Proposal of the stretch detection hypothesis of the Meissner corpuscle

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Abstract. In order to realize artificial tactile sensation, we are researching the natural nerve activity timing of mechanoreceptors. Considering the energy conversion system of the Meissner corpuscle, we insist that the corpuscles encode the normal strain, particularly detecting horizontal normal strain. We observed a clear difference in the thresholds between the pushing and pulling cases. This finding suggests that horizontal stretch preferentially induces nerve activity in the Meissner corpuscle.

Key words: Mechanoreceptor, strain, nerve activity

1 Introduction

Several studies have reported on tactile displays that employ mechanical stimulation. These studies proposed the replication of (1) the surface property of the object or (2) skin deformation. There are two strategies for implementing these abovementioned proposals-the use of vibration or the exertion of pressure. Many vibration-based tactile displays employ the vertical vibration of a pin array to change the physical amplitude and oscillation frequency on the surface of the skin [1]. Researchers have also proposed methods based on the properties of human tactile information processing. We are able to feel tactile sensations because of the mechanoreceptor units. Mechanoreceptors are classified into four groups according to the receptive fields and the adapting speed. Rapidly adapting type I and type II (RAI and RAII) mechanoreceptors are called Meissner corpuscles and Pacinian corpuscles, respectively. Slowly adapting type I and type II (SAI and SAII) mechanoreceptors are called Merkel 's disk and Ruffini endings, respectively. Some researchers have developed tactile displays that stimulate each mechanoreceptor selectively [2, 3]. However, the researchers were unable to demonstrate sensations clearly in the intended manner because they had not determined the parameters of the major proportions of tactile information. Consequently, ad hoc stimulations were used for the tactile devices. We believe that tactile displays should provide rich information with a simple structure. Based on this motivation, we intend to determine the human tactile perceptual mechanisms. Some researches have been conducted on the elastic transfer property of human skin. By using a simulation of dynamics of elasticity, the prediction of elastic deformation already has a certain accuracy. There also exist a few hypotheses on the relation between receptor modification and nerve activity. In this study, we wish to provide an answer to the question " When does the nerve activity arise concretely in a transitive situation? " Unlike electophysiological experiments, nearly all daily experiences are transitional. For example, the experiences that one might undergo during the course of daily life differ from a situation in which a regularly fixed vibration continues to be given to the skin. Thus, in this paper, we propose an explanation for the energy conversion system of Meissner corpuscles, which exist in the superficial layer of the skin. The response of this receptor is supposed to be important especially for active touch. This discussion will help us determine an effective strategy for signal design of tactile displays.

2 Related Research

Meissner corpuscles have a relatively low characteristic frequency of around 40 Hz. They are localized in the papillary dermis with a height of around 150 μm and a diameter of 40-70 μm. Observations revealed that the sensory corpuscles are composed of a stack of discoid components consisting of flattened axon terminals sandwiched between Schwann cell lamellae. Mechanoreceptors encode the surface deformation of their axons into nerve activity when the skin is deformed.

2.1 Electrophysiological finding

By applying vibrations to a fingertip, many electrophysiological experiments were conducted [4]. Physiological studies have characterized Meissner corpuscles as rapidly adapting mechanoreceptors that monitor the velocity of skin indentation caused by mechanical stimuli. 1 shows the sine wave vibration applied to

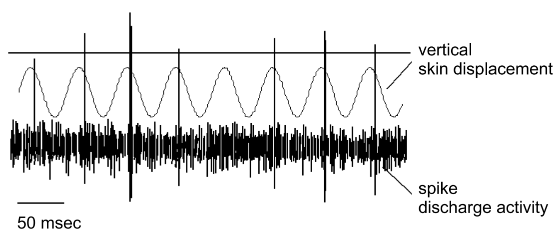

Fig. 1. Nerve activity of a single RA skin afferent fiber and mechanical vibration (reconstructed from [4])

a fingertip together with the RA nerve activity recorded at the arm. The nerve activity is synchronized with the mechanical vibration. Nerve activity occurs in a specific phase with one pulse per cycle or a couple of pulses per cycle. This finding is a good index for considering the nerve activation timing of Meissner corpuscles.

