The Control of Muscles in Speech

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I — MUSCLES AND NERVES

This section summarises some of the available literature concerning the operation of muscles and nerves.

All skeletal muscles comprise groups or bundles of smaller muscle fibres; these muscle fibres are of many different shapes and sizes depending on the muscle in question. Cylindrical gamma shaped muscle fibres are comparatively short compared with, say, flagelliform or laneolate muscle fibres. In addition there are spindle-shaped muscle fibres, so named because they have a thick central region with pointed ends. Sometimes a muscle fibre may extend the whole length of the muscle; other fibres are shorter, overlapping with other short fibres (Buchthal and Lindhard 1939). Several researchers give figures of the order of 10µ for the diameter of a muscle fibre, but several centimetres for its length (Fromkin and Ladefoged 1966).

Muscles are attached at both ends, sometimes to bones or membranes attached to bones, sometimes (as with *m. orbicularis oris* — used in rounding and protruding the lips) to themselves. It is by *contraction* that a muscle causes. movement in whatever it is attached to, or can enable a greater load to be borne by *tensing*. Individual fibres composing the muscle contract or tense, causing the muscle as a whole to contract or tense.

Liddel and Sherrington (1925) consider the muscle as comprising *motor units*. A motor unit may be regarded as "a motor cell, its axon process and the groups of muscle fibres innervated by this one nerve cell" (Fromkin and Ladefoged *op. cit.*; see also Cooper 1965). According to Fromkin and Ladefoged no estimate has been made of the number f fibres in the tongue and lip muscle motor units; however it is known that in general the larger the muscle as a whole the greater the number of fibres to each motor unit.

Contraction occurs within the fibres of the motor unit when impulses arrive causing a chemical change at the junction between nerve and muscle, followed by a muscle action potential. The electrical changes in the muscle precede the actual contraction. If the attachment of the fibres is moveable then actual shortening will occur, if not then tensing will occur. The contraction of any one fibre or the fibres associated with a single motor nerve (or motor neuron) lasts only a few milliseconds; contraction of the entire muscle may of course last very much longer depending on the non-simultaneous contraction of different motor units. After contraction of the muscle fibre — the decay time of the contraction may not always be the same for all types of fibres — there is a short period of time while the original chemical balance is restored; after this time the fibre is able to contract again upon receiving a suitable stimulus (i.e. a stimulus above the threshold required to initiate the chemical change associated with contraction). Rate of contraction of the individual motor units will not normally exceed 5 cps. for a single twitch.

As mentioned above a muscle fibre will contract as a result of chemical change brought about by an appropriate stimulus. There is a threshold of acceptance of the incoming impulse below which there will be no chemical action and above which the chemical action will take place. In a simple diagram (Fig. 1) therefore we can imagine a cline of possible stimulus ‘intensity’ below the threshold resulting in no contraction and a continuing cline above the threshold resulting ultimately in *maximum contraction* .

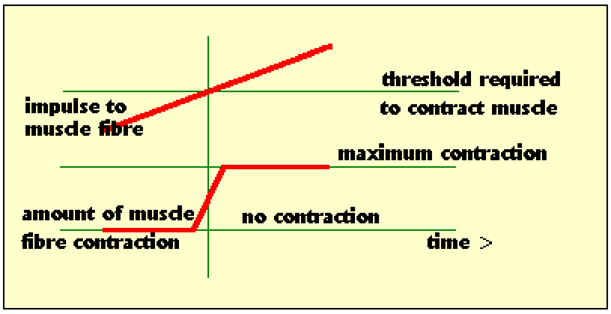

Fig. 1 Diagram illustrating how below a certain intensity of stimulating impulse there is no muscle fibre contraction; above this critical threshold intensity there is maximum muscle fibre contraction.

Thus a binary or flip/flop mechanism operating at the level of fibre contraction results from what may not necessarily be a binary input. In fact however if we assume that the acceptance threshold is always constant when the impulse arrives the muscle fibre will normally fire providing the stimulus is at threshold intensity.

