THE ROLE OF THE AUDITORY ANALYZER IN THE PERCEPTION OF RHYTHM AND IN RHYTHMIC MUSCULAR ACTIVITY*

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In rhythmic muscular activity, in work or sports movements of a cyclic nature (running, walking, etc.), stimuli enter the cerebral cortex from almost all the analyzer apparatuses. This is true in particular of those stimuli to whose rhythm the individual must make the movements and which have the specific importance of conditioned stimuli, and also those arising in the activity itself, in each motor act – kinesthetic, cutaneous, auditory, etc. The significance of these stimuli in the chain of conditioned reactions is not all the same, and it calls for thorough study.

In the work described here we attempted to study the role of the auditory analyzer and the cutaneous analyzers in perception of rhythm of external stimuli and in the accomplishment of rhythmic movements in the healthy adult individual.

METHOD

We based the investigation on measurement of the thresholds of conditioned motor reactions to increases in the frequency of rhythmic signals. For this purpose we used an electric metronome of our own construction, consisting of a low-frequency relaxation oscillator, which permitted us to change the frequency of rhythmic electric signals easily and with a high degree of precision (within 0.5% of the original value). We sent these signals either through an attenuator into a telephone (short auditory signals like metronome strokes) or through an active electrode to one part or another of the skin surface – usually the forearm (electrocutaneous stimuli, jolt-like). The subject was placed in an isolation chamber and the stimuli were administered at a specific (original) frequency. After 7-10 seconds this frequency was increases somewhat. In accordance with instructions, the subject, on noting the increase in the rhythm of the signals (sonic or electrocutaneous), notified us orally or pressed a special key. If the subject did not perceive the increase in the frequency of the rhythmic signals (30-40 signals), the original frequency was resumed after a pause of 15-20 seconds, and again its frequency was stepped up "while underway", this time somewhat more than before. The minimum acceleration of signals evoking an oral or motor reaction was taken as the threshold of the conditioned reaction or, what amounts to the same thing, as the threshold for perception of an increase in the frequency.

In the second series the subject was directed to produce rhythmic movements (tapping with the finger on a contact surface) to the rhythm of the singals and to correct the tempo of his own movements as the tempo of the signals was stepped up. The minimum increase in the frequency of the signals (as in the first case) for which the subject was able to correct the tempo of his movements was taken as the threshold of correction. The thresholds for perception of increased frequency and the thresholds of correction were expressed by the ratio of the minimum increase in frequency to the original frequency in percent.

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The frequencies used ranged from 360 to 24 per minute. In a number of cases in order to facilitate analysis we expressed these frequencies by the intervals between the rhythmic signals, the length of these being inversely proportional to the frequency. The studies were made on 8 persons ranging in age from 20 to 35.

RESULTS

Fig. 1 shows the change in the thresholds for perception of an increase in the frequency of rhythmic signals or, what is the same thing, of a decrease in the intervals between rhythmic electrocutaneous and sonic stimuli, expressed in percentage of the original length of the intervals. As will be seen from the figure, all the curves have a similar trend. For intervals of 0.3-0.5 seconds (frequency 200-120 per minute) the thresholds have the smallest value, i. e. a peculiar optimum for perception of an increase in the frequency of the rhythmic signals is observed here. However, the same curves show that according to the character of the perception the frequencies studied may be divided into two groups: more than 90 per minute (intervals less than 0.7 second), and less than 90 per minute (intervals greater than 0.7 second). In the first group the outstanding feature is the superiority of the auditory analyzer. The thresholds for the auditory signals are lower than for the electrocutaneous signals throughout the whole range of frequencies employed, but for the intervals of less than 0.7 second the difference is especially large; for intervals of more than 0.7 second it levels out. The various subjects detected the increase in the original frequency with approximately the same degree of precision for the electrocutaneous and auditory stimuli.

