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THE SOUNDS FROM SINGLE MOTOR UNITS IN A CONTRACTING MUSCLE

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Most people are familiar with the roaring sound which may often be heard in their ears during strong contraction of the jaw muscles when the external meatus of the ear is blocked at its outer end. We have, however, been able to hear in quiet surroundings a succession of discrete clicks or pops occurring during much slighter degrees of muscular contraction. These clicks occur with a fairly regular rhythm whose frequency varies with the strength of the contraction. We were struck by the resemblance of these rhythms to a loudspeaker reproduction of the action currents from single motor units, and it seemed probable that the sounds were the mechanical counterparts of the muscle action currents. This paper deals with the relation between these two phenomena.

APPARATUS AND METHODS

All the experiments to be described were carried out on intact human subjects.

Whenever muscle action potentials were recorded, they were picked up through the skin by means of bipolar electrodes. The electrodes consisted of a pair of parallel wires of enamelled constantan between 0·06 and 0·12 mm. in diameter. The ends of the wires were cut square, and the flat uninsulated surfaces were applied to the skin, with the axis between their centres in line with the main axis of the muscle fibres. The separation of the electrodes varied, in different experiments, between 0·1 and 1·5 mm. The subject was earthed through a silver plate which he held in his mouth, and this procedure reduced interference from the mains enough to make the use of a shielded room unnecessary.

When investigating the mechanical disturbances underlying the clicking sounds, two types of electro-mechanical instrument were used. The sounds were recorded by means of a crystal microphone. Alternatively, a stiff piezo-electric system, in direct contact with the skin, was used to record mechanical movements of the underlying muscle, without the intervention of a column of air. In order to record simultaneously the electrical action currents and the mechanical effects, a pair of wire electrodes, like those just described, was incorporated in each of these instruments. The potentials from the wire electrodes and from the microphone or mechanical device were led separately to two resistance-capacity coupled push-pull amplifiers having degeneration of in-phase signals. The amplifier used for action potentials has an overall time constant of about 10 msec.,

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and the one used for recording sounds and movements has an overall time constant of about 0·5 sec. When, however, a piezo-electric recording instrument forms part of the input circuit of this second amplifier, the capacity of the crystal greatly reduces the time constant of the whole system (see below).

The apparatus for the simultaneous recording of action potentials and sounds is shown in Fig. 1. It consists of a pair of wire electrodes (*B*) in the middle of a microphone orifice, which are held in position by a narrow strip of rubber (not shown in the figure). This orifice fits in an airtight fashion on the skin (*A*). The microphone chamber (*C*) is closed at its other end by the diaphragm (*D*), thus forming a completely enclosed space. Movements of the diaphragm deform the Rochelle salt crystal (*E*), which has piezo-electric properties, and therefore gives rise to potentials which are led through screened cable to the amplifier (*F*).

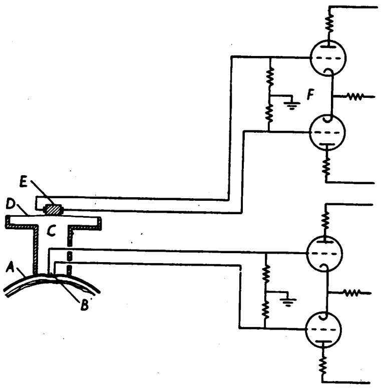

Fig. 1.

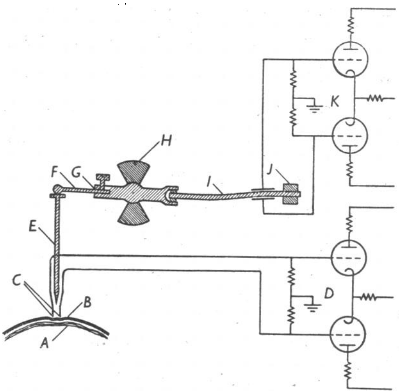

Fig. 2.

Fig. 1. Apparatus for the simultaneous recording of action potentials and sounds (for explanation, see text).

Fig. 2. Apparatus for the simultaneous recording of action potentials and muscle movements (for explanation, see text).

