Mach Band Type Lateral Inhibition in Different Sense Organs*

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ABSTRACT Experiments were done on the skin with shearing forces, vibrations, and heat stimuli and on the tongue with taste stimuli to show that the well known Mach bands are not exclusively a visual phenomenon. On the contrary, it is not difficult to produce areas of a decreased sensation magnitude corresponding to the dark Mach bands in vision. It is shown on a geometrical model of nervous interaction that the appearance of Mach bands for certain patterns of stimulus distribution is correlated with nervous inhibition surrounding the area of sensation. This corroborates the earlier finding that surrounding every area transmitting sensation there is an area simultaneously transmitting inhibition.

INTRODUCTION

The importance of lateral inhibition in sensory perception has become more and more evident from recent research. Formerly, lateral inhibition was considered a small side effect. But it now appears that without lateral inhibition much sensory stimulus localization would be lost.

To illustrate the magnitude of lateral inhibition in hearing, we can for instance arrange 20 to 40 loud-speakers extending 10–20 ft. in a single row. Common sense would lead us to expect to perceive a sound source with a size comparable to the length of the row. Instead of this, when the distance between the loud-speakers and the observer is about 3 ft, the observed size of the sound source is of the order of the diameter of one single loud-speaker. This indicates that, for localization phenomena the lateral loud-speakers are practically unnoticed, and one of the loud-speakers—the one closest to the observer—dominates the picture.

To perform this experiment, we used loud-speakers 13 cm in diameter placed with their centers 16 cm apart. They were connected in series and supplied with white noise with a band width of 0–20 kc. They were carefully checked to assure that the sound pressures were all in phase.

The lateral inhibition is so strong that, as we walk parallel to the row of

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loud-speakers (Fig. 1), we have the impression that there is only one loud-speaker present which is carried by a person walking beside us.

A type of lateral inhibition observed easily in vision produces the Mach bands, which were discovered in 1866 (Mach, 1866). Unfortunately, their neurological significance has been realized only in the last two decades, since they are easily observed but are not very spectacular. Their importance became evident, however, after Hartline (1949) and Ratliff and Hartline (1959) showed that they are one of the psychological phenomena which can also be easily demonstrated electrophysiologically.

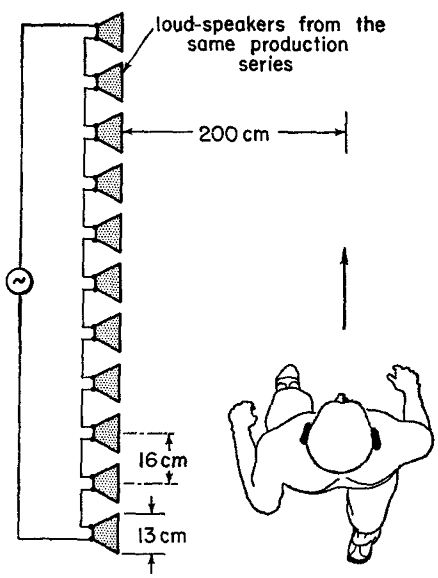

FIGURE 1. A row of loud-speakers supplied by the same electrical source does not produce a longitudinal sound image. The impression is that only one of the loud-speakers is activated. The others seem to be suppressed.

The appearance of the Mach bands is illustrated in Fig. 2. We observe parallel with the y-axis a dark band and a light band which appear at discontinuities in the light distribution. The white line seems to be much brighter than the local light intensity would produce on an evenly illuminated surface. The dark line, on the contrary, is much darker than we would expect. As a consequence of the two bands, the pattern of local sensation magnitude is quite different from the light intensity distribution. Ratliff described the literature and experiments on this subject fully in his book entitled Mach Bands (1965). My interest in Mach bands was to find out whether they are present only in vision or are a common feature of all the sense organs with large surface areas. In the latter case, most of the properties of Mach bands in vision should also be found for other sense organs. This would give lateral inhibition and the whole field of neurology a common ground.

