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RE-EVALUATION OF RESPIRATORY REFLEXES.

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In cats anæsthetized with chloralose it was found that below about 18° C. the rhythmic pattern of discharge in low-threshold pulmonary stretch fibres is reversed in relation to the respiratory cycle. This reversed pattern is apparently responsible for the reversal of the Hering Breuer inflation reflex (Head's paradoxical reflex). Evidence favouring this is that reflex inhibition of respiration, produced by high frequency electrical stimulation of pulmonary stretch fibres applied against a background of low frequency stimulation, is converted to excitation between 9 and 11° C. Head's paradoxical reflex appears when the total discharge in low- and higher-threshold pulmonary fibres during inflation becomes less than the total discharge in the former before inflation. A nomogram showing the relation between temperature and the peak frequency of a train of impulses in fibres of different conduction velocities is presented. The likely mechanism responsible for the quantitative variation of the inflation reflex (and its reversal) with temperature is given.

SOME of our present concepts [*cf.* Aviado and Schmidt, 1955; Widdicombe, 1964; Wyss, 1964] regarding the reflex effects of cardio-respiratory and cardiovascular afferent fibres have arisen from experiments in which the vagus was cooled to various temperatures [Head, 1889; Hammouda and Wilson, 1935 *a*; 1935 *b*; Partridge, 1939; Whitteridge and Bülbring, 1944; Hammouda *et al.*, 1943; Torrance and Whitteridge, 1948; Dawes *et al.*, 1951; Widdicombe, 1954 *a*; 1954 *b*; 1959]. The conclusions in the more recent of these studies (from 1948 onwards) have rested on the tacit or stated assumption that faster conducting fibres are blocked at higher temperatures than the slower fibres. No experimental support for this assumption has been obtained so far. On the other hand, in a recent paper it has been demonstrated conclusively that (apart from individual variations) conduction in all medullated fibres is blocked at about the same temperature of about 8° C. regardless of conduction velocity [Paintal, 1965 *a*; 1965 *b*]. Other relevant and important new findings are (1) that the absolute refractory period (ARP) of nerve fibres varies inversely with their conduction velocities, *i.e.* fibre diameter [Hursh, 1939]; (2) the maximum frequency of a train of impulses that can be conducted in a fibre without any block is determined by the ARP after the second (or subsequent) impulse; and (3) that under appropriate conditions total block of a train of impulses can occur if the frequency of discharge is greater than this maximum transmissible frequency [Paintal, 1965 *b*].

In view of these findings it follows that our concepts regarding the effect of temperature on reflex effects in relation to the sensory input need to be reconsidered. The present paper provides an interesting example for this need. It demonstrates that Head's paradoxical reflex [Head, 1889] can be

attributed entirely to the reversed pattern of activity in low-threshold pulmonary stretch afferent fibres at cold temperatures without postulating a different set of fibres for this reflex response. In fact, Head's paradoxical reflex must be regarded as a 'physiological artifact'.

Throughout this paper the afferent fibres of pulmonary stretch receptors identified in the usual way with intact chest [Adrian, 1933] will be referred to as pulmonary stretch fibres. This definition includes fibres from slowly adapting bronchial receptors, because as pointed out recently [Paintal, 1963], there is no means of distinguishing the slowly adapting bronchial receptors of Widdicombe located in the main bronchus [Widdicombe, 1954 *a*] from those located in the intra-pulmonary bronchi apart from the actual location of the ending itself.

The basic assumption made in the present paper is that the Hering Breuer inflation reflex is produced by the activity in pulmonary stretch afferent fibres, an assumption that is generally accepted [Widdicombe, 1964; Wyss, 1964].

Methods

Experiments were carried out on adult cats anæsthetized with chloralose (75 mg./kg., i.v.). The methods of isolating filaments containing pulmonary stretch afferent fibres, recording their impulses and determining their conduction velocities were

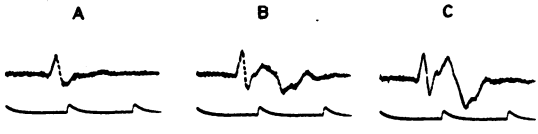

Fig. 1. Compound action potentials of the intact cervical vagus recorded diphasically (inter-electrode distance = 3 mm.) near the nodose ganglion. A shows the fastest component, with a conduction velocity of 79 m/sec. (corrected to 37° C.); the stimulus strength was 0·08v. In B, the stimulus strength was increased to 0·2 v (just above threshold for second component) and it shows the presence of the second component with a maximum conduction velocity of 61 m/sec. (at 37° C.) which can be attributed to pulmonary stretch fibres. C shows the response when the stimulus was increased to 0·35 v (2 × threshold for 2nd component); the conduction velocity of the slowest fibres activated was 32 m/sec. (at 37° C.). Average temperature of the vagus in the above experiment was 35° C.

identical with those described initially [Paintal, 1953]. For cooling a stretch of the vagus, the technique of immersion cooling was used [Paintal, 1965 *a*]. The length of nerve cooled was roughly 12 mm. The temperature of the cooled nerve was measured with a thermocouple and galvanometer, which provided readings correct to 0·1° C.