2.2 Existing hypothesis

Generally, when using the finite element method, Meissner corpuscles are approximated to encode the strain energy density of skin. This approximation is reasonable if the receptor has an ideal elastic body and an axon spreads omnidirectionally such that it becomes equally sensitive in all directions. However, this hypothesis appears to contradict certain electrophysiological findings. Based on this hypothesis, mechanoreceptors should activate two times per cycle with a 180 ° phase difference with the vibrations. This fact is contrary to the electrophysiology findings. Therefore, we rejected this strain energy hypothesis. Another possibility is that the Meissner corpuscles encode the strain. Since strain can be classified into normal strain and shear strain, it is necessary to verify the hypothesis for each type.

There is another hypothesis that considers Meissner corpuscles to encode shear stresses [5]. Approximating the axon ending of Meissner corpuscles to a coiled structure, it was shown that Meissner corpuscles can preferentially encode shear strain because of the vibration mode of the coiled structure. In order to explain the electrophysiological findings according to the shear strain hypothesis, mechanoreceptors are required to distinguish between the shear directions. With regard to this problem, an argument was made regarding the expansion and contraction of the coil. Depending on the direction of twist, the coil would extend nonlinearly even if fixed displacement was added in all directions. However, in order to support both the electrophysiological findings and this hypothesis, the direction of twists of all the axons from the Meissner corpuscle units need to be constant. Such a structural finding has not been reported till date. In addition, according to the research findings in recent years, an axon is not shaped so much as a coil but as an accordion. However, for structural reasons, this hypothesis is also rejected.

Based on the discussion so far, only normal distortion coding appears relevant. Here, we review the structure of Meissner corpuscles and propose a new hypothesis: Meissner corpuscles encode the normal strain, particularly detecting the horizontal normal strain.

3 Hypothetical proposal

3.1 Previous work

The fine structure of Meissner corpuscles in monkey dermal papillae was examined [6]. Iwanaga et al. reported that each corpuscle was completely covered by a connective tissue capsule, which was linked with the basal aspect of the epidermis by dermal collagen fibers. Their findings indicate a possible mechanism for the propagation of mechanical stimuli to the receptor axon in the corpuscle: a deformation in the epidermis is followed by a distortion of dermal collagen fibers, which continue into the corpuscles. It is very difficult to actually observe " the actual stretching of the mechanoreceptors by the collagen fibrils ", and there is no conclusive evidence for the same. However, their model does not employ a structurally extreme assumption, but a structurally reasonable one.

3.2 Hypothesis

Inspired by Iwanaga's finding and the hypothesis of Meissner corpuscles, we propose a detection hypothesis, as shown in 2. (The top and middle diagrams were reconstructed from Iwanaga's hypothesis.) If the skin surface is pushed in

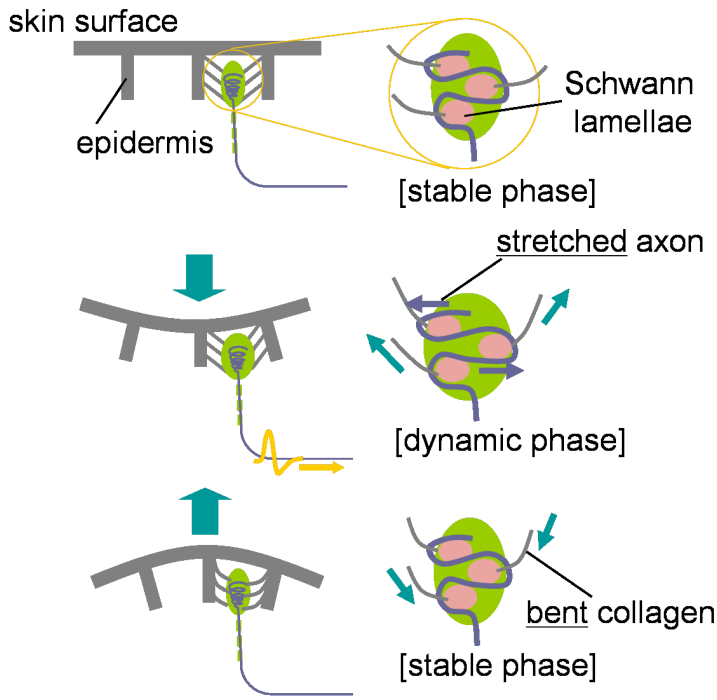

Fig. 2. Supposed nerve activity mechanism of the Meissner corpuscle

or if it stretches from a basal phase (middle diagram), the epidermal basement membrane under the stimulated point will open, and the Meissner corpuscles will be extended in the direction of their diameter. As a result, a nerve axon is stretched and it leads to nerve activities. On the other hand, when some part of the skin is considered to be pulled or shrunken (lower diagram), it is estimated that the collagen fibril bends. As a result, in case of pulled or shrunken deformation of skin surface will propagate to Meissner corpuscles inefficiently. According to this hypothesis, nerve activity does not occur when the skin surface shrinks, but it occurs when the skin is extended. Thus, it is possible to realize nerve activation in a specific phase synchronized with mechanical vibrations. Here, we propose the following hypothesis: Meissner corpuscles encode the normal strain, particularly detecting the horizontal normal strain.