Mach Bands in Various Sense Organs

It is easy to show lateral inhibition on the surface of the skin by pressing different shaped pieces of cardboard against it (Békésy, 1928). The pressure sensation produced is easily recognizable as an exaggeration of the curvature of the cardboard. Thus, all the edges seem to be much sharper than they really are. We can observe the pressure distribution by looking at the deformation of the surface of the skin. It is obvious that there is a complicated relationship between the stimulus pattern and the sensation pattern. The surprising fact is that any sudden increase in pressure produces a pronounced

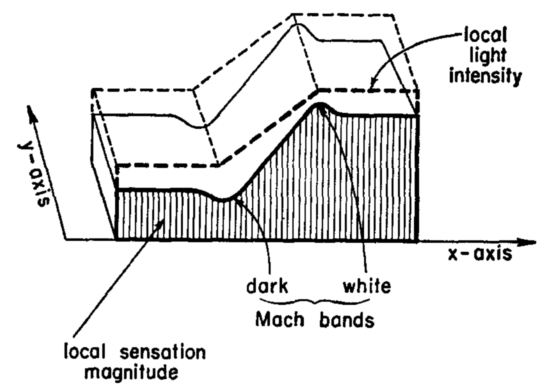

FIGURE 2. A light intensity distribution that is constant along the y-axis of a surface but changes along the x-axis, can produce a brightness pattern very different from the physical light intensity pattern. Some sections of the field are depressed and others are enhanced in their brightness. For the light intensity distribution shown in the figure, a dark and a white band, called Mach bands, will be visible.

decrease in sensation magnitude at that point. It is this fact that indicates an inhibition. The inhibition can become so strong that sections of the stimuli are not felt at all.

Pressure sensations along the surface of the skin are not very well defined, since they are a composite of vertical and shearing displacements. We can also observe the Mach bands by using only shearing displacements and shearing forces. To do this we used an equipment (Fig. 3) consisting of a highly elastic Latex rubber tubing 20 cm long. The ends of the tubing were glued to two metal platforms which slid along a track parallel with the length of the tubing. Two chains were attached to these slides, and when a knob was rotated, the slide on the right in the figure moved three times as fast as the slide on the left. This stretched the rubber tubing between the two slides. The stretching, in turn, produced a constant displacement on the left end of the tubing. The displacement between the slides increased continuously until it reached the edge of the slide on the right side of the figure. From there on again the shearing displacement remained constant. The arm was placed lightly on the tubing. The observer was then asked to draw the local sensation magnitudes along the surface of the arm. There was an area where no shearing sensation could be observed in spite of the fact that the shearing displacement of the skin was visible without magnification. The blackout of shearing sensation in a section around the point where the stimulus magnitude changes from a constant value to a slowly increasing value is analogous to the black line of the Mach bands. A detailed examination of this phenomenon shows the great similarity between the sensation distribution along the

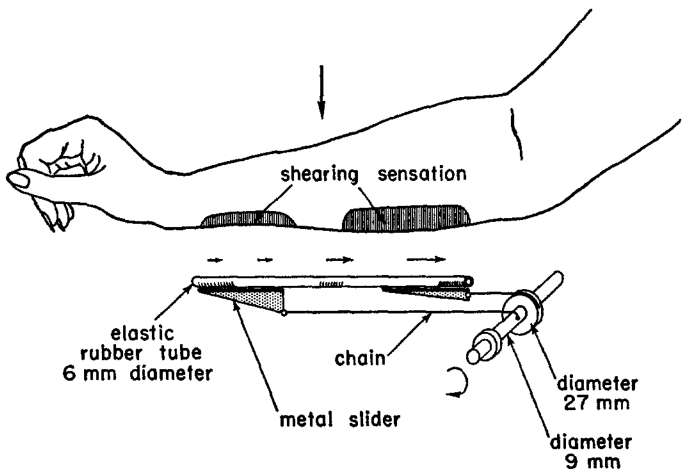

FIGURE 3. Shearing sensations produced along the surface of the skin are also different from the actual shearing displacements. Under some conditions, inhibition can become so strong that shearing sensations disappear completely at certain points.

surface of the skin and the sensation distribution we would obtain for a light intensity distribution similar to the shearing displacement described above.

