice of which time epoch contained the signal. The force data were used to identify trials on which the force was inconsistent. These trials were redone at the end of each block so that each participant completed five valid trials for each combination of signal level, noise level, and signal frequency in each block. The dependent variable of interest, percentage correct responses (closely related to the d' measure of signal detection theory in the 2IFC paradigm), was analyzed using an analysis of variance (ANOVA) with the following factors: age (young or old), signal frequency (25 Hz, 50 Hz, 250 Hz, or 400 Hz), signal level (80% or 90% of signal threshold energy), and filtered noise level (0%, 33%, 50%, 67%, 83%, or 100% of noise threshold energy). All factors except age were repeated measures factors. Greenhouse-Geisser corrections (original degrees of freedom are reported) were used to correct p values for sphericity violations for factors with more than two levels. Statistically significant ANOVA findings were further analyzed using the Tukey post hoc method.

RESULTS AND DISCUSSION

The results of the experiment are summarized in Figure 3. Performance varied significantly with age, $F(1, 10) = 17.5, p = .002, \eta^2 = .009$; signal level, $F(1, 10) = 42.9, p < .0001, \eta^2 = .005$; and noise level, $F(5, 50) = 512.9, p < .0001, \eta^2 = .747$; performance did not vary significantly with frequency. Noise level interacted significantly with signal level, $F(5, 50) = 35.3, p < .0001, \eta^2 = .086$, but not with age or frequency. For each signal level, there was a nonzero, optimal noise level that maximized percentage correct responses, with the weaker signal (80% of threshold) requiring a greater level of noise for maximum performance. Thus, SR occurred at each frequency and signal level, although performance varied with noise level slightly differently for different frequencies, as indicated by the significant three-way interaction of frequency, signal level, and noise level, $F(15, 150) = 3.1, p = .0002, \eta^2 = .009$. There were also slight differences in this three-way interaction with age, as indicated by a marginally significant four-way interaction of noise level, signal level, frequency, and age, $F(15, 150) = 1.8, p = .04, \eta^2 = .005$. At the optimal noise level and several others for each condition, performance was significantly different from the 50% level predicted by random responding ($p < .05$ by Tukey test; see also standard error bars in Fig. 3).

As mentioned, the optimal noise level was dependent on the signal level (Table 1). Previous research has shown that particular nonzero levels of noise produce maximum performance. These optimum noise levels, however, have previously not been expressed generally, in terms of the relationship of a target signal to a threshold. At the 90%-of-threshold signal level, 33% noise produced maximum performance for the young at all frequencies, whereas the optimal noise level was 50% for all but the 25-Hz stimuli for the elderly. At the 80%-of-threshold signal level, either 50% or 67% noise produced maximum perfor-

