Noise in human muscle spindles

SIR — Stochastic resonance is a phenomenon in which the response of a nonlinear system to a weak input signal is optimized by the presence of a particular non-zero level of noise[1,2]. It has been demonstrated in several biological systems, ranging from ion channels[3] to sensory neurons[4] to human psychophysics[5]. Here we demonstrate stochastic resonance *in vivo* in the human proprioceptive system. We show that the sensitivity of muscle-spindle receptors to a weak movement signal can be maximally enhanced by introducing noise through the tendon of the parent muscle.

We recorded firing activity of individual muscle-spindle afferents from the wrist and hand extensor muscles from the radial nerve in healthy human subjects. When a suitable afferent is isolated, the subject's right wrist is passively rotated by a manipulandum, with a low-amplitude sinusoidal waveform (Fig. 1). We applied a random noise input by a tendon stimulator to stretch the appropriate muscle, and varied the intensity of the noise input between trials.

To characterize stochastic resonance in the spindle afferents, we calculated the output signal-to-noise ratio from the power spectrum, defining it as the ratio of the strength (area) of the signal peak to the mean amplitude of the background noise at the input signal frequency. The output signal-to-noise assesses the coherence of the system response (its spiking activity) with the input signal at the frequency of wrist rotation.

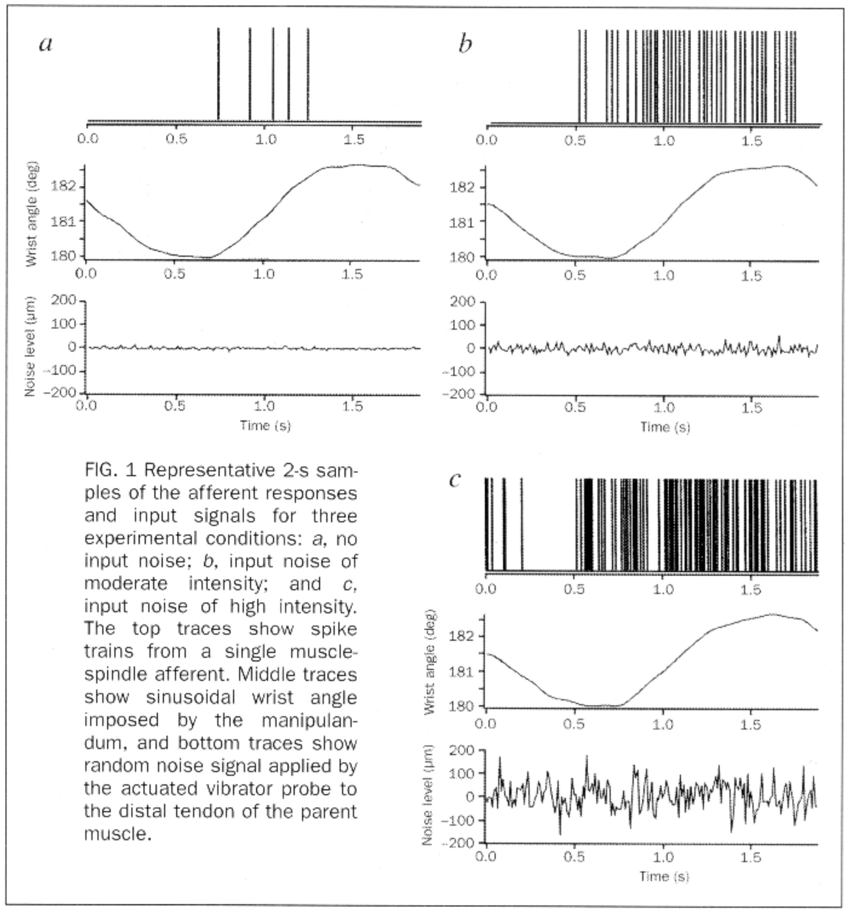

FIG. 1 Representative 2-s samples of the afferent responses and input signals for three experimental conditions: *a*, no input noise; *b*, input noise of moderate intensity; and *c*, input noise of high intensity. The top traces show spike trains from a single muscle-spindle afferent. Middle traces show sinusoidal wrist angle imposed by the manipulandum, and bottom traces show random noise signal applied by the actuated vibrator probe to the distal tendon of the parent muscle.

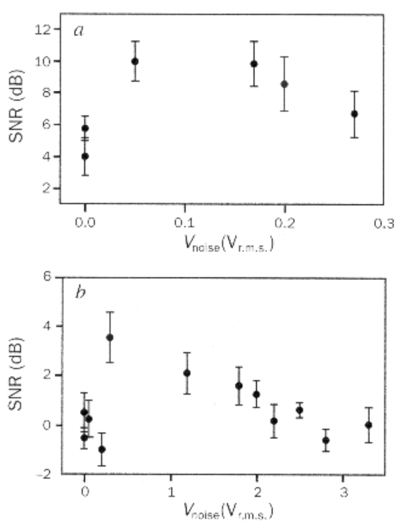

FIG. 2 Values of the output signal-to-noise ratio (SNR) versus the input noise r.m.s. voltage for single spindle afferents in two different subjects: *a*, a healthy subject; *b*, a subject who was administered an anaesthetic block of the brachial plexus. The output SNR for each noise intensity level was computed from the spike-train power spectra in 1-Hz increments. Error bars on the SNR values represent the standard deviation of the noise value of the centre frequency of each 1-Hz bin.

Six of the eight afferents we examined showed clear stochastic resonance behaviour: as input noise intensity increased, the output signal-to-noise ratio rapidly increased to a peak and then slowly decreased (Figs 1 and 2). Thus, in each of these cases, the presence of a particular, non-zero level of noise optimally enhanced the sensitivity of the muscle spindle receptor to the weak input signal (see also ref. 6).

Stochastic resonance from mechanical stimulation of the arm could occur directly on the muscle-spindle receptor or indirectly through cutaneous fusimotor reflexes[7,8], because the noise input presumably activates cutaneous receptors beneath the probe as well as muscle spindles in the muscle proper. To control for a possible cutaneous fusimotor reflex, we inactivated the fusimotor system in the right arm of one subject with an anaesthetic block of the brachial plexus, functionally denervating the arm at the shoulder. The afferent recordings from that subject exhibited clear stochastic resonance characteristics (Fig. 2*b*), suggesting that the positive effect of noise reported in this study is due to a direct effect on the muscle-spindle receptor rather than as a result of cutaneous fusimotor reflexes.

Our results raise the possibility that the fusimotor system uses a stochastic resonance-type mechanism to increase the sensitivity of muscle spindles to stretch. It is known that fusimotor activity and muscle spindle output is enhanced during postural tasks and novel movements[9]. Fusimotor activation, which increases the random properties of muscle spindle firing[10], could provide the stochastic input required by a stochastic resonance mechanism. Thus, fusimotor neurons may serve as a beneficial,

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intrinsic noise source for the proprioceptive system.

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Noise-enhanced tactile sensation