There are several small points which have to be kept in mind during this experiment: The skin near the elbow is a little less sensitive than the skin near the wrist. It is very important that the whole length of the arm is in touch with the tube so that it can all be stimulated, since there is no inhibition without stimulation. We also have to be careful not to touch anything but the top of the rubber tubing with the surface of the skin. It is unavoidable that during rotation of the knob the whole arm will be moved a little, and if any other section of the arm touches the supporting area, the displacement it produces on the skin will be opposite to the shearing displacement of the tubing. This therefore can produce a sensation indicating a movement which is opposite to the movement of the tube. To minimize the displacement of the arm, it is preferable to apply the shearing forces to the surface of the skin only along a very thin line. When the shearing forces are applied to a larger surface of the arm, the displacement of the whole arm increases.

To show the Mach bands for vibratory sensations (Békésy, 1959) on the surface of the skin, we can press the edge of a vibrating plastic sheet against the skin (Fig. 4). Here again the vibrating amplitude is constant over the left section, increases slowly from left to right across the center section, and remains constant over the right. The lever system used to produce this vibration distribution along the surface of the arm can be seen in detail in the figure. The sensation distribution again shows a blackout at the section where the stimulus magnitude starts to increase, and an overshot when the increase

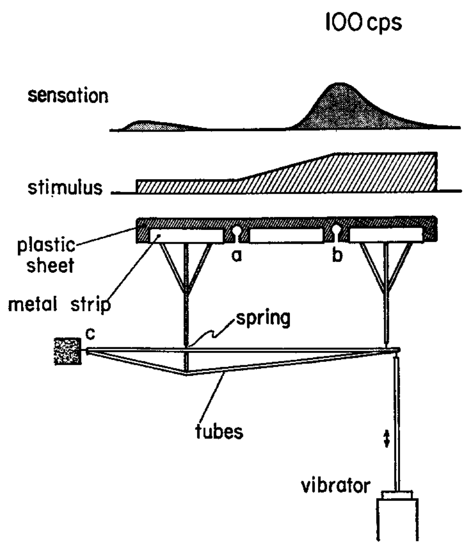

FIGURE 4. When a vibratory stimulus presented to the lower arm is increased in intensity along the arm, it can produce inhibition such that there is a complete black-out at the place where the vibratory stimulus starts to increase. The inhibited area is analogous to the dark Mach band in vision.

in stimulus magnitude ceases. The blackout and the overshoot are again analogous to the black and white Mach bands.

A more interesting question was whether we can produce analogous phenomena on the tongue. On the surface of the tongue it is quite easy to localize taste stimuli, but taste observations are quite hard to make, since the adaptation is very strong. It is therefore difficult to make observations on local sensation magnitudes. Fig. 5 shows the equipment used to investigate this question. It consists basically of a plastic block into which tube C_1, carrying a solution of hydrochloric acid, was introduced. To make this solution, about 20 cc of 40% hydrochloric acid solution were dissolved in 7 liters of tap water. The speed with which the fluid was introduced into the plastic block was 30 cc per minute. The plastic block had an opening 3 mm wide and 27 mm long, through which the fluid was administered to the surface of the tongue. From the back of the tongue the fluid was carried to the upper surface of the block and to an outlet. In addition, there was a third tube drilled into the plastic block in order to carry a more concentrated solution (60 cc per 7 liters). On the left side in Fig. 5 are shown small capillaries connecting this tube with the opening on the surface of the tongue. These capillaries were used to inject into the fluid stream C_1 increasing amounts of the more concentrated solution. In this way it was possible to produce a constant concentration of the solution flowing along the opening and after a short distance, to increase the concentration continuously. The resultant concentration distribution is shown in the drawing. Here again we proved that inhibition occurs by producing a section where we do not observe any taste at all. The local sensation magnitude distribution along the opening is shown in the drawing at the top. This demonstrates that inhibition analogous to the Mach bands is present for taste sensation also.