It therefore follows that the amount by which a muscle fibre contracts is a property not only of the incoming impulses but also of the fibre itself. The rate of firing depends on two things:

- the rate at which impulses arrive at the bundle of nerve fibres associated with each motor neuron (the fibres firing more or less simultaneously) and
- whether or not the individual fibre has had sufficient time to regain its original chemical state.

Impulses arriving too fast (i.e. before the original state has been regained) will either have no effect or, or a brief period before absolute restoration of chemical equilibrium, result in somewhat reduced contraction. Most muscle fibres contract to very roughly half their length, although their overall volume does not vary very much — i.e. their diameter is greater when they are shorter. The binary nature of firing is often referred to as an ‘all or none response’. As mentioned earlier not all motor units will be activated at the same time. The effect of this — since not all fibres run the whole length of the muscle and since the load will prevent it — is that the muscle itself will not contract as a whole to half its length. Thus some energy is expended in moving the muscle as well as moving the load placed upon it.

The amount of load a muscle can support or the degree of muscle activity is dependent upon the number of motor units which have been recruited and upon the rate at which these are firing. It can be seen therefore that a measure of motor unit activity might be its rate of firing and a measure of muscle activity the number of motor units recruited equated with the rate of firing of each.

II — MUSCLE SPINDLES

Muscle spindles occur intermixed with muscle fibres. They can be several millimetres long and contain from two to twelve intrafusal fibres each of which may have a diameter of six to twenty eight (Matthews 1964). The central region of the spindles usually has an overall diameter of between 80 and 200. The bundles of intrafusal fibres are each encased in a capsule containing a fluid; it is this which provides the characteristic fusiform shape of muscle spindles.

The number of spindles per muscle varies but in general small muscles undertaking fine movement with precision have a greater ratio of spindles; the actual ratio of spindles to motor units has not yet been accurately determined for facial muscles or other muscles involved in speech although a good deal is known about muscles controlling eye movements.

A principal function of muscle spindles is the signalling of mechanical events to higher level motor centres and as such they play a large part in the accurate co-ordination of muscle movement.

This signalling of mechanical events is carried on *via* the output from the spindle — the afferent nerve fibres. Information is sent this way to the central nervous system in terms of the spindle discharge. This discharge results in a measure of the relative lengths of the intra- and extra-fusal fibres. In spindle behaviour related to posture passive stretching of the muscle (i.e. stretching caused by something external to the muscle — contraction of an adjoining muscle, movement of a bone to which the muscle is attached, etc.) increases the rate of repetitive firing of the muscle spindles, the frequency of this firing being proportional to muscle lengthening. Thus the firing rate is a measure of the lengthening to which the muscle is put from the outside. Contraction of the gross muscle causes a decrease or cessation of spindle firing — indicating that the external lengthening has been counteracted. Thus a very elementary model of the function of the spindles in normal posture would posit that upon the lengthening of the muscle by some external force there is an increase in spindle firing; this is signalled to the central nervous system resulting in excitation of the muscle vi (at least) the downward alpha route; upon subsequent contraction of the muscle the spindles are no longer being lengthened, so their firing ceases or returns to a slower normal rate. This model is a gross over-simplification and we can attempt to build up a more complete picture of the part muscle spindles have to play in muscular control.

The spindles are therefore important in maintaining postural reactions but as mentioned above they play a large part in providing the nervous system as a whole with information about the mechanical state of the muscle in question. It is important to differentiate between this kind of information and, say, consciously felt proprioceptive information which may, for example, be provided by pressure sensors on the surface (of, say, the tongue or lips).

There are normally two excitation paths to the muscle: the alpha route and the gamma route. gamma efferent nerve fibres are motor to the spindle and it has been found that in many muscles spindle nerve fibres (both afferent and efferent) are considerably greater in number than the alpha nerve fibres which are motor to the extrafusal muscle fibres. It is probably the case that some -fibres may be shown to be ‘fusimotor’ (i.e. that they may control spindles), but Matthews (*op. cit.*) together with others generally refers to ‘gamma efferent fibres’ to mean any fibre motor to the spindle irrespective of its diameter (alpha fibres are greater in diameter than gamma fibres). alpha and gamma routes may well perform distinct functions, though apparently working in co-operation.