For studying reflex respiratory responses in three cats, both vagi were cut and the central end of the right vagus was stimulated at the lower end of the neck with trains of stimuli of known frequency. The stimulus intensities used were 2 to 2·5 times the threshold strength required to generate the second component (pulmonary

stretch fibres) of the compound action potential recorded diphasically near the nodose ganglion (fig. 1B). The first component (conduction velocity, 67–79 m/sec.) shown in fig. 1A was ignored since it is produced by motor fibres of the vagus [*cf.* Paintal, 1963]. Since the maximum conduction velocity of the second component ranged from 51 to 61 m/sec. in the three experiments, it can be safely attributed to the largest diameter afferent fibres, namely the pulmonary stretch fibres [Paintal, 1953; 1963]. At the stimulus intensities used, the conduction velocities of the slowest fibres stimulated were about 33 m/sec. (fig. 1). This means that in addition to the pulmonary stretch fibres, some fibres from arterial baroreceptors and rapidly adapting tracheal receptors must also have been stimulated [Paintal, 1953]. Considering the mean and range of conduction velocity of the latter, and the fact that there are relatively few of them [Paintal, 1953], it was assumed that they contributed little to the net reflex effects observed. Therefore, in view of the fact that the reflex respiratory effect of arterial baroreceptors is the same as that of pulmonary stretch receptors [*cf.* Aviado and Schmidt, 1955; Heymans and Neil, 1958] namely respiratory inhibition, it can be safely assumed that the reflex effects observed in the present experiments were produced by fibres causing respiratory inhibition, the majority of which are pulmonary stretch fibres.

The intrapleural pressure was recorded with a pressure transducer. It served as an index of respiration.

For studying the effect of relatively high frequency stimulation, applied during one breath on the same breath, the stimulator was triggered as soon as the intrapleural pressure started falling (fig. 7); stimulation lasted as long as a normal breath (2·4 sec. in the case of fig. 7). The maximum delay between the onset of inspiration and beginning of tetanization was of the order of 50 msec.

Results

The pulmonary stretch fibres were divided into two categories, low-threshold fibres and higher-threshold fibres. The former fired impulses during the respiratory pause in addition to their characteristic discharge during inspiration (figs. 2 and 3); the latter discharged impulses only during inspiration.

As expected, it was confirmed that the threshold of inflation for stimulating the low-threshold fibres was, in the majority of fibres, slightly less than that for the higher-threshold fibres. In higher-threshold fibres the threshold was determined by noting the level of intrapleural pressure at which the discharge started during spontaneous inspiration. In low-threshold fibres the intrapleural pressure at which the discharge started increasing was taken as the threshold. However, no quantitative values for threshold can be given because the intrapleural pressure was not calibrated against the volume of air inspired.

Reversal of Rhythm in Low-threshold Pulmonary Stretch Fibres. – As the fibres are cooled to lower and lower temperatures the peak frequency of discharge in them becomes less and less until total block occurs. Below 20° C. impulses start dropping out during inspiration or inflation (fig. 2B) and this becomes more marked as the temperature is lowered further. However, the most interesting observation made was that between 18 and 10° C., the rhythmic pattern of activity in low-threshold pulmonary stretch fibres was reversed in relation to the respiratory cycle, *i.e.* the activity was more during the respiratory pause than during inspiration or inflation (fig. 2). For studying

