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10. It should be noted that a patient diagnosed as a manic-depressive, depressed, might be neurotic. Our diagnosis was based on a history of at least one prior manic and one prior depressive episode requiring hospitalization. For the study, the illness at the time needed not to have been of psychotic proportions (manic-depressive illness).
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20. Supported in part by research funds from the Veterans Administration, by research training grant TR-29 from the Veterans Administration and by NIMH training grant 5-TO1-MH-11178. We thank Michael Kane and Steven Seltzer for technical assistance.
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Proprioceptive Illusions Induced by Muscle Vibration: Contribution by Muscle Spindles to Perception?

Abstract. When vibration of 100 hertz was applied to the tendon of the biceps or the triceps muscle, the subject made a systematic misjudgment of the angle at the elbow. During contraction the error could be as much as 40 degrees. The subject thought that the elbow was in the position that it would have assumed if the vibrated muscle had been stretched.

The mechanisms underlying kinesthesia or "position sense" have long been debated. Sherrington (1) attributed position sense solely to the central perception of the discharges from the appropriate proprioceptive end organs. Others (2), following Helmholtz, have argued that the sensory centers are informed by recurrent pathways of the dispatch of commands from the higher motor centers, and that this of itself can lead to changes in the perception of position. Both mechanisms are now usually accepted as being capable of paying a part. Sherrington (1) produced the first evidence that muscle spindles are sensory end organs and suggested that they should be included among the mechanoreceptors that contribute to kinesthesia. Since the arrival of the electronic era it has been shown that the muscle spindle afferents do indeed signal the mechanical state of the muscle, but there has been a parallel accumulation of evidence against the spindle discharges having any access to conscious sensation. Instead, the spindle has been seen as reserved for the subconscious control of movement, notably by the cerebellum. The various receptors in joints have accordingly been allocated the sole responsibility for providing the peripheral contribution to kinesthesia.

The evidence for this view has been firmly based on human studies. First, the regional anesthetization of a finger joint produces a gross loss of awareness of the position of the finger when it is moved passively, even though the muscle spindles in the relevant muscles may be presumed to be behaving normally (2, 3). Second, the passive stretching of a muscle in the conscious subject by pulling upon the exposed tendon fails to produce any clear proprioceptive sensation (4). Thus the muscle spindle has appeared to be excluded from contributing to sensation. Until recently, this view was supported by the inability of electrophysiologists to discover a cortical representation of spindle afferents by the recording of an evoked potential in response to stimulation of a muscle nerve at an appropriate strength. However, with refinements in technique such projections have now been amply demonstrated in both cat and monkey (5). The following proprioceptive illusion, which may be produced in the normal human subject, suggests that under suitable circumstances spindle afferent discharges can contribute to perception.

The illusion has been produced as follows. The blindfolded subject sat with his upper arms lying parallel and horizontal on a support. His forearms

were free to move in the vertical plane. A light wooden splint was tied to each forearm and connected via a string to a potentiometer to allow recording of the angle at the elbow. The recording arrangement was nonlinear, but gave a reproducible reading that was accurate to within 2°; this was adequate for the present experiments. One arm was designated as the experimental arm. The spindles in either its biceps or its triceps muscle were then excited by manually applying a physiotherapy vibrator to the appropriate tendon (Pifco vibrator; frequency of vibration, 100 hz; amplitude of movement, of the order of 0.5 mm when loaded). The other arm was designated as the tracking arm, and the subject was asked to keep it aligned with the vibrated arm. The tracking arm thus was an objective indication of the subject's estimate of the position of the vibrated arm. The subject was told to maintain the position of the vibrated arm against gravity, but was asked not to oppose any movement which tended to take place when the arm was vibrated or moved by the experimenter. Essentially similar results were found when the arm commenced moving reflexly from a position of complete rest against a stop.

Figure 1 shows the typical effect of vibrating the biceps muscle. Shortly after the vibration began, the vibrated arm started to move into flexion under the influence of the tonic vibration reflex. This phenomena is now well known and is attributed to the excitation of the spindle primary endings by the vibration; this excitation is believed to lead to a stretch reflex type of response, although there may well also be contributions from higher centers (6). The initial part of the reflex movement was not perceived by the subject, but when movement of some 10° had occurred the subject became aware of the motion and began to move his tracking arm also. But the tracking arm moved more slowly than the vibrated arm so that the misalignment between them increased progressively.