Thus muscle spindles are found in large numbers in small muscles controlling fine movement and perform two functions:

- they can be stimulated by their own motor nerve fibres and contract in the normal manner and
- they are ‘stretch receptors’ reporting back to a higher motor centre information about certain mechanical events about stretch which they are undergoing — thus reporting back information about the conditions under which the muscle as a whole is operating.

According to Matthews the precise nature of the information emanating from muscle spindles is not known, neither is the way this information is used by the nervous system as it regulates muscle contraction fully understood. It is possible however to construct a working model of the system according to the available data. I shall first outline this model and then show how it can be applied to muscle control in speech.

A muscle spindle has been found to have three different kinds of nerve endings attached to it: primary, secondary and plate nerve endings (Matthews *op.cit.*). It is not necessary to go into detail here about the relative function of these different endings, but it does seem that the spindle primary endings are responsible for signalling the nervous system with two different kinds of information:

- they indicate facts about the length of the muscle at any given moment;
- they indicate, again at any given moment, the velocity at which the muscle is being stretched.

Perhaps it should be remembered that there is no conscious feeling provided by this information — the spindle is simply playing a role in the subconscious control of muscle contraction.

A simple model would consider spindles together with the fusimotor fibres nerve fibres to the spindles bringing impulses resulting in contraction) as part of a ‘follow-up length servo’, as Matthews calls it, which will enable the length of a muscle to be set *refexly* to any required value.

The conception of this control loop as a servo mechanism is an important contribution to the understanding of precision of control in muscle movement. In engineering terms a servo mechanism is any control system which is automatic; the system comes into operation when a so-called ‘error signal’ is generated. When, for example, a device is in danger of becoming unstable a mechanism operates signalling that an error is occurring; this brings into play a correction signal which decreases the instability and therefore the error signal; the entire control cycle comprises a closed-loop system which must in addition possess some form of power amplification.

In muscle control of posture reacting against, say, gravity or other external force, contraction is signalled by the primary endings of the spindle. A correction signal arrives and equilibrium is re-established. The main function of the fusimotor fibres is seen as providing the control mechanism of various parameters of the servo system (such as, for example, stiffness, damping, etc.); this seems to fit the model better than to assume that they directly alter the balance turnover point of the servo loop by biasing the spindle.

As stated above, the spindle is controlled by two efferent fibre inputs and the discharge from the spindle is modified (with respect to its rate) by two factors:

- extrinsic muscle lengthening;
- the intrinsic contractile status of the intrafusal fibres

Spindles do not act directly as specific indicators of muscle tension or length but provide parametric information from which these facts may be deduced.

It is by means of the discharge from the fusimotor fibres (causing spindle contraction) that a muscle may be set reflexly to a variety of lengths (according to Matthews’ model). Any *increase* in fusimotor activity will result in an increase of primary ending discharge. The result of this, reflexly employing the servo loop, will be a shortening of the muscle until the primary ending discharge is reduced to its original value. Any *decrease* in fusimotor activity will cause the muscle to relax to a new and greater length. Provided the gain in the reflex loop-is great enough, the new length assumed by the muscle at any instant in time should be independent of both load and fatigue. The stretch reflex loop can operate independently of the cortex in an entirely automatic manner; the original increasing or decreasing of fusimotor activity is however controlled and capable of setting the system to the desired value. The power amplification necessary in a servo circuit is provided by the muscle contraction.

The precise operation of the servo mechanism to hold equilibrium once the desired length has been established follows this closed loop cycle operation: tension on muscle — muscle stretches — primary endings become excited — results in monosynaptic excitation of the motor neurons (alpha-neurons) of the same muscle — muscle contracts — tension in muscle — etc. This basic loop control mechanism operates therefore on the principle of negative feedback which is essential for any degree of stability in a system. What is happening is that muscle contraction is opposing the applied tension with the result that under the servo control a constant length is maintained no matter what the external force tending to disrupt the equilibrium. In practice, all servo mechanisms contain a delay caused by inertia of certain components within the system; this results sometimes in ‘over-correction’ oscillating in either direction about the equilibrium point, but gradually settling down. The faster the operation of the loop the more rapidly and finely is equilibrium established. It is important to note that this model is about setting the muscle to a particular length and then maintaining that length despite external disturbing forces. Any model attempting to account for a complex continuous movement of a muscle or integrated system of muscles will be vastly more complex. It is not necessary to go into this; it may be enough to indicate that the next degree of complexity of the model would suggest that *controlled* (either spatially or temporally) muscle contraction could be accomplished by a temporal super-imposition of many desired length settings and servo operations — but then we would have to account for the rhythm of the super-imposition.