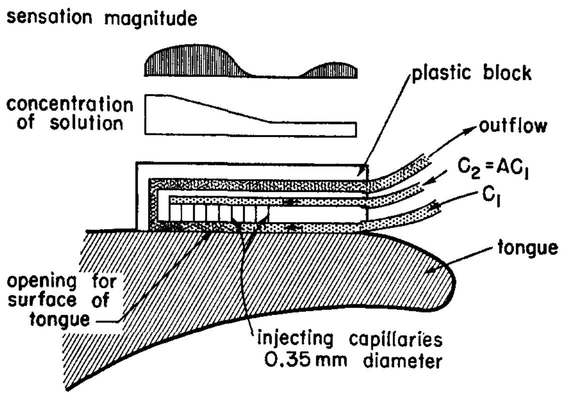

FIGURE 5. The phenomenon observed on the skin for shearing forces and vibrations can also be shown for taste sensations on the tongue.

Since adaptation on the tongue is so strong, the taste solution was presented for only 10 sec. Tap water was constantly flowing through the tube C_1, and solution was introduced only at intervals of about 30 sec. If there is very little pressure through tube C_2, we feel an almost equal sensation magnitude along the opening under these conditions. It is necessary to adjust the concentration so that for each observer the taste is not too weak and not too strong. There are large individual differences in this respect. After this preliminary adjustment, the pressure of C_2 is increased during the period of stimulation until the back of the tongue feels a stronger taste than the tip. After this second adjustment, we localize the local taste sensations in two separate areas with a blackout between them. The switching system for exchanging the tap water and the solution was described in an earlier paper (Békésy, 1964). The same results were found for other tastes (such as sugar, quinine, etc.), but hydrochloric acid has the advantage that the injecting capillaries do not get clogged up. A little food coloring was added to the taste solution so that the change in concentration of the solution along the plastic block opening on the surface of the tongue could be easily observed visually.

A method similar to that used in Fig. 5 can be used to investigate whether heat or cold sensation on the skin shows Mach inhibition. Again a plastic block 22 cm long had an opening 5 mm wide along which tap water of 35°C was constantly flowing (Fig. 6). This small heat sensation disappeared after a short while because of adaptation. There was also a pressure chamber with injection capillaries adjusted much like those in the system used in Fig. 5. At periodic intervals, the tap water was replaced in tube C_1 by water of 39°C and in the pressure chamber, tube C_2, by water of 42°C. This produced a temperature distribution as shown in Fig. 6. In this case again the heat sensa-

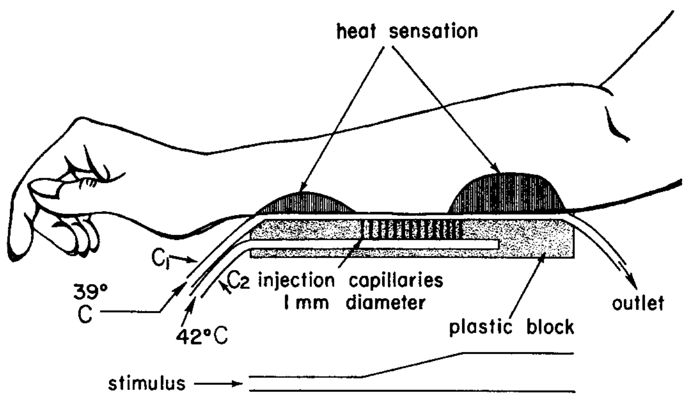

FIGURE 6. An experiment analogous to the ones in Figs. 4 and 5 using heat sensation on the arm.

tion consisted of two peaks, separated by an area definitely lacking in heat sensation. The correct method of carrying out the experiment was again first to increase the temperature flowing through the opening until a constant heat sensation was felt along the arm, and then to raise the temperature going through the injection capillaries until the heat sensation near the elbow was higher than the heat sensation near the wrist. Under these conditions, there was usually no sensation in the middle of the plastic block. The fluid going through the injection capillaries was again slightly stained. The opening was covered with a plastic plate in order to adjust the operation properly, and the darkening of the color gave a measure of the temperature increase near the wrist. The fluid speed was approximately 500 cc per min, and the crosssection of the tube with the opening corresponded to a round opening 6 mm in diameter. Since the cross-section was everywhere constant, there was little eddy formation.