After the vibrated arm had moved through about 40°, its movement was gently arrested without the subject's knowledge. As a result of the reflex movement itself, a long string was gently pulled tight; one end of the string was attached to the splint and the other was fixed. The subject then had a strong sensation that his arm was being moved in the opposite direction to that in which it had just been

moving (that is, that the movement was changing from flexion to extension). This did not surprise him, as he had no knowledge of what was actually happening; and in some trials the experimenter did indeed forcibly extend the vibrated arm. The movement of the tracking arm (Fig. 1) provides an objective measure of the extent of the subjective sensation of the reversal of movement. At the end of the period of vibration, there was an error of more than 40° in the alignment of the subject's forearms, although the subject believed that he was successfully managing to keep them parallel. At the end of the period of vibration he immediately became aware of his error and made the appropriate correction.

Figure 2 illustrates the analogous experiment on the triceps muscle. In this case the tonic vibration reflex induces an extension rather than a flexion, and the illusion is the mirror image of that when the biceps muscle is vibrated. But in principle what happened was the same. First, the subject moved his tracking arm with a lag. Second, when the vibration-induced movement was checked the tracking arm reversed its direction of motion; indeed, it soon overshot its initial position.

Such reactions have been observed in more than 20 subjects, many of whom were initially new to this kind of experiment. The illusions are so clear-cut that they could still regularly be reproduced in experienced subjects, even though subjects knew that they were suffering from a delusion. The effects might, however, vary in size in successive repetitions of the experiment and were not always as great as those illustrated. Nonetheless, the reversal of the tracking movement when the reflex movement was resisted was a consistent feature. In one subject, vibration regularly failed to elicit a reflex contraction. This subject felt that his arm moved in the opposite direction to that in which the reflex would have taken it, just as if the reflex had been arrested from the very beginning. Several other subjects had a similar sensation when the vibration was turned on and before any appreciable reflex movement had occurred. These findings help dispel the objection that the main results were essentially dependent upon the subject's voluntarily changing his motor commands the moment he perceived that his vibrated arm was beginning to move.

Passive movements imposed on the

subjects by the experimenter could of course be tracked with a much higher degree of accuracy. This is illustrated in Fig. 3. The subjects did not experience any significant local cues, from pressure or other sensations, that the

movement had been resisted; local cues were minimized by the movement being stopped gradually rather than abruptly. Cues were further eliminated in a few control experiments by applying the resisting force to the hand