Before going on to applying this notion of muscle control to the operation and control of muscles in speech there are one or two further observations to be made. The so-called 'error signal' to the servo system can be regarded as the difference in frequency of firing of the primary ending on the muscle spindle when the muscle is unloaded and when it is loaded. During control, the direct voluntary excitation of the muscle *via* the alpha route must be sufficiently powerful to prevent the situation whereby the diminished spindle discharge due to shortening will reflexly oppose the direct excitation of the motor neurons by higher centres (cf. Matthews *op. cit.*). The alpha-route would therefore be used at its most effective when operating in conjunction with sufficient fusimotor activity to *prevent* any decrease in the spindle discharge during contraction.

III — CONTROL OF MUSCLES IN SPEECH*

[*I am greatly indebted in this section to the work of Sven Ohman, KTH, Stockholm. In particular to his very important paper 'Peripheral Motor Commands in Labial Articulation' which recently appeared (*STL-QPSR* 4.1967). His model represents a considerable step forward in our understanding of the neuro-muscular mechanisms operating in speech.]

As mentioned earlier muscles consist of bundles of muscle fibres each of which is associated with a particular motor (or alpha) neuron. Impulses arrive at the muscle fibres *via* the descending neural pathway and the muscle contracts appropriately. Muscle fibres are, at a simple level, divisible into those fibres or bundles of fibres which receive signals to contract *via* gamma neurons and possibly by some alpha neurons) but also act as stretch sensors relaying information about the mechanical state of the spindle and therefore of the muscle as a whole.

Extrafusal (or non-spindle) fibres vary in their speed of response to incoming stimuli. This speed of response is simply a measure of the rate at which the fibre reaches the peak of its response from the onset of response (Ruch *et al.* 1963). Most muscles in man contain extrafusal fibres varying in a wide range from fast to slow (Bessou *et al.* 1963) and, as Ohman (1967) points out (p.40) "there is a certain correlation between the speed of a muscle fibre and the optimal frequency of firing of the motor neuron [- neuron] that is connected to it...; faster fibres are in general innervated by higher frequency motor neurons and vice versa" (see also Henneman *et al.* 1965). It is the muscle fibre which becomes adapted to the average firing rate of its associated motor neuron and not the other way round (Eccles *et al.* 1962). The usual range of firing rate of the motor neuron is directly proportional to its size (Kernell 1965).

The number of excitatory synaptic knobs on the soma-dendritic complex of different size motor neurons varies from muscle to muscle. In the particular case where all motor neurons have the same number of synapses, it is clear that a uniform presynaptic excitation of moderate frequency will recruit a greater proportion of the slower motor neurons than of the faster ones. Under the same conditions, a presynaptic excitation of increasing frequency will not only result in increasing firing frequencies of the motor neurons but also in a gradual coming into play of faster and faster motor neurons (Ohman 1967, p.41).

A fundamental function of the muscle spindles seems to be that of accelerating the firing of the motor neurons during the initial phase of a central excitation command (Matthews 1964). The afferent neuron originating in the receptor organs of the spindle and ending in excitatory synapses on the soma and dendrites of the motor neurons (or of neurons which in their turn terminate on the motor neurons) transmits a train of action potentials the frequency of which depends on how much and how quickly the spindle is stretched either because of passive stretching of the muscle or because of active contraction of the spindle itself through excitation of its motor neuron. Ohman 1967, p.41

Ohman, reporting findings by v. Euler (1966) and Leksell (1945) mentions that central commands are usually sent to most of the innervatory motor neurons including those of the muscle spindle. Since some of the smallest fibres in the efferent nerve are spindle motor neurons these will respond early to the command. "Consequently, the muscle spindles will start contracting earlier than the majority of the extrafusal fibres." (1967 p.41) Stretch will occur in the spindles and the receptor organs will be activated transmitting a discharge to the extrafusal fibre motor neurons, thus adding an excitatory synaptic current (i.e. not originating from higher command centres) to the command already descending to the extrafusal fibres. Thus the motor neuron firing frequency increases during the initial phases of a contraction and will be higher than it would have been without the gamma loop system.