4 Experiments

In order to describe how strain will be spatially distributed under the skin, we consider a part of an ideal elastic body as a simple example. For the verification of these three hypotheses, we considered how the small volume deforms just under a vibrator when perpendicular vibrations are added to an elastic body. The small volume will be stretched horizontally when pushed and stretched vertically when pulled. The key point of this argument is that the strain energy density will be equal in all places when pushed or pulled. The shear stress distributes symmetrically about the stimulus point, and the maximum strain in both processes will be equal. On the other hand, the horizontal normal strain only takes the maximum value when pushed. According to our hypothesis, nerve activity will occur when the vibrator is pushed into the skin if the amplitude of vibration is near the threshold. This phenomenon was verified in the experiment.

Experiment with low frequency In order to verify the possibility of the horizontal normal stretch detection mechanism of a Meissner corpuscle, we use three techniques in this experiment, based on a previous report.
1) Use of subject 's thumb: In order to presume semi-infinite elastic body assumption, we used thumb as an ideal finger.
2) Small pin as a vibrator: Pacinian corpuscles (RAII) are known as very sensitive receptors to vibration. It is well known that spatial addition will be performed with these receptors [7]. Conversely, we used a small pin vibrator so that the Pacinian corpuscles were not stimulated.
3) Superglued fingers of subjects on a vibrator pin: We stuck a vibrator on to a finger physically so that the skin would certainly follow the vibrator 's displacement.

Apparatus We constructed an experimental system, as shown in 3. A stainless steel pin of diameter 0.8 mm was placed at the center of an aluminum board with a hole of diameter 2.8 mm. The pin was vertically driven by a linear actuator through the hole in the board. The actuator can output 800 N. The subjects placed their right-hand first fingers on the pin.

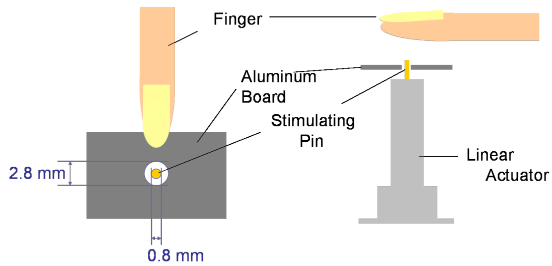

Fig. 3. System configuration: top (left) and side (right) views

Experimental procedure We selected a frequency of 30 Hz for the experiments, which is a low characteristic frequency of Meissner corpuscles. The addition of half a wave of a 30 Hz vibration intermittently gives rise to two modes, namely, the " Push " mode and the " Pull " mode. The tactual motion was presented every 1s with duration 16.6 ms. The subjects answered either " per-

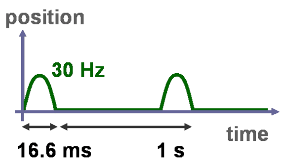

Fig. 4. Push mode mechanical stimulation

ceptible " or " not perceptible. " This experiment was performed under two experimental conditions (push mode and pull mode). The mechanical pulse height was 0 through 7 μm, and a displacement of 9 steps was randomly performed. For each pulse height, ten sets of experiments were conducted. A total of 180 trials were performed for each subject (10 trials $\times$ 9 steps $\times$ 2 conditions).
The subject group comprised four people between the ages of 24-26 years. The subjects who were unable to hear the sound of the vibrations kept their eyes open to maintain their arousal level.