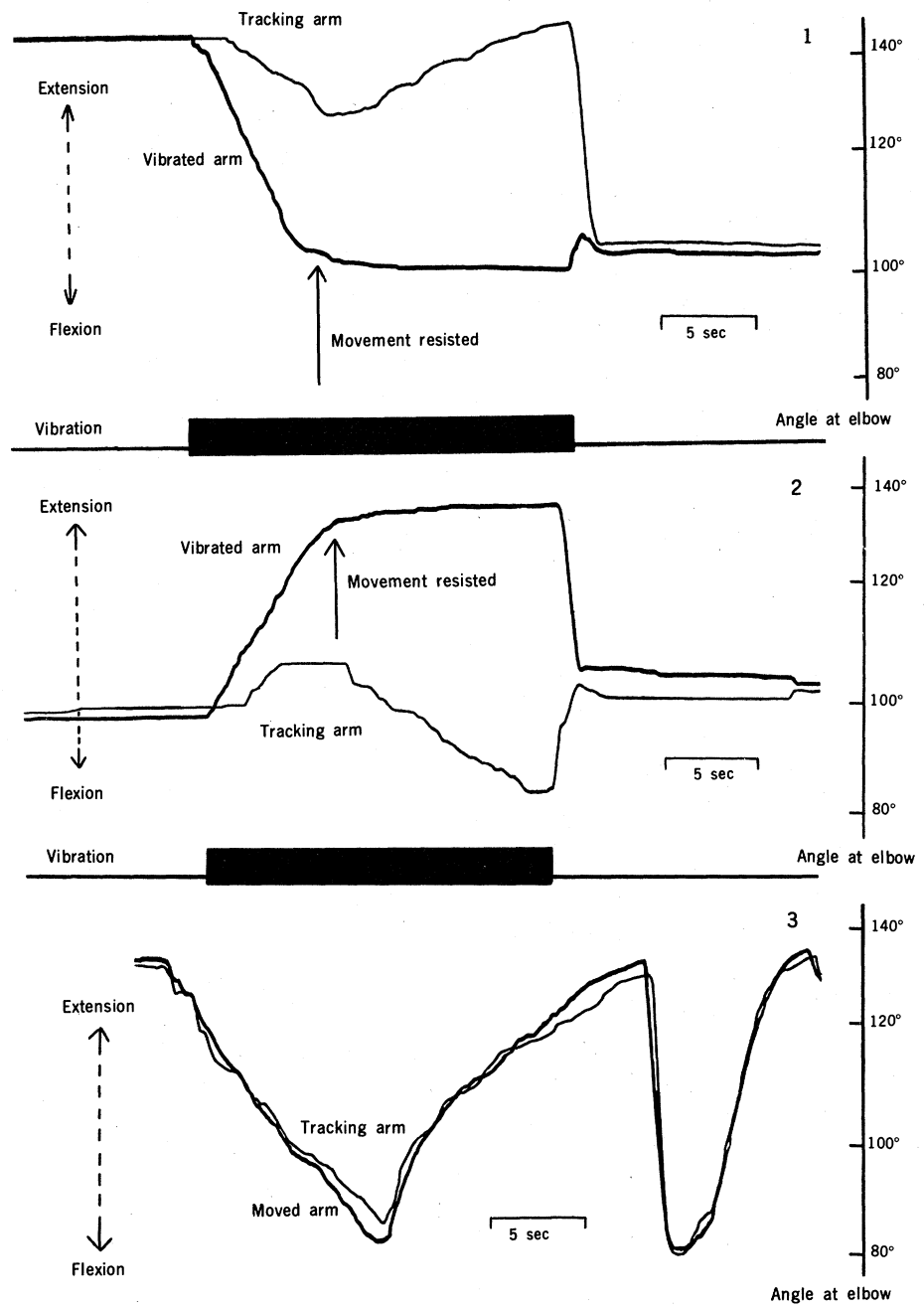


Fig. 1. The effect of vibrating the tendon of the right biceps muscle so as to produce a tonic vibration reflex, which moved the arm into flexion. The blindfolded subject used the left arm to track what he believed to be the position of the vibrated right arm. From the arrow onward, any appreciable further flexion of the vibrated arm was prevented because the movement gradually pulled taut a long string that was attached to a splint on the arm and fixed at its far end. Fig. 2. The effect of vibrating the tendon of the right triceps muscle so as to produce a tonic vibration reflex, which moved the arm into extension. The blindfolded subject used the left arm to track what he believed to be the position of the vibrated right arm. From the arrow onward, any appreciable further extension of the vibrated arm was prevented as in the experiment in Fig. 1. Fig. 3. The accuracy of tracking of passively imposed movements. The right arm was moved by the experimenter, and the subject was asked to track it with his left arm. Same subject (still blindfolded) was used as in Figs. 1 and 2. The experimenter held a splint on the subject's arm and not the arm itself.

after it had been made insentient; this was done by inflating a pressure cuff around the wrist and occluding the circulation for the appropriate time. We have also observed, but not measured, similar illusions concerning motion at the knee and ankle joints, although these illusions have not been nearly as well developed as those for the elbow. Others have found that at these sites, vibration may induce misjudgments of a few degrees in estimates of the steady position of the joint (7).