Ohman is using the model to account for variations in EMG measurements for ‘same’ phonemes in varying contexts. Cooper (1966) suggested that the gamma loop system might play an important role in speech because this particular model provides a very convenient solution to the problem of how the articulators can approximate a fairly constant target position and predictably miss that target position according to context (Ohman 1964, 1966 etc.; et a.). Such a servo system providing information on the state of muscles prior to the particular phoneme, added to the oncoming relatively constant a-neuron command caters for otherwise insoluble context effects. MacNeilage and Declerk (1967) suggest that the gamma loop model might adequately account for some left-to-right effects they observed in a series of EMG experiments, where variations in the EMG of a particular phoneme gesture were predictable from the gesture of the preceding phoneme.

It is clear that if muscle spindles are subject to the voluntary (and we assume for the moment, relatively stable and constant) downward command earlier than the extrafusal fibres then by the time the extrafusal fibres begin to contract they will be receiving not only that voluntary command but also a modifying command bearing information about their present state. Any overshoot or undershoot will be due to time lags in servo operation or sheer inability of the muscle to reach targets due to inertia or mass — not due to a different context-sensitive alpha command from the motor centre. This is a convenient hypothesis that awaits testing.

Elaborating on this basic model, let us posit the entire working as follows: a particular vocal tract configuration is required for uttering one particular phoneme (at the moment in isolation); this will involve the positioning of certain speech organs and require activation of certain muscles associated with these organs. Some of these muscles will be antagonistic. Let us consider just one muscle. It is ‘known’ by the motor control centre what degree of contraction is required by this muscle given that it is a neutral position to achieve movement of the organ to the desired position. Descending fusimotor neurons provide fast information regarding the equilibrium point for the muscle contraction. Possibly simultaneously delivered (but arriving later) commands arrive at the extrafusal fibres. These have been mixed with a signal from the sensors of the spindles modifying them

- with respect to the previous ‘posture’ of the muscle (in this case neutral),
- with respect to the reaching and maintaining of the set desired value of contraction.

In addition the initial movement from neutral will be greater because of the additive effect of the alpha command and the gamma loop signals.

In the case where the particular phoneme exists in context — does not start its gesture from the neutral position — signals from the muscle spindles will already be indicating the mechanical state of the muscle before the commands for this new gesture are delivered; both signals will mix in the normal way. Missing of target position may be the result of inertia of the mass of the organ being moved; *despite* the gamma loop servo system and the use of fusimotor fibres to signal in advance the desired contraction of the muscle, because of the lack of time the target is missed. We shall now see that there is evidence that in the case of right-to-left influence it may be necessary to take into consideration other factors.

MacNeilage and Declerk (1967) refer to the suggestion made by Jung and Hassler (1960) that "impulses leading to readiness of the peripheral motor system could be initiated over extensive connections between ‘psychomotor levels’ (such as Broca’s Area) and the substantia nigra, a brain stem nucleus". Normally any intention of moving will produce an increase of muscular tone. Ohman (*op. cit.*) points out that central commands to the peripheral circuits can be divided into different types of differing function. Control of posture (muscle tone) seems to be under the charge of a separate system (Lundberg 1966) which at least to a certain degree functions *via* the spindle neural inputs. As referred to above, posture in skeletal muscles involving comparatively slow changes in these muscles, which are generally set antagonistically, involves a balanced contraction under the control of the muscle spindles. EMG data presented by Ohman support the hypothesis that immediately prior to speaking a *basic speech posture* is set up involving a steady tonic activity in some muscles (Ohman mentions specifically m. levator labii superioris).