Results 5 shows the rate of " Perception " responses obtained. The horizontal and vertical axes represent the amplitude of the mechanical stimulus and the rate of a subject 's response of " Perception. "The red circles and green inverted triangles represent the averages of 10 trials in the Push and Pull modes, respectively. A thin red line and a broken green line indicate the fitted line with the cumulative normal distribution. When the strongest stimulus was presented, all subjects in almost all trials answered " Perceptible. " On the other hand, when

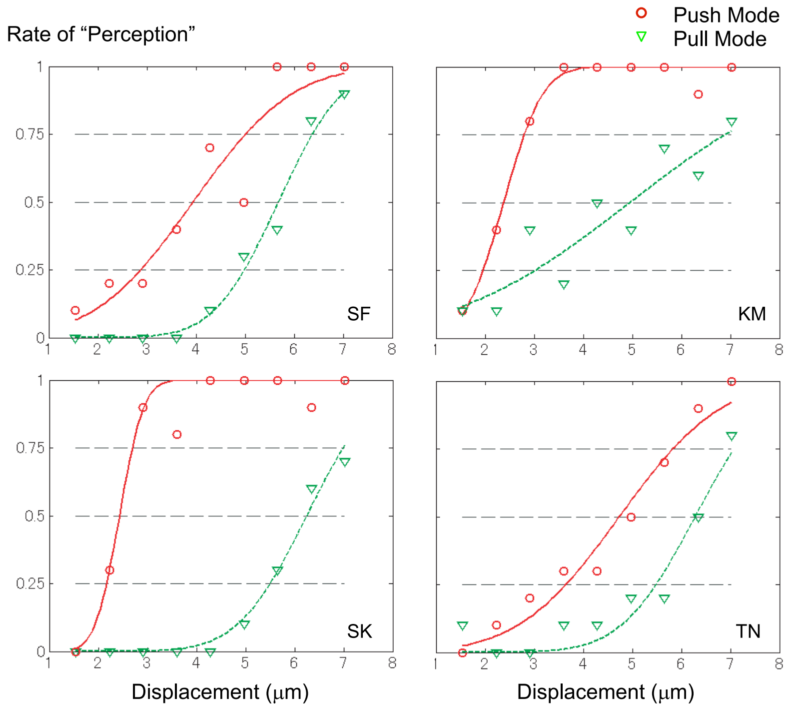

Fig. 5. Results of the experiment with low frequency

the weakest stimulus was presented, the rate declined to zero. When the Push mode was presented, higher " Perception " responses were obtained as compared to the Pull mode. These tendencies were observed for all subjects. The perceptual thresholds for the Push mode and the Pull mode for each subject are [4.7, 2.4, 3.9, 2.4 μm], and [6.3, 5.0, 5.7, 6.2 μm], respectively. In all the subjects, the Push mode thresholds were lower than the Pull mode thresholds. This implies that a smaller amplitude is sufficient for perception when the skin is pushed rather than pulled.

4.1 Experiment with very low frequency

As described in section 4.1, we conducted an experiment to verify the detection mechanism of a Meissner corpuscle. This result was derived from the structure of Meissner corpuscles. In this section, we describe another experiment using very low frequency stimulus to verify the reason for the difference in the threshold values between pushing and pulling. In this experiment, a sufficiently low vibration frequency is selected so that it cannot be detected by the Meissner corpuscles. This vibration can be perceived by Merkel 's disk (SAI). Physiological studies have characterized Merkel 's disk as monitoring the displacement of skin indentation caused by mechanical stimuli. Merkel 's disk does not have a structure such as the fibrils in an elastic body and it exists in a superficial layer of the skin similar to the Meissner corpuscles. If the threshold difference arises due to the structure of the Meissner corpuscles, it would not be observed in this experiment. Since Merkel 's disk is a slowly adapting mechanoreceptor, we replaced the aluminum board with a new one having a hole of diameter 4.8 mm, in order to prevent the receptors field from being disturbed. Since there were considerable differences between the perceptive thresholds of different individuals in this experiment, we changed the stimulus amplitude range for each subject.