Analogous results were obtained for cooling. A temperature difference of 2° (for instance 22°C and 24°C) was usually enough. But here again, the optimum temperatures have to be adjusted separately for every individual subject.

Since it turned out that Mach lateral inhibition is common to most of the sense organs with large surface areas, the next question is, what is the common underlying feature of the nervous system which produces Mach inhibitions and distortion of the stimulus distribution in the sensation pattern?

One method for investigating this question is the analysis of different nerve models to find out under what conditions Mach inhibitions may occur. As can be seen in the next paragraph, models of nervous interaction do give preference to certain types of lateral inhibition.

Geometrical Model to Illustrate the Formation of Mach Bands

There are many ways to illustrate the formation of Mach bands as a consequence of lateral inhibition. It can be done purely mathematically or by the

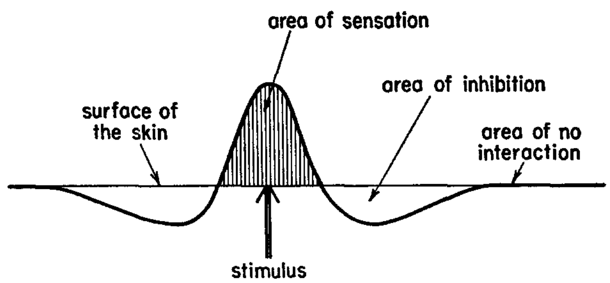

FIGURE 7. The stimulation of a small spot produces an area of sensation surrounded by an area of inhibition. We shall call the combination of sensation with its surrounding area of inhibition a "neural unit."

use of a geometrical model. I prefer the geometrical model mainly because it allows one to follow step by step the production of the Mach bands to see how their magnitudes depend on the stimulus distribution along a sense organ with a large surface area.

It was concluded mainly from research done on the surface of the skin (Békésy, 1960) that two sharply localized stimuli can eliminate each other under certain conditions. This led to the conclusion that every stimulus produces an area of sensation surrounded by an area of inhibition (Fig. 7). Methods were developed to describe approximately the width of the area of sensation and the width and the extension of the area of inhibition for a sharply localized stimulus. It was also possible to give a relative magnitude estimation for the sensation and the inhibition. All these values are different for the different sense organs. Very similar descriptions were given by many investigators, and as Ratliff (1965, p. 122) showed, there are at least six different models that are practically the same.

The basic concept that every sharply localized stimulus produces an area of sensation surrounded by an area of inhibition has lately been corroborated by electrophysiological observations: Rose and Mountcastle for skin sensations (1959), Suga for hearing (1965), and Hartline, Ratliff, and Miller for vision (1961).

We can simplify our geometrical inhibitory unit to a model (Fig. 8). As a first approach, we can assume that the inhibitory units add together, and that the sensation magnitude and the inhibitory magnitude are proportional to the stimulus. The final sensation distribution is then the difference between the sum of the sensation magnitudes and the sum of the magnitudes of inhibition of the neural units. In carrying out such a summation, we find that the

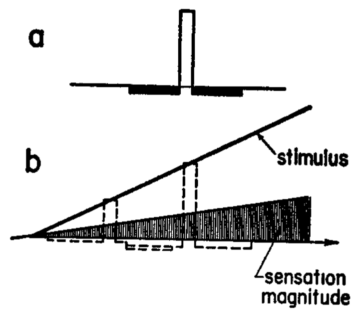

FIGURE 8. In the model the sensation magnitude can be geometrically determined from the stimulus distribution by adding together neural units adjusted to the local stimulus magnitude. A linear summation of sensation magnitude and inhibition magnitude was assumed. A continuously increasing sensation magnitude corresponds to a continuously increasing stimulus. This is in agreement with observations in vision and other sense organs. Drawing a represents a single neural unit. The white area stays for the sensation magnitude and the black area for the inhibition. In drawing b the linear summation of a series of single units is shown, when the stimulus continuously increases from left to right.

sensation magnitude for a continuously increasing stimulus along the surface of a sense organ will be of the same type as the stimulus. This is illustrated in Fig. 8 *b*.