MacNeilage and Declerk (*op. cit.*), extending Jung and Hassler are in agreement. "It is conceivable that ... somewhat more specific [than in general posture control ‘anticipatory’ modifications in amount of muscle contractions for a phonemic command could be produced during the previous phoneme or representation." (p.25) They suggest that a greater amount of anticipatory contraction in a particular muscle may be observed by EMG when the following ‘invariant phoneme command’ will involve greater contraction for that muscle — i.e. amount of anticipatory contraction and amount of required contraction for a given phoneme are directly proportional.

Furthermore, it is perhaps not too far fetched to believe that a phoneme command could partly consist of an inhibitory component directed to muscles antagonistic to the movement it requires. If so, the anticipatory action could consist also in inhibition of some muscles in proportion to the hindrance their contraction imposes on the later movement. MacNeilage and Declerk *op. cit.* p.25

Thus, if it is true that changes in degree of muscle contraction cause a variation in the amount of anticipatory contraction preceding the contraction proper, then this would overlap in a right-to-left direction on to the preceding phoneme gesture. One would expect therefore a greater (or different) EMG signal for orbicularis oris for /b/ in /bu.../ than in /bo.../ than in /bi.../ etc. MacNeilage and Declerk’s data point towards this and likewise similar results in Harris, Lysaught and Schvey (1965), Ohman (1967), Tatham and Morton (1968b). Researchers differ considerably in the degree of difference in the two signals but most agree that there is a small but recognisable and fairly consistent right-to-left effect in such cases.

Fromkin (1965) however states:

> For the bilabial stops /b/ and /p/ different motor commands produce different muscular gestures for these consonants occurring in initial position and in final position. There is, however, an apparent invariance in the gestures which produce the allophones of these phonemes. In other words the neuro-muscular characteristics of /b/ in initial position in an utterance were found to be relatively identical regardless of the vowel which followed. Fromkin 1965, p. 161

Tatham and Morton (1968a) infer from their data that "there is a marked similarity for amplitude and durational measurements for the orbicularis oris muscle action ... irrespective of vowel context ..." (p.20); this was later corrected (1968b): "... variations are quite small and not significant in a sample of this size but are relatively stable and worth noting" (p.44).

Thus there are at least two ways in which a right-to-left effect can occur: signals from the phoneme command proper may cause the muscle spindles to react before the extrafusal fibres, causing a slight contraction during the offset of the previous phoneme and modifying the observable EMG signal for that phoneme; or there may be a special mechanism setting up a basic posture to receive the command for the phoneme proper — this increased tonic activity will be superimposed on the preceding phoneme gesture. There is also the possibility that these two mechanisms may operate together.

However, it is quite possible that both these explanations of right-to-left effects may be (or amount to) one and the same thing. There is a certain amount of evidence (Gårding 1967, Ohman 1967, Chomsky and Halle 1968, etc.) that the basic speech posture (approximating to the neutral vowel [s]) can be detected before and after an utterance (Gårding shows this as an inference from the acoustic waveform during juncture phenomena) and it is suggested by Ohman that the gestures of speech proper can be regarded as superimposed upon this posture which obtains during the whole length of the utterance (utterance boundaries are undefined). I infer that Ohman does not want, as I do not, to make this notion of basic speech posture language-specific.

If this 'carrier and modulation' effect is a true statement, then Gårding's finding of a tendency toward the neutral vowel at a juncture (also observable in the data of Lehiste 1959) is to be expected. Where, for some linguistic reason, delivery of phoneme commands is suspended, one would expect the basic speech posture to be left unmodulated for a certain length of time (Tl) followed by a setting up of that posture again for a certain time (T2) before the next phoneme delivery. If the context was such that the gap between the pre-juncture phoneme gesture and the post-juncture phoneme gesture were less than Tl + T2 then there would be a continuous holding of the neutral position of the articulators.

The gamma efferent mechanism setting up muscle posture proportional to the motor command for the following contraction coupled with the gamma loop servo mechanism reporting on the mechanical state of the muscle during this assumption of the basic speech posture and during the subsequent gesture, and at the same time allowing the balance point of the stability of the entire system to be regulated, constitutes a powerful model of the control and organisation of speech gestures. The model is comparatively simple in conception, but would be complex in operation. 'There seems to be no contradictory evidence in the recent available neuro-physiological literature.

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