The apparatus for the simultaneous recording of action potentials and movements through the skin is shown in Fig. 2. It records the electrical action potentials arising under the ends of a pair of wire electrodes (*C*), and at the same time records the mechanical force exerted on both the flat ends by the underlying muscle (*A*). This is achieved by connecting the two electrodes through screened cable to one amplifier (*D*): at the same time a rod (*E*), to which the electrodes are rigidly attached, actuates a crystal gramophone pick-up whose output is connected to the other amplifier (*K*). The rod (*E*) is 30 mm. long and 1 mm. in diameter, and is made of a magnesium alloy. The electrodes are attached to the sides of the rod with silk thread and shellac, and the ends project 0·5 mm. beyond the lower end of the rod on to the skin (*B*). The upper end of the rod, which has a flat head like a nail, bears against the spherical knob at the end of a second rod (*F*) which is 20 mm. long, and also of magnesium alloy. In this way a universal joint is formed, and for convenience of manipulation the two members of the joint are held together with a treacly mixture of castor oil and resin. The second of these rods is inserted in the chuck (*G*) of a Rothermel piezo-electric gramophone pick-up ('bender' type). In the pick-up, the chuck member rotates on rubber bearings (*H*), and is attached by means of rubber pads to the free end of the Rochelle salt crystal (*I*). The other end of the crystal is clamped between a second pair of rubber pads (*J*). The time constant of the crystal, screened leads, and the pair of 1 MΩ. grid leaks was found experimentally to be 15 msec.

When this apparatus is used for investigating the facial muscles (e.g. m. orbicularis oculi), the subject lies on his back with his head in a moulded plaster support. A loop, or 'halo', of lead piping is rigidly attached to this support, and the pick-up is fixed to the part of the loop which overhangs the appropriate muscle by means of a rack-and-pinion mounting. This allows fine adjustment of position.

RESULTS

The sounds heard by the ear during the contraction of adjacent muscles

One of the simplest ways of hearing the muscle sounds is to close the external meatus at its outer end, for example, by lying with one's head on a pillow. Once one has learnt to recognize these sounds, they are heard in this way with great clarity, and may even prevent one from going to sleep at night. The sounds may also be heard well when the outer end of the meatus is blocked with soap suds, or when the meatus is filled with water.

It is frequently possible to hear sounds like the rhythm from a single motor unit. They occur when the jaw is closed or deviated to the same side as the ear one is using, and cease when the jaw is opened or deviated to the opposite side: they probably arise in m. masseter. The lowest rate of regular firing is about 5 per sec., and occurs during very slight maintained contraction. Rhythms of this order of frequency are often heard during postural activity of the jaw muscles, and without any voluntary effort of contraction. It sometimes seems impossible to achieve complete relaxation even with one side of the head lying on a pillow. At rates below about 5 per sec. the rhythm becomes irregular. As the strength of contraction increases the rhythm from a single unit becomes faster and may be distinguished up to 10 or 15 per sec., but becomes involved in a rapidly mounting roar as more and more units become active and increase their rates of firing. One of us is able to hear very distinctly the sounds from m. auricularis superior when the pinna is raised in voluntary contraction, but sounds from a single unit can only be distinguished in one ear. This particular unit can be followed even during a maximal contraction, which suggests that it happens to be very favourably placed anatomically for conducting its sounds to the ear. It was possible, by means of a miniature microphone inserted a short distance into the meatus, to make a record (see Fig. 3*a*) of the sounds of a maximal contraction of this unit. The best results were obtained when the canal was partially filled with soap suds. The sounds were, of course, simultaneously heard by the subject, the microphone and soap suds effectively closing the meatus.

It is not always entirely clear how these sounds are conducted to the internal ear. It seems most probable that the motor units cause movements of the walls of the meatus, and that these in turn cause pressure changes in the meatal air-column which actuate the ear drum. The following observations support this theory. The sounds are only heard when muscles in the immediate neighbourhood of the meatus are contracted. Blocking the external end of the meatus makes the sounds audible, presumably because the air-pressure changes, due