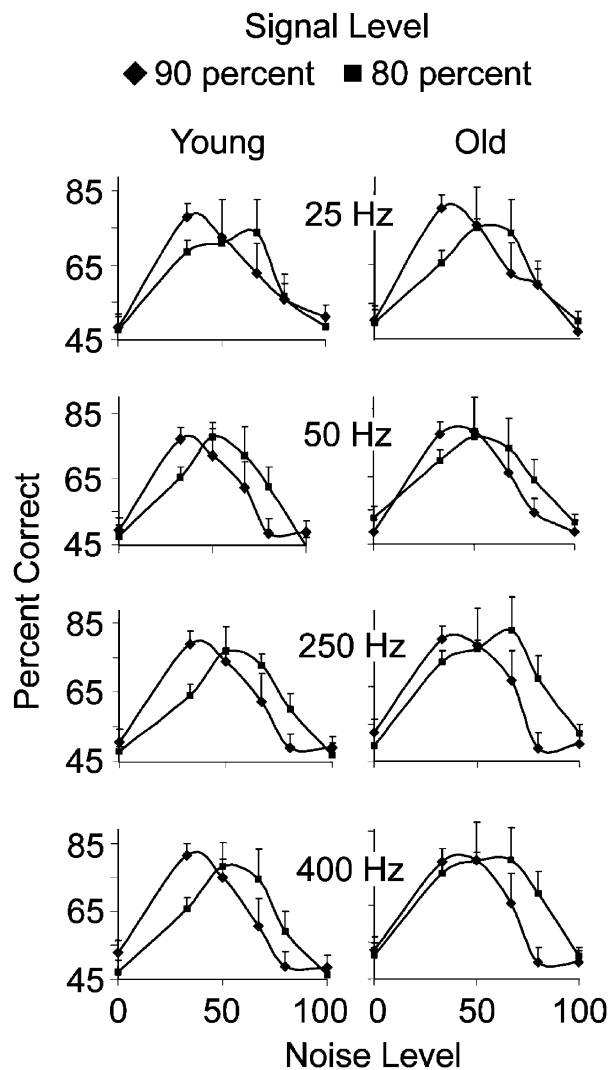


Fig. 3. Percentage correct as a function of noise level for young (left) and older (right) adults. For each age group, results for the four vibration frequencies are presented in separate graphs, with separate curves for the 80% and 90% signal levels. Each graph shows the signature of sub-threshold resonance: Percentage correct rises quickly to a maximum with increasing noise level and then declines slowly. Error bars represent standard errors.

mance; however, there was no statistically significant difference between the performance maxima produced by these noise levels at any frequency. For all frequencies, signal levels, and age groups, responding was at chance for the 0% noise and 100% noise levels.

That the optimal level of noise was higher for the 80% signal level than the 90% level is reasonable, because one would expect a lower signal level to require a higher noise level for there to be sufficient threshold crossings to transmit information about the signal. Greenwood, Ward, and Wefelmeyer (1999) showed mathematically 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.

TABLE 1

Optimal Noise as a Function of Signal Strength and Frequency

Age group and signal strength	Signal frequency			
	25 Hz	50 Hz	250 Hz	400 Hz
Young				
90% signal	33%	33%	33%	33%
80% signal	50%	50%	50%	50%
Old				
90% signal	33%	50%	50%	50%
80% signal	50%	67%	67%	67%

Performance improved to similar levels (relative to individual thresholds) at both FAI-mediated (25 Hz for young, 25 Hz and 50 Hz for old) and FAII-mediated (50 Hz, 250 Hz, and 400 Hz for young; 250 Hz and 400 Hz for old) frequencies for both young and old participants. At 50 Hz, 250 Hz, and 400 Hz, however, greater amounts of noise were required to achieve these performance levels in old than in young participants. These frequencies are mediated by FAII receptors in the young, although, because of declining number and function of FAII receptors, 50-Hz vibration is mediated by FAI receptors in the old. Given the decrease in the number of FAII receptors as a function of age, it is possible that more noise was required in order to engage the remaining receptors of the old participants to the same level of activity as stimulated in the more plentiful receptors in the young participants.

CONCLUSIONS

Using a 2IFC paradigm, this study showed that SR is effective in aiding the detection of subthreshold signals in both young participants and old participants with elevated touch thresholds. The 2IFC design improved upon previous 1IFC and yes/no experiments by eliminating criterion effects. Further, the present experiment showed that the mechanism of SR does not just increase the energy in a stimulus, but also increases the information that an organism can derive from a stimulus.

Based on the results of the experiment, two main conclusions regarding the use of SR in the elderly can be drawn. First, the use of SR rendered subthreshold signals detectable to both young and old age groups. Given the uniformity of the effect of SR over individuals, the degree to which noise can improve sensation in older people could be expressed compellingly in terms of the average number of years of age for which SR compensates. Because at present only the endpoints of the function relating absolute threshold to age are known, we can only guess at the exact magnitude of the effects represented by our results. Nonetheless, any reduction of absolute threshold implies the possibility of using SR as an aid to reclaim functionality in the old, and possibly to reduce injury resulting from lost functionality (cf. Liu et al., 2002).

Second, because the results show that the optimal amount of noise is related to the degree to which the target signal is below threshold, it is possible to know a priori what level of noise will optimize the transmission of a signal through the tactile system and to use this knowledge to design prostheses. Consider, for example, using SR to facilitate the sensation of frequencies commonly felt by the plantar surface of the foot during walking or running. This could alleviate some of the effects of gait dysfunction caused by diminished feeling in the foot. It has been hypothesized that plantar vibration sensation plays an important role in gait (Diener, Dichgans, Guschlbauer, & Mau, 1984; Kennedy & Inglis, 2002; Wells et al., 2003), and, further, increased sensation thresholds on the plantar surface of the foot have been shown to cause gait dysfunction (Perry, McIlroy, & Maki, 2000). This age-related decrepitude in plantar vibration sensation may lead to pathological gait and falls, the major cause of accidental death in people over age 75 (Azar & Lawton, 1964). Were it possible to determine the amplitudes of vibration frequencies felt in the foot during walking, and the elevated thresholds for these frequencies, useful sensations at these critical frequencies could be facilitated by adding precisely calculated, individually optimum amounts of noise to the foot sole. It has already been shown that facilitation of other types of plantar sensation can be helpful in the old by improving the effectiveness of stabilizing reactions evoked in response to unpredictable postural perturbations (Maki, Perry, Norrie, & McIlroy, 1999) and by improving balance control while standing (Priplata, Niemi, Harry, Lipsitz, & Collins, 2003). The present results provide the kind of scientific basis needed to build useful SR-based prostheses for people whose sensory thresholds have been raised by age or disease.