As is evident from the same figure, the intensity of the rhythmic signals is also of great importance in the perception of an increase in the original frequency. The less the intensity, the higher the thresholds and the more difficult it is to perceive an increase in the frequency. However, this relationship appears only for intervals of less than 0.7 second, and it is much less pronounced for auditory than for electrocutaneous signals. Thus, when the intervals are 0.2 second (frequency 300 per minute), for weak, barely supraliminal electrocutaneous stimuli, the threshold for perception of a change in their frequency is 32%, and for strong signals 9.5%. With the same interval, when the loudness of the auditory signals is 0.3 neper above the auditory stimulus threshold, the thresholds for perception of an increase of the frequency are only 3-4% higher than for loud stimuli (40 nepers above the threshold) [1 neper = 8.686 decibels].

More detailed study showed that when the loudness of the auditory signals is increased to only 0.5-0.7 neper above the absolute threshold (when they are still barely audible) the thresholds for perception of an increase in frequency reach a constant value, and they do not change with a further increase in the loudness of the signals. For electrocutaneous stimuli, however, the thresholds do not reach a constant level until the intensity has risen to 3-5 times the absolute threshold, by which time these stimuli have the character of strong jolts.

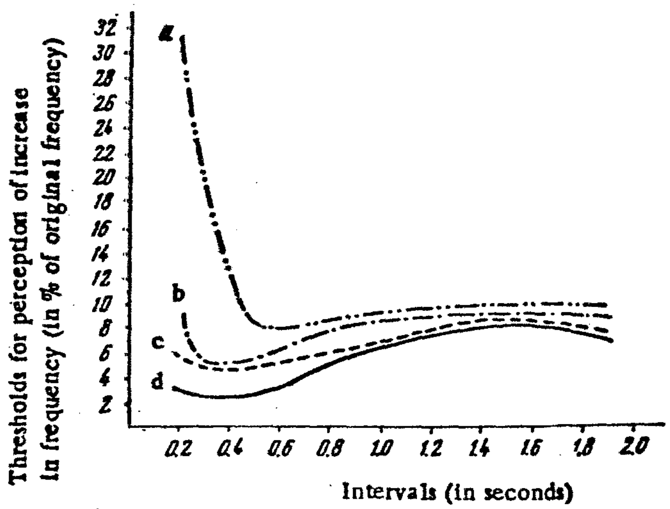


Fig. 1. Change in the thresholds for perception of a decrease in intervals between rhythmic signals, expressed as percentage of original length of the intervals. Average data for all subjects. a) Barely supraliminal electrocutaneous stimuli; b) strong electrocutaneous stimuli; c) barely supraliminal auditory signals; d) loud sonic signals.

For simultaneous, synchronized stimulation of the cutaneous and auditory analyzers the thresholds for perception of an increase in the original frequency correspond to the thresholds for the auditory signals, i. e., they are at their lowest. In other words, the strongest component in such a complex stimulus is the auditory stimulus, even at its slightest intensity.

The above relationships were established for intervals of less than 0.7 second between signals. For greater intervals, however (with frequencies of less than 90 per minute) the dependence of the thresholds on the intensity of the stimulation fully levels out. The degree of precision in perception of an increase in the original frequency is identical for both cutaneous and auditory stimuli, regardless of their intensity.

We also undertook to determine how many rhythmic signals of a new frequency (increased over the original by the threshold magnitude) were required for perception of this change. In other words, we sought to find whether there is any special summation of stimulation from several signals at an increased tempo, or whether one signal coming at a shorter interval than the original is enough to bring about a motor reaction (pressing on a particular key).

Number of Cases of Appearance of Motor Reactions (in percent) After Indicated Number of Rhythmic Signals at Shorter Intervals (Data for all subjects)

Original frequency (per min)	Nature of rhythmic stimulus	Number of rhythmic signals after increase of original frequency by threshold magnitude														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
300	Cutaneous	2	7	15	12	10	11	11	9	6	4	6	3	2	1	1
	Auditory	33	26	15	14	6	6									
120	Cutaneous	32	42	9	9	3	4	1								
	Auditory	54	29	17												
60	Cutaneous	75	25													
	Auditory	84	16													
30	Cutaneous	100														
	Auditory	100														