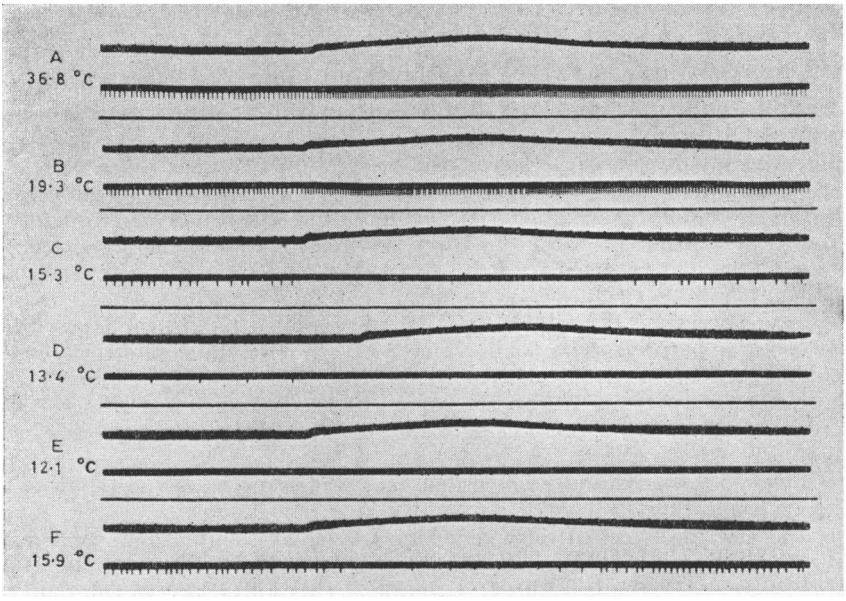

FIG. 2. Reversal of rhythmic activity in a low-threshold pulmonary stretch fibre at low temperatures. A, shows the typical pattern of discharge in the fibre with increase of activity during inflation of the lungs (rise in intra-tracheal pressure, upwards). In B, at about 19·3° C., there is some dropping out of impulses. In C, there is clear reversal of the rhythm with silence during inflation of the lungs. In D, the reversal is still present at 13·4° C. In E, there is complete block of the discharge at 12·1° C. In F, on rewarming to 15·9° C., the reversed pattern of discharge reappears. The fibre regained its normal pattern at higher temperatures (not shown). The conduction velocity of the fibre was 47 m/sec.

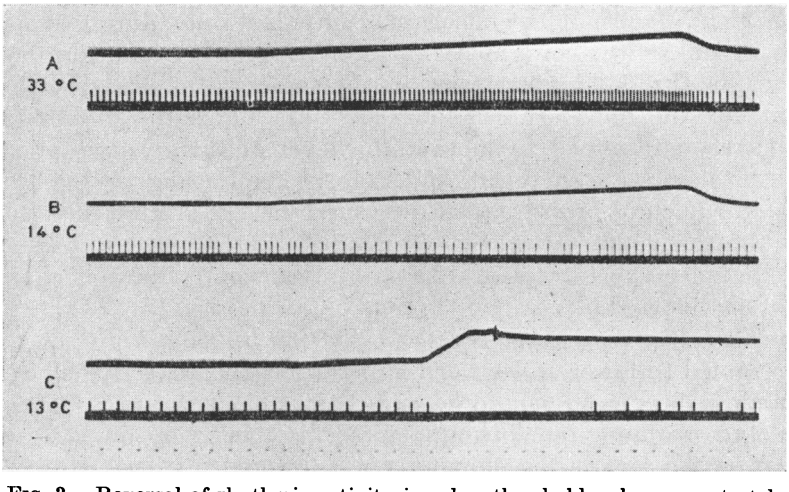

FIG. 3. Reversal of rhythmic activity in a low-threshold pulmonary stretch fibre. A, shows the normal pattern of activity recorded at 33·2° C. In B, there is clear evidence of reversal (although not conspicuous) since there is a reduction in the frequency of discharge during inflation of the lungs. In C, inflation of the lungs rapidly with 130 ml. silences the pre-inspiratory discharge for some time. The conduction velocity of the fibre was 40 m/sec.

this reversal systematically, the cat was ventilated with a respiratory pump using a constant volume of air, and the pattern of discharge examined at different temperatures in twelve low-threshold pulmonary stretch fibres. In all twelve of them reversal of rhythm was observed at some range of temperature between 10 and 18° C. In some the reversal was dramatic (fig. 2C) and in others just noticeable (fig. 3B).

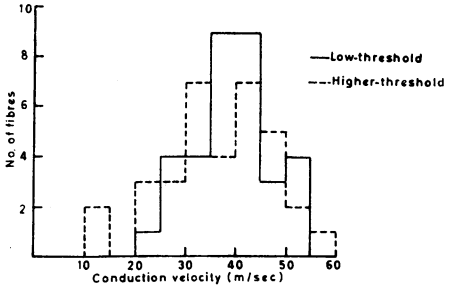

FIG. 4. Frequency distribution of the conduction velocities of low-threshold and higher-threshold pulmonary stretch fibres. Total number of fibres in each group, 34.