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REFERENCES

- Azar, G., & Lawton, A. (1964). Gait and stepping as factors in the frequent falls of elderly women. *Gerontologist, 4*, 83–103.
- Bolton, C., Winkelman, R.K., & Dyck, P.J. (1966). A quantitative study of Meissner's corpuscles in man. *Neurology, 16*, 1–9.
- Collins, J.J., Imhoff, T.T., & Grigg, P. (1996a). Noise enhanced information transmission in rat SA1 cutaneous mechanoreceptors via aperiodic stochastic resonance. *Journal of Neurophysiology, 76*, 642–645.
- Collins, J.J., Imhoff, T.T., & Grigg, P. (1996b). Noise-enhanced tactile sensation. *Nature, 383*, 770.
- Collins, J.J., Imhoff, T.T., & Grigg, P. (1997). Noise mediated enhancements and decrements in human tactile sensation. *Physical Review E, 56*, 923–926.
- Cordo, P.J., Inglis, J.T., Verschueren, S., Collins, J.J., Merfeld, D.M., Buckley, S., Rosenblum, S., & Moss, F. (1996). Noise in human muscle spindles. *Nature, 383*, 769–770.
- Diener, H., Dichgans, J., Guschlbauer, B., & Mau, H. (1984). The significance of proprioception on postural stabilization as assessed by ischemia. *Brain Research, 296*, 103–109.
- Douglass, J.K., Wilkens, L., Pantazelou, E., & Moss, F. (1993). Noise enhanced information transfer in crayfish mechanoreceptors by stochastic resonance. *Nature, 365*, 337–340.
- Dyck, P.J., Dyck, P.J.B., Kennedy, W.R., Kesserwani, H., Melanson, M., Ochoa, J., Shy, M., Stevens, J.C., Suarez, G.A., & O'Brien, P.C. (1998). Limitations of quantitative sensory testing when patients are biased toward a bad outcome. *Neurology, 50*, 1213.
- Dyck, P.J., O'Brien, P.C., Kosanke, J.L., Gillen, D.A., & Karnes, J.L. (1993). A 4,2 and 1 stepping algorithm for quick and accurate estimation of cutaneous sensation threshold. *Neurology, 43*, 1508–1513.
- Freeman, R., Chase, K.P., & Risk, M.R. (2003). Quantitative sensory testing cannot differentiate simulated sensory loss from sensory neuropathy. *Neurology, 60*, 465–470.
- Gammaitoni, L., Hänggi, P., Jung, P., & Marchesoni, F. (1998). Stochastic resonance. *Review of Modern Physics, 70*, 223–287.
- Gescheider, G., Verrillo, R.T., & Pelli, D.G. (1992). Effects of noise on detection of amplitude increments of sinusoidal vibration of the skin. *Journal of the Acoustical Society of America, 91*, 348.
- Gingl, Z., Kiss, L.B., & Moss, F. (1995). Non-dynamical stochastic resonance: Theory and experiments with white and arbitrarily coloured noise. *Europhysics Letters, 29*, 191–196.
- Greenwood, P.E., Ward, L.M., & Wefelmeyer, W. (1999). Statistical analysis of stochastic resonance in a simple setting. *Physical Review E, 60*, 4687–4695.
- Hamer, R., Verrillo, R.T., & Zwislocki, J.T. (1983). Tactile masking of Pacinian and non-Pacinian channels. *Journal of the Acoustical Society of America, 73*, 1293.
- Johansson, R., Landstrom, U., & Lundstrom, R. (1982). Responses of mechanoreceptive afferent units in the glabrous skin of the human hand to sinusoidal skin displacements. *Brain Research, 422*, 17–25.
- Kennedy, P.M., & Inglis, J.T. (2002). Distribution and behaviour of glabrous cutaneous receptors in the human foot sole. *Journal of Physiology (London), 538*, 995–1002.
- Kenshalo, D.R. (1977). Age changes in touch, vibration, temperature, kinesthesia and pain sensitivity. In J.E. Birren & K.W. Schaie (Eds.), *Handbook of the physiology of aging* (pp. 562–579). New York: Van Nostrand Reinhold.
- Kenshalo, D.R. (1986). Somesthetic sensitivity in young and elderly humans. *Journal of Gerontology, 41*, 732–742.
- Kitajo, K., Nozaki, D., Ward, L.M., & Yamamoto, Y. (2003). Behavioral stochastic resonance within the human brain. *Physical Review Letters, 90*, Article 218103.
- Laming, D.R.J. (1986). *Sensory analysis*. Orlando, FL: Academic Press.
- Levin, J.E., & Miller, J.P. (1996). Broadband neuronal encoding in the cricket cercal sensory system enhanced by stochastic resonance. *Nature, 380*, 165–168.
- Liu, W., Lipsitz, L.A., Montero-Odasso, M., Bean, J., Kerrigan, D.C., & Collins, J.J. (2002). Noise-enhanced vibrotactile sensitivity in older adults, patients with stroke, and patients with diabetic neuropathy. *Archives of Physical Medicine and Rehabilitation, 83*, 171–176.
- Maki, B.E., Perry, S.D., Norrie, R.G., & McIlroy, W.E. (1999). Effect of facilitation of sensation from plantar foot-surface boundaries on