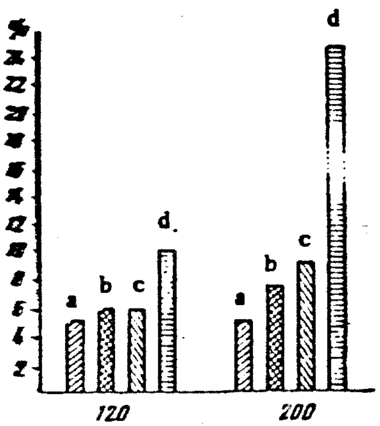
It will be seen from the table that summation of the process of stimulation is required for perception of a change in the original frequency, but only when the frequency is greater than 60 (more exactly, 90) per minute. At these frequencies the motor reaction arises in most cases not at the first signal with the new interval, but at the second, third, etc., the serial number being higher with the frequency rise. Under these conditions the superiority of the auditory analyzer shows itself again: the motor reaction to a change in the rhythm of the auditory signals comes much faster than to a change in the electrocutaneous signals. However, for frequencies less than 90 per minute (60 per minute) this relationship fully levels out. The motor reaction appears after the very first signal (both auditory and electrocutaneous) with a shorter interval.

As was stated above, in the second series we requested the subject to tap rhythmically with his finger to the rhythm of the stimulations. In the case of auditory signals the subjects were able to make movements immediately to the rhythm of these signals throughout the whole range of frequencies used (up to 360 per minute) and to change the tempo of their movements to correspond exactly to the change in the rhythm of the signal. Under these conditions the thresholds for correction of the tempo of the movements corresponded accurately to the thresholds for perception of a change in the rhythm of the auditory signals. When rhythmic electrocutaneous signals were applied at the same frequencies (higher than 90 per minute) the subjects were unable to produce movements to the rhythm of the signals (regardless of their intensity). The tempo of their movements was sometimes considerably above the frequency of the signals, sometimes below; they would stop and "attune" themselves to the rhythm of the cutaneous stimulations and then would try again unsuccessfully to "get on" it. Here the thresholds for perception of a change in the original tempo doubled or tripled. The greater the frequency of the signals, the more marked this phenomenon was.

Adding the auditory signals to the electrocutaneous signals fully restored ability to work at the given rhythm. The thresholds were lowered accordingly. Thus, at frequencies above 90 per minute even in these investigations the auditory analyzer proved to be superior, and the auditory signals, being the strongest componen of the complex, proved to be more adequate for perception of the rhythm of the external stimuli.

Significantly, however, at intervals of more than 0.7 second between rhythmic electrocutaneous signals (frequencies of less than 90 per minute) disruptions in the rhythm of movements were not observed. The subjects were able to perform movements accurately to the rhythm not only of the auditory but also of the cutaneou stimuli and to modify the tempo of their movements to correspond fully to changes in the rhythm of the signals. In these cases the thresholds for correction of the tempo of movements corresponded exactly to the thresholds for perception of a change in the rhythm of the signals.

In the last series of studies we undertook to determine why the rhythm of movements was disrupted in the case of electrocutaneous stimuli. We conjectured that there was a complex interaction here of our conditioned electrocutaneous stimuli and of the stimuli arising from each movement – kinesthetic, cutaneous (tapping the contact platform surface with the finger), and auditory (on closing the contacts). In order to determine the role of these stimuli a special method was used which made it possible to eliminate them practically altogether or ot change their intensity at will. A very light lever was fastened to the last joint of the subject's finger and an active electrode, also very light, was included in the Bourguignon chronaximeter circuit. As the finger moved down, the lever – through a mercury cup – silently closed the relay circuit, and discharged the selected capacity of the chronaximeter, whereupon the current entered either the above-mentioned electrode or the microphone. Thus, each movement of the subject's finger was accompanied either by a mainly kinesthetic stimulation (without electrocutaneous and auditory stimulation) or by an electrocutaneous stimulation of any intensity (in its character almost fully imitating the touching of the finger to the contact surface) or an auditory stimulation (a cracking sound). Finally, all these stimuli could be sent together, imitating the circumstances of the preceding experiments. Here, as previously, thresholds for perception of changes in the rhythm of electrocutaneous stimulations (administered to the other arm) and thresholds for correction of movements were determined.