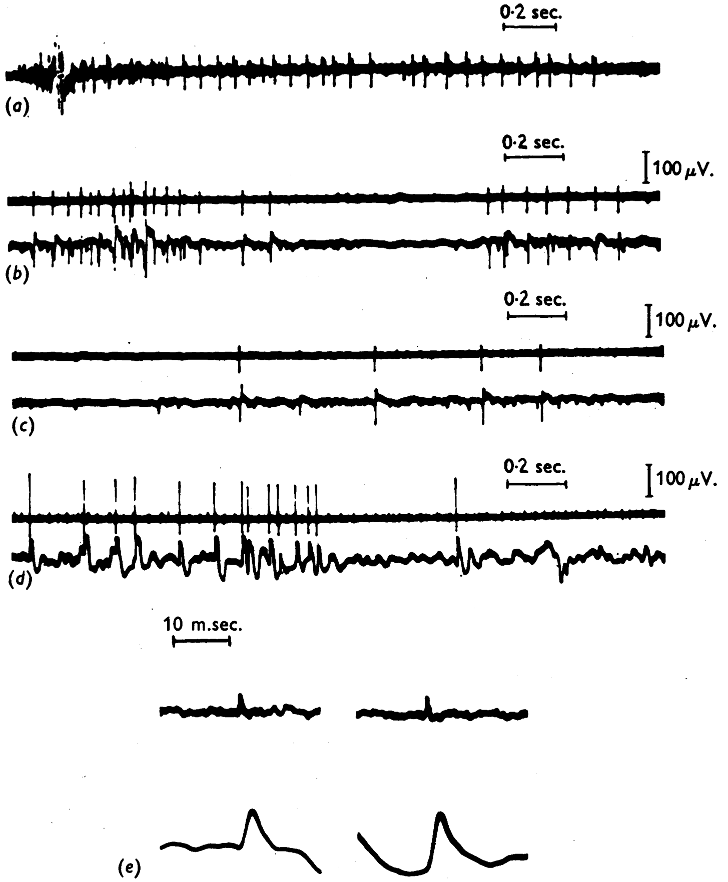

Fig. 3. (*a*) Record of sounds picked up by a microphone inserted in the external meatus of the human ear. A single sustained contraction of m. auricularis superior occurs during the record. The large complex oscillation at the beginning is an artefact caused by the slight displacement of the microphone which occurs as the pinna moves upwards. The sounds from one motor unit stand out clearly throughout the contraction. (*b*) Simultaneous record of action potentials (top line, bipolar electrodes 1 mm. apart) and of sounds (bottom line, microphone with 6 mm. diam. orifice) taken from the upper eyelid (m. orbicularis oculi). Two light closing movements of the eye occur during the record, the first stronger than the second. The activity of the same motor unit stands out in both lines. The scale of μV. refers to the top line. (*c*) As (*b*) above. Four very slight movements were made, as though to close the eye: each movement is represented by one action potential. (*d*) Simultaneous record of action potentials (top line, bipolar electrodes) and of mechanical movements (bottom line, piezo-electric instrument), each taken from the same small area of contact with the upper eyelid (electrode separation 0·2 mm.). The eye was kept closed throughout, the tension being steadily increased, then relaxed, and finally increased again slightly, giving rise to the final action potential. The activity of the same motor unit stands out in both lines. The scale of μV. refers to the top line. (*e*) As (*d*) above. Two records taken at higher speed, to show the relation in time of an action potential (top line) to its accompanying mechanical movement (bottom line).

to movements of the meatal wall, are greater when the air is confined. The sounds are sharper when the outer end of the meatus is closed with soap suds instead of a hard object, presumably because of their well-known property of damping out reverberation in an air-column: the sounds are louder, on the other hand, when the meatus is filled with water even when open at its outer end, presumably because water, having greater inertia than air, is a better transmitter of the movements of the meatal wall to the ear drum. This dependence of the phenomenon on local conditions in the meatus makes it likely that the sounds were actually produced by the muscles which we have named, and not by a synergic or fortuitous contraction of the middle ear muscles. While we are inclined to the view that closing the meatus acts by increasing the pressure changes in the air-column, the exclusion of external noise may also play a part in increasing the clarity of the muscle sounds.

The sounds from other muscles

It is well known that a low-pitched rumble is heard when a stethoscope is applied over contracting muscle. When the area covered by the stethoscope is sufficiently reduced, the rumble resolves itself into more discrete sounds, and, when listening over the thin palpebral portion of m. orbicularis oculi, the sounds from single units may be heard distinctly. The most satisfactory form of 'stethoscope' is an 8 in. length of 3 mm.-bore pressure tubing, one end of which is inserted in the ear and the other, cut accurately flat and preferably wetted, placed flat on the upper eyelid. With this instrument, the sounds from single units are heard with such clarity as to justify the use of this experiment in class teaching. The sounds resemble those from a distant motor-cycle.

M. orbicularis oculi was used in all the remaining experiments owing to the thinness both of the muscle itself and of the overlying skin and subcutaneous tissue. Records of the sounds from single units were never obtained so clearly from any other muscle investigated, even in the face region, and the thicker and deeper-lying muscles of the limbs only gave a complex rumbling sound.

The correlation of the electrical and the mechanical events in a contracting motor unit

(*a*) *The recording of electrical action potentials.* When using the bipolar electrodes previously described, it is easy to obtain records from single units of m. orbicularis oculi. It is unnecessary to clean the skin or prepare it in any other way. After the upper eyelid has been fully exposed by stretching it downwards and fastening with adhesive cellulose tape, the electrodes are pressed firmly against selected areas. The subject then makes graded voluntary contractions of the muscle.