- postural stabilization in young and older adults. *Journal of Gerontology*, 54A, M281–M287.
- Morse, R.P., & Evans, E.F. (1996). Enhancement of vowel encoding for cochlear implants by the addition of noise. *Nature Medicine*, 2, 928–932.
- Perry, S., McIlroy, W.E., & Maki, B.E. (2000). The role of plantar cutaneous mechanoreceptors in the control of compensatory stepping reactions evoked by unpredictable multi-directional perturbation. *Brain Research*, 877, 401–406.
- Priplata, A.A., Niemi, J.B., Harry, J.D., Lipsitz, L.A., & Collins, J.J. (2003). Vibrating insoles and balance control in elderly people. *The Lancet*, 362, 1123–1124.
- Pubols, B. (1987). Effect of mechanical stimulus spread across glabrous skin of racoon and squirrel monkey hand on tactile primary afferent fibre discharge. *Somatosensory Research*, 4, 273–308.
- Richardson, K.A., Imhoff, T.T., Grigg, P., & Collins, J.J. (1998). Using electrical noise to enhance the ability of humans to detect suprathreshold mechanical cutaneous stimulus. *Chaos*, 8, 599–603.
- Rothwell, J. (1986). *Control of human voluntary movement* (2nd ed.). New York: Chapman and Hall.
- Tougaard, J. (2000). Stochastic resonance and signal detection in an energy detector—implications for biological receptor systems. *Biological Cybernetics*, 83, 471–480.
- Verrillo, R. (1979). Change in vibrotactile thresholds as a function of age. *Sensory Processes*, 3, 49–59.
- Verrillo, R., Gescheider, G.A., Calman, A.G., & Van Doren, C.L. (1983). Vibrotactile masking: Effects of one- and two-site stimulation. *Perception & Psychophysics*, 33, 379–387.
- Ward, L.M. (2003). Is stochastic resonance just an epiphenomenon? In S.M. Bezrukov (Ed.), *Unsolved problems of noise and fluctuations* (pp. 84–93). Melville, NY: American Institute of Physics.
- Ward, L.M., Desai, S., Rootman, D., Tata, M., & Moss, F. (2001). Noise can help as well as hinder seeing and hearing. *Bulletin of the American Physical Society*, 46, N23.002.
- Ward, L.M., Neiman, A., & Moss, F. (2002). Stochastic resonance in psychophysics and in animal behavior. *Biological Cybernetics*, 87, 91–101.
- Wells, C., Ward, L.M., Chua, R., & Inglis, J.T. (2003). Regional variations and changes with ageing in vibrotactile sensitivity in the human footsole. *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences*, 58, B680–B686.
- Zeng, F., Fu, Q.J., & Morse, R. (2000). Human hearing enhanced by noise. *Brain Research*, 869, 251–255.

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