Frequency of electrocutaneous stimuli per minute

Fig. 2. Change in thresholds for perception of frequency of rhythmic signals in relation to stimuli accompanying the motor reaction. a) Usual thresholds for perception of increase in frequency (without any movements); b) for movements not accompanied by either cutaneous or auditory stimuli; c) for movements accompanied by electrocutaneous stimuli; d) with addition of auditory stimuli to electrocutaneous stimuli.

Figure 2 shows the results of such experiments, typical for all the subjects. As will be evident from the figure, the lowest thresholds are those for perception of a increase in the frequency (a). The kinesthetic and electrocutaneous stimuli (b and c) somewhat raise the thresholds, i. e. they disrupt perception of the rhythm of the electrocutaneous stimuli (the more so as the frequency is raised). However, adding auditory signals to them raised the thresholds so much that the whole system of rhythmic activity is highly disorganized. Here the same picture is observed as was described above: the subjects were unable to produce movements to the rhythm of the electrocutaneous signals administered. It was shown that under these conditions the intensity of the stimuli accompanying the movement itself is of great importance. For example, when the strength of the electrocutaneous stimulation of the finger was increased, imitating the tapping on the contact surface with the finger, the thresholds could be raised so much that the same picture of disorganization of the rhythmic activity was observed here as with the auditory stimulations. However, for this a considerable strengthening of the electrocutaneous stimulations was required, whereas in the application of the auditory stimuli the same effect was achieved with a barely supraliminal intensity.

Thus, this data shows the importance of the stimuli accompanying a motor conditioned reaction for analysis of external stimuli (in our case, of their rhythm), a consideration that is usually given little attention in studies of a similar sort. In rhythmic conditioned reactions these stimuli interweave themselves into the system of external conditioned signals, forming with them a compound complex stimulus, in which the components may differ in importance. Thus, when the frequencies of the external stimulations are more than 90 per minute the auditory analyzer is stronger and subordinates the whole rhythm of the movements to itself, although the auditory stimulus is a result of the movement itself.

The data given here show that perception of rhythmic stimuli with a frequency of more than 90 per minute is based on certain physiological mechanisms different from the mechanisms for perception of lower frequencies. For the higher frequencies there emerges clearly not only the dominant importance of the auditory analyzer, insuring the greatest precision in the production of rhythmic conditioned reactions and differentiation of the frequencies, but also dependence of perception of rhythm on the intensity of the conditioned stimuli. On the other hand, for lower frequencies the importance of the analyzer to which the rhythmic stimulations are directed and the importance of their intensity are leveled out.

It may be suggested that the dominant importance of the auditory analyzer for frequencies greater than 90 per minute is determined by the law of the strength of conditioned stimuli. However, there is some peculiarity in this manifestation of the law. We must consider the rhythmic stimulations which we employed as a rhythmic series of identical conditioned signals following each other at a set interval. Under these conditions each signal (auditory, cutaneous, etc.) proves to be not only a conditioned stimulus evoking a reaction (for example, touching the contact surface with the finger) but also a strengthening of the following condition of the cortical cells after the preceding conditioned signal. This strengthening contributes to the elaboration of the conditioned reaction time, which as we have shown previously [1, 2] is more clearly observable for relatively short intervals between rhythmic conditioned signals (less than 1 second). On the other hand, for intervals greater than 1 second the conditioned reaction to time plays a relatively minor role.

It may be suggested that all the relationships which we have described here are determined to a considerable degree by the interrelationships of these two factors – the conditioned reaction to time and the conditioned reaction to the external signal. It is quite possible that the auditory signal being a physiologically stronger stimulus at the same time is also a greater strengthener for the conditioned reaction to time and, consequently, contributes to its speedier and more stable elaboration. It, by itself, determines the most complete flow of rhythmic conditioned reactions and the most accurate perception of the rhythm of external stimulations.

LITERATURE CITED

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