The recorded potentials from single motor units are largest when the electrodes are near the inner end of the eyelid, and may reach 0·2 mV. with an interelectrode gap of 0·2 mm. They are usually diphasic or polyphasic, the total duration of the diphasic potentials lying between 1 and 2 msec. The activity of a particular unit may usually be followed for as long as desired. The lowest frequency of regular discharge is about 3 per sec.: when we have been able to observe a single unit during maximal contraction its frequency has not exceeded 45 per sec.

(*b*) *The recording of the sounds from single motor units.* When the orifice of the microphone is applied to the skin of the eyelid the sounds from single units can be amplified and recorded on a cathode-ray tube. Provided the microphone orifice fits perfectly on the skin, the sounds may usually be recorded well from any part of the upper eyelid.* The spikes as recorded on the screen are usually diphasic and the total duration of each is 5–15 msec. The initial deflexion in each spike corresponds to an increase in pressure such as might result from a lateral expansion of the motor units. The frequency of the microphone spikes varies, just like the frequency of action potentials (see (*a*) above), with the strength of contraction: as the durations of the microphone spikes are much greater than those of action potentials, and as no record in a maximal contraction is ever confined entirely to one unit, it is difficult to follow microphone spikes individually to a frequency as high as 45 per sec. In one experiment, however, spikes from a single unit were followed up to this frequency; it was found that they preserved their original size and individuality, and there was no rise in the base-line as there is in the usual mechanical record of a tetanus.

Simultaneous records of the electrical action potentials and of the 'sounds' can be obtained with the microphone shown in Fig. 1, which has a pair of electrodes centred in its orifice. Although it is a fairly simple matter to obtain a record from a single unit with a microphone alone or with a pair of electrodes alone, one has usually to make a number of trials before finding a place from which simultaneous electrical and microphone records may be made from the same unit: a loud-speaker on the output of the channel recording the action potentials is almost essential. Records of this kind are seen in Fig. 3, *b* and *c*. Here the activity of one particular unit is conspicuous, and it is clear that each action potential from this unit is accompanied by a 'sound'. This confirms the expectation put forward at the beginning of this paper.

The 'sounds' recorded by the microphone must be caused by minute movements in the motor units lying under its orifice. In the hope of investigating the nature of these movements more precisely, and of measuring the brief time interval between the electrical action potential and the movement itself, and also, possibly, of recording from a smaller area, we have used the piezo-electric system shown in Fig. 2. This instrument has the advantage of picking up both action potentials and mechanical movements from the same small area of

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* This method was demonstrated at the XVII International Physiological Congress (Oxford, July 1947).

contact with the skin. Even though this area is small, it is clear that both the electrical and the mechanical changes may be produced by units lying some distance away. Since the piezo-electric instrument records any movement of its point relative to the main body of the instrument, it was impossible to hold it sufficiently steady by hand. The head was therefore supported in a plaster rest to which the piezo-electric instrument was rigidly attached, and the subject tried to relax his neck muscles as completely as possible. Even then, the base-line of the records was never as steady as it was with the microphone. In other ways the records (see Fig. 3*d*) were similar to the microphone records, and showed the same range of frequencies of spikes and the same relationship to the action potential records. The spikes were monophasic, or more commonly diphasic, with a comparatively slow return to the base-line, the diphasic spikes having a total duration of 30–40 msec. The initial deflexion corresponded, as in the microphone records, to an outward movement of the surface of the eyelid.

In order to measure the time interval between the electrical and the mechanical spikes, snapshots of single sweeps of the cathode-ray tube were taken at intervals of about 3 sec. In using this hit-and-miss method of making records, it was necessary to make sure before starting that the electrical and mechanical traces were from the same unit. The sweep was run as fast as was compatible with fitting a complete mechanical spike on to the face of the tube. It was found that the beginning of the electrical action potential preceded the beginning of the mechanical movement by an interval which lay, in different experiments, between 0·4 and 2 msec.; in any one experiment on one unit, the interval was consistent to about 0·5 msec. The results shown in Fig. 3*e* illustrate two extremely brief intervals. Even if the conditions of the experiment allowed the use of a faster sweep, there would be little or no increase in accuracy, since the point of rise of the mechanical spike is not sufficiently well defined.

DISCUSSION

The work described in this paper shows that an electrical action potential in a single motor unit is accompanied by a mechanical change which starts rapidly enough to produce a sound. The action potential and the brief mechanical change are physiologically related, and the correspondence between them was not due to any interaction between the electrical and mechanical recording systems: if it had been an artefact, there would always have been some correspondence, whereas, as previously explained, lengthy adjustment was usually necessary in order to achieve it.