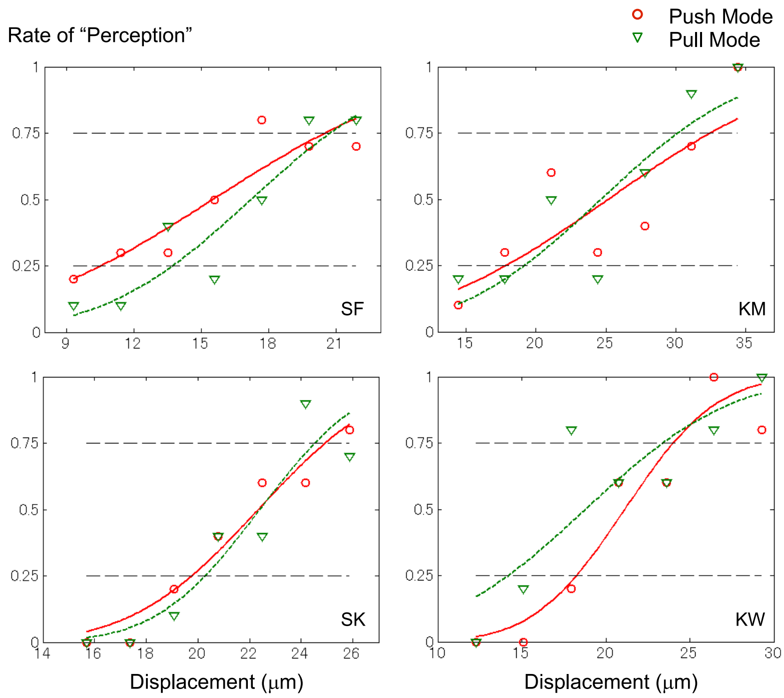

Fig. 6. Results of the experiment with very low frequency

Result When a stronger stimulus was presented, all subjects in every trial tend to answer" Perceptible. "However, there is no significant threshold difference between the Push and Pull modes. These tendencies were observed for all subjects. The perceptual thresholds in a Push mode and a Pull mode for each subject are [21.1, 25.2, 15.5, 22.3 μm], and [18.8, 24.7, 17.2, 22.4 μm], respectively.

5 Discussion

We divided the vibration into two groups (push mode and pull mode). The measured thresholds of both modes were recorded with a low frequency (30 Hz) and a very low frequency (3 Hz) each. An experiment conducted by using half a

Table 1. Results of two experiments (Push mode threshold, Pull mode threshold, Rate)

Subjects	Low frequency (30 Hz) Thresholds (μm) [Push, Pull]	Low frequency (30 Hz) Threshold rate [Pull/Push]	Very low frequency (3 Hz) Thresholds (μm) [Push, Pull]	Very low frequency (3 Hz) Threshold rate [Pull/Push]
Subject A	[4.7, 6.3]	1.34	[21.1, 18.8]	0.89
Subject B	[2.4, 5.0]	2.08	[25.2, 24.7]	0.98
Subject C	[3.9, 5.7]	1.46	[15.5, 17.2]	1.11
Subject D	[2.4, 6.2]	2.58	[22.3, 22.4]	1.00

wave of a 30 Hz vibration revealed that the Push mode thresholds were definitely lower than the Pull mode thresholds. These results suggest that the deformation of the pushed skin, which stretches the Meissner corpuscles in the horizontal direction, was preferentially connected with nerve activation. We insist that the strain energy density on the skin was equal in all places when the skin surface was pushed or pulled. The shear stress was distributed symmetrically about the stimulus point; therefore, the maximum strain in both the pushing and pulling processes would be equal. Therefore, only the normal strain hypothesis can explain this unexpected but clear threshold difference between these two conditions.

On the other hand, an experiment in which half a wave of a 3 Hz vibration was used did not reveal any differences between the Push and Pull mode thresholds. Based on these observations, we can conclude that the threshold difference did not arise from the elastic element of skin but from the mechanical structure of the Meissner corpuscles, which is similar to fibrils in an elastic body.

6 Conclusion

The objective of this study is to determine human tactile perceptual mechanisms. We focused on the transitive problem and attempted to describe the timing of nerve activity. In this paper, we proposed a mechanical filtering system of Meissner corpuscles. Based on the previous research, we considered that the Meissner corpuscles tend to stretch in the horizontal direction, and proposed the following hypothesis: Meissner corpuscles encode the normal strain, especially detecting the horizontal normal strain. In order to verify the hypothesis, it was experimentally shown that the perceptual thresholds of a fingertip for the pushed and pulled conditions are clearly different. This result cannot be explained in terms of the strain energy or shear strain, but it can be explained by our normal strain hypothesis. A design and experiment is required for verifying the method. Once the physical quantity that is encoded by mechanoreceptors is clarified, we can easily calculate that quantity either by theoretical formula or by means of simulation. If it becomes possible to describe the spatiotemporal distribution of the nerve activity of tactile receptors, it will be possible to obtain a signal design for showing a natural tactile sense. This will lead to the development of a better tactile display.

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