However, if the stimulus distribution shows discontinuity (upper drawing of Fig. 9), the sum of the adjusted units representing the final local sensation magnitude will show at places of discontinuity an undershoot or an overshoot (lower drawing of Fig. 9). These deviations from the stimulus pattern are of the same type as the dark and the light Mach bands. Just like the Mach bands in vision, the undershoot and overshoot depend on the change in the gradient of the stimulus distribution (Fig. 10). The undershoot and overshoot reach their maximum for a step function.

The calculated width of the Mach bands depends very much on the width of the lateral spread of inhibition in the inhibitory unit. We can estimate the actual width of the inhibitory area of the unit by comparing the width of observed Mach bands with Mach bands calculated for different units. In this way it is possible to indicate (Fig. 11) the lateral spread for vision and touch. There are also other methods which allow us to make this comparison, and they all indicate that lateral inhibition in vision extends over a very large area, whereas lateral inhibition on the skin is very small. The calculated width of the Mach bands can be increased substantially by moving the inhibited area away from the sensation area (Fig. 12). This might be valuable

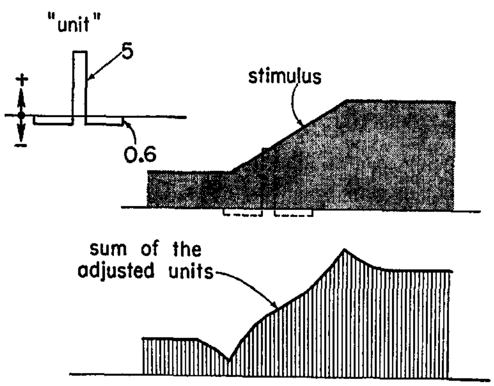

FIGURE 9. Any break in the rise of the stimulus pattern produces an undershoot or overshoot in the sensation magnitude (lower drawing). These are the dark and light Mach bands.

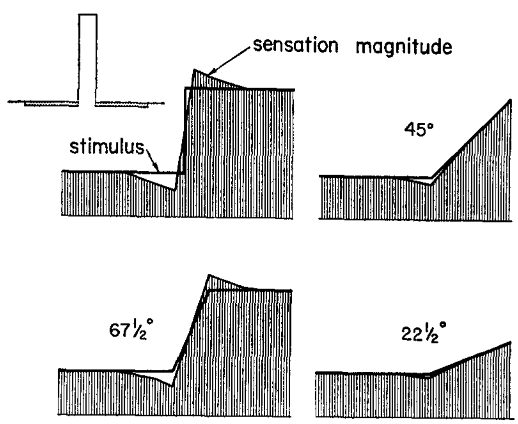

FIGURE 10. The over- and undershoots of the sensation magnitude increase with the degree of discontinuity of the stimulus. They reach their maximum for a step function.

for electrophysiological interpretations. At the moment I do not see a way of making a clear decision between the two possibilities shown in the upper and the lower drawings. However, the over-all width of the Mach bands is determined by the maximal lateral spread of the outer edge of inhibition.

In all the previous figures, the undershoot and the overshoot of a sensation magnitude are exactly the same. This is a consequence of our assumption that there is a linear summation of the units. Therefore it is interesting to know whether we can produce an overshoot different from the undershoot. In Fig. 13, it is illustrated that, for a unit which increases the lateral extension of the inhibition proportional to the magnitude of the stimulus, the overshoot will be larger, and the width of the light Mach band will also increase. This difference between the overshoot and the undershoot is not present when the stimulus shows a single discontinuity (upper drawing of Fig. 13). Since the change in the lateral spread of the unit also occurs in a single step, inhibitory

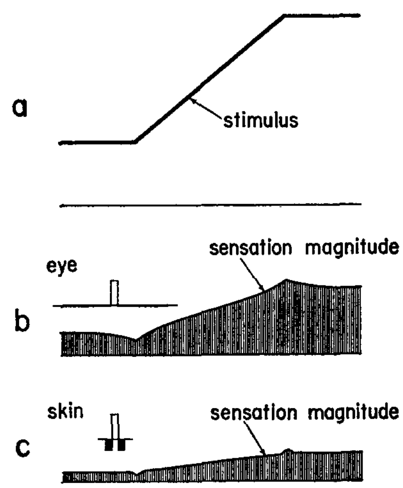

FIGURE 11. The width of the Mach bands is closely correlated with the inhibitory spread of the neural unit. It is large for vision and relatively small for the skin.