Inspection of the spikes recorded with the microphone and with the piezo-electric instrument has shown some obvious similarities and some differences (compare (*b*) and (*d*) in Fig. 3). This calls for a closer analysis of the properties of these two instruments and of the response of each to muscular contractions.

A wave of muscular contraction cannot travel along the fibres comprising a single motor unit unaccompanied by a wave of lateral expansion. If the orifice of the microphone is placed on a region of skin under which there is an active motor unit, then, when the front edge of the travelling wave of lateral expansion reaches the region under the orifice, the skin will be forced to bulge slightly into the microphone chamber, thereby increasing the pressure in it and actuating the diaphragm. It is to be expected that an initial deflexion will occur when the sharp front edge enters the orifice, and a deflexion in the reverse direction when it leaves. This might explain the brief and diphasic spikes on the microphone record.

The charge on the crystal of the piezo-electric instrument is proportional, on the other hand, to the force exerted at any instant by the motor unit, except that it leaks away at a rate depending on the time constant of the input circuit (15 msec.). The sharp rise of the recorded spike occurs in a time considerably less than this time constant, and is therefore a fairly true representation of the force exerted on the pick-up point by the motor unit at any instant: it probably corresponds to the complete diphasic spike in a microphone record. Since the rest of the spike occurs more slowly, it is a less true picture of the contraction process: the apparatus does not give a faithful representation of the rise in mechanical base-line during a tetanus. It seems probable that the contracting motor unit exerts a force on the pick-up point not only by means of its lateral expansion, but also by means of its lengthwise contraction, because the pick-up point makes a dimple in the skin which the motor unit tends to flatten out when it contracts.

We have mentioned that the measured interval between the beginning of the electrical action potential and the beginning of the mechanical spike in a single motor unit varied considerably from one experiment to another. Although our figures indicate that the interval is a brief one, there may be a serious source of error in any measurements of this kind. It is known that synchronization of the discharges of different motor units can occur in powerful voluntary contraction of human limb muscles (Adrian, 1932, 1947), and from a few experiments we suspect that this occurs in m. orbicularis oculi even with moderate contraction. It is clear that the electrical and the mechanical records might, on occasion, be derived from different motor units which were discharging synchronously or nearly so, and if this were to happen the measurement of the interval between the electrical and mechanical spikes would be misleading.

Cooper & Eccles (1930), in a comparison of the twitch durations of different mammalian muscles, measured the stimulus frequency necessary to achieve an apparently smooth contraction. The frequency for m. gastrocnemius was 100 per sec., and for m. rectus internus 350 per sec. The palpebral part of m. orbicularis oculi, which is used for making extremely rapid movements, probably has a relatively high fusion frequency, and single units of this muscle could not achieve smooth contraction in the range of frequencies which we have observed in voluntary movements (less than 50 per sec.). It is doubtful, indeed, whether the contraction of single units even in a relatively slowly acting limb muscle is ever completely smooth, since Rutherford (1886) stimulated a whole muscle repetitively, and was able to hear a sound from the muscle whose frequency followed the stimulus frequency up to 352 cyc. per sec. These sounds were presumably produced in the way we have previously described, and were only observable from a whole muscle because all the motor units were being stimulated synchronously. The complex rumbling sound which is heard from large muscles during voluntary contraction must be due to the asynchronous activation of many motor units: the overall contraction of the muscle is then relatively smooth.

SUMMARY

1. The sounds heard by the human ear during the contraction of muscles adjacent to the meatus may be resolved into sets of rhythmic clicks, each set corresponding to the contraction of an individual motor unit. The sounds heard during the contraction of a single unit of m. auricularis superior have been recorded from a microphone inserted in the meatus. The optimal conditions for hearing these sounds, and the probable method of their conduction to the ear-drum, have been discussed.

2. The sounds produced by single motor units of m. orbicularis oculi were heard with a 'stethoscope' applied directly to the skin overlying the muscle, and were recorded by applying a microphone to the skin. In other experiments, the movements underlying these sounds were recorded through the skin with a piezo-electric instrument.

3. Each movement or sound in a series is associated with an electrical action potential which was recorded simultaneously from the same motor unit: the frequency of discharge varies with the strength of voluntary contraction, the highest recorded figure being 45 per sec.

4. Each movement lags behind its accompanying action potential by an interval of 2 msec. or less: the errors in making this measurement have been discussed.

5. The method by which a muscle achieves a smooth voluntary contraction is briefly discussed.

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