The illusions of position can be attributed to the excitation of intramuscular receptors rather than of extramuscular receptors, since the effects were not obtained when the vibrator was applied directly over the elbow joint or to regions of skin overlying bone. Nor did such nonspecific application of vibration distort position sense, since the subjects did not then make systematic tracking errors when the vibrated arm was moved by the experimenter. Thus the widespread excitation of Pacinian corpuscles, which must undoubtedly have occurred, seems to have produced merely a sensation of vibration itself and cannot be held responsible for the illusory sensations of limb position. Of the intramuscular receptors, the muscle spindle primary endings may reasonably be held responsible, for these are far more powerfully excited by vibration than are any of the other muscle receptors (8). However, both the Golgi tendon organs and the spindle secondary endings do show some sensitivity to vibration, and so it is impossible to say whether or not they contributed to the development of the present illusions; all three types of proprioceptors have been believed to be denied access to consciousness.

The findings are compatible with the idea that during muscle contraction, the spindle primary discharges that are set up by the vibration are interpreted by the higher neural centers as if they were due to excitation of the spindles by stretching the muscle; the increased discharges would then indicate that the vibrated muscle was longer than it actually was and would so produce a corresponding error in the central judgment of the angle at the elbow. In addition, the illusion induced by vibration may be as much one of velocity of movement as of position per se. This may perhaps be why the reversed motion of the tracking arm continued for so long after the reflex movement was arrested (Figs. 1 and 2); the volume of driven spindle discharge may be pre-

sumed to have risen to a plateau soon after the reflex movement was impeded. Be that as it may, the present illusion appears sufficient to throw serious doubt on the current view that muscle afferent firing is without influence on perception. The perceived position of a limb may thus be attributed to the compounding of three kinds of signals: afferent from joint receptors, efferent from motor centers, and afferent from muscle spindles.

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A Neural Effect of Partial Visual Deprivation in Humans

Abstract. *Certain human subjects have considerable sensitivity differences in the visual resolution of vertical gratings as compared to horizontal gratings. Although only subjects with pronounced ocular astigmatism exhibit this effect, the differences are of neural, rather than optical, origin. It is argued that the resolution anisotropies result from early abnormal visual input caused by astigmatism. This abnormal input permanently modifies the brain.*

The influence of early visual experience on the organization of cortical neurons in the developing brain has been strikingly demonstrated in two recent studies. Hirsch and Spinelli (1) raised kittens so that each kitten had one eye viewing horizontal bars and the other eye viewing vertical bars. After the rearing period, they found that all cortical neurons with elongated receptive fields responded to input from only one eye. Furthermore, the receptive field orientations were coincident with the bar pattern to which the eye had been exposed. Blakemore and Cooper (2) limited the binocular visual environment of kittens, during the period from 2 weeks to 5 months of age, to only vertical or horizontal stripes.

They found that stimuli presented in the orientation of the earlier visual exposure produced essentially normal behavioral and neurophysiological responses. However, when stimuli were presented in an orthogonal orientation, behavioral blindness was evident and no responsive neurons were encountered. These experiments show that functional neural connections can be altered, in a predictable and selective manner, by visual environment.

We propose here that an analogous modification in the organization of neurons in the human visual system can be induced by early abnormal visual input. We have found subjects who show considerable differences in their resolution sensitivities for vertical and

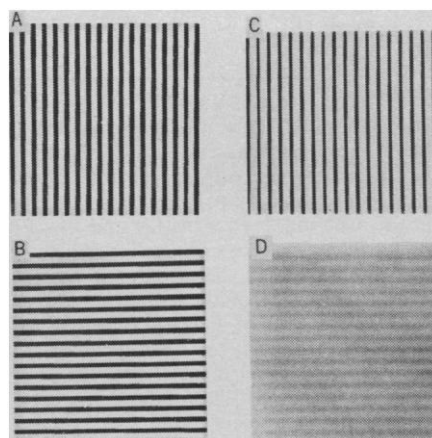


Fig. 1. The effect of astigmatic optics on image formation. In astigmatism, a point source in object space is imaged as two mutually perpendicular focal lines separated by a distance that is determined by the amount of astigmatism. (A and B) Identical square wave gratings which consist of alternate black and white bars oriented vertically and horizontally. (C and D) The gratings shown in (A) and (B) are imaged through an astigmatic lens which defocuses the vertical meridian. In (C), the bars are parallel to the direction of blur and it is evident that image quality is unaffected except for slight bar narrowing and edge blur. But in (D), the grating bars are perpendicular to the direction of blur which results in severe image degradation.