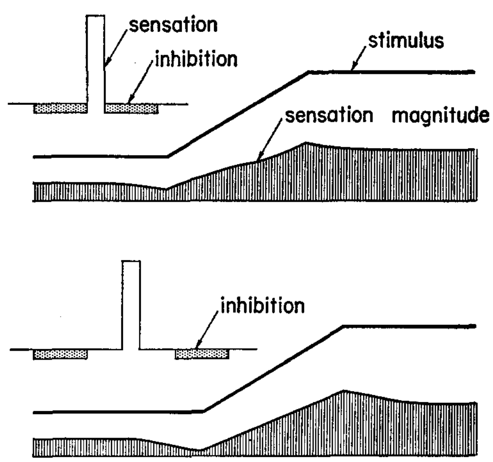

FIGURE 12. The width of the Mach bands is increased when the inhibitory area of the neural unit moves away from the stimulus. This fact makes it difficult to determine the exact value of an inhibiting area, since the Mach band width depends on the maximal lateral spread.

areas on the left and the right are the same. Differences in the band width of the dark and light Mach bands seem, therefore, to indicate that the lateral extension of the inhibitory section of the unit depends on the stimulus magnitude. If the magnitude of the inhibition does not change at all and only its lateral spread increases with the stimulus, as shown in the top drawing of Fig. 14, then the difference between the magnitude and the width of the overshoot and undershoot still remains.

It can be also asked if it is possible to have inhibitory units which do not produce any Mach bands at all. Using the same methods as before, we can see from the lower drawing in Fig. 14, that if the magnitude and lateral spread of the inhibition stay constant, no Mach bands are present.

From these geometrical models we may conclude that a neural unit of the type represented in Fig. 8 *a*, with a slightly increasing lateral spread of

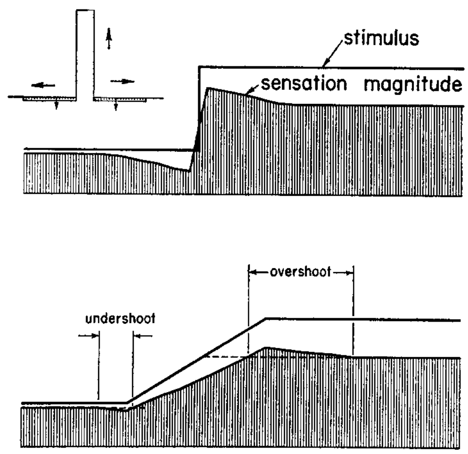

FIGURE 13. We can assume that the lateral spread and the magnitude of inhibition increase with the stimulus. Under these conditions, the over- and undershoots for a step function of the stimulus remain equal. But for a smaller break in the stimulus increase, the magnitude and width of the undershoot may be different. Many observations of Mach bands indicate that a similar situation may be the case in the actual nervous system.

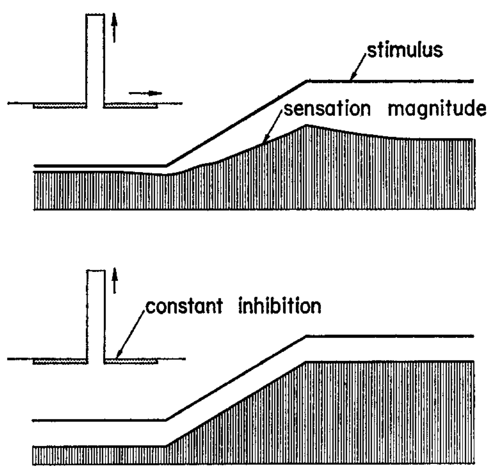

FIGURE 14. If we assume that the magnitude of inhibition does not change, and only its lateral spread changes in proportion to the stimulus magnitude, we calculate the sensation magnitude pattern shown in the upper drawing. Of special interest is the situation when the inhibition stays constant. In this case, as the lower drawing shows, there are no Mach bands.

inhibition (Fig. 13), will give an adequate description of the observed Mach bands.

The unit described before and redrawn in Fig. 15, drawing A, is equivalent to the unit shown in drawing B. Physiologically they might be quite different, since in unit B we assume that every localized stimulus produces an inhibition along a large surface surrounding the stimulus *in addition* to producing an area of sensation. From this geometrical approach there is no way to decide in which of the ways illustrated in the lower drawings of Fig. 15 a local stimulus inhibits and stimulates the sensory cells. However, the usual assumption is that the inhibited area is larger than the stimulated area. This seems to be the basic prerequisite for the formation of Mach bands which are dark

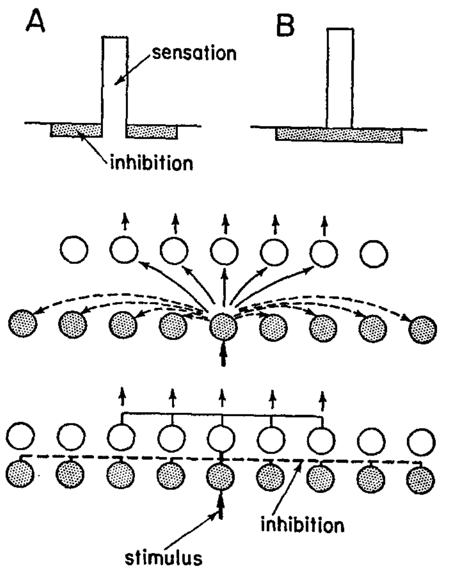

FIGURE 15. The neural unit can be represented either as in scheme A or as in scheme B. The transmission of excitation or inhibition can also be assumed to work in several ways (two lower drawings). In both cases, the expected Mach bands will be the same. Therefore we cannot draw conclusions about the way inhibition spreads laterally from the appearance of the Mach bands.

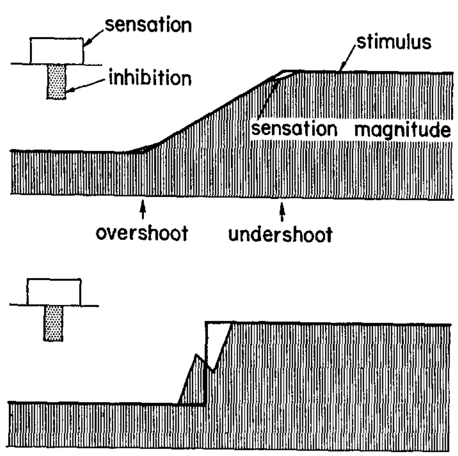

FIGURE 16. Constructing different types of neural units, we find that the lateral spread of the inhibiton has to be wider than the lateral spread of the sensation area: in the opposite situation with an inhibition area smaller than the sensation area, the Mach bands would reverse and we would have a dark Mach band where a light Mach band was found experimentally for all tested sense organs.

when the stimulus pattern starts to increase, and light at the point where the stimulus pattern stops increasing. This can be shown easily by using the inhibitory unit shown in Fig. 16, where the lateral spread of the sensation area is larger than that of the inhibited area. Under these conditions, we have a reversal of the Mach bands, and the dark Mach band is expected to appear where calculation shows the white Mach band, and vice versa. Therefore, the observations seem to indicate that the inhibitory area has a larger extent than the sensation area for sharply localized stimuli.

I believe that these simple geometrical models indicate a direction in which electrophysiological observations could be done to find out how Mach bands are produced. But they are oversimplified and do not describe many aspects of the Mach bands. The largest discrepancy seems to be in the prediction of the local sensation magnitude, especially the sensation magnitude at the peak of the over- and undershoot. Unfortunately, it is difficult to measure local sensation magnitude since it is influenced by simultaneous contrast, which has in vision a very large lateral spread and can be an inhibitory process different from the processes producing Mach bands. For small changes in the spatial stimulus gradient, the undershoot and overshoot are about equal in magnitude, and the simplified linear model describes the Mach bands pretty well. But for larger changes in the stimulus gradient or sudden steps, the overshoot is usually much larger in magnitude than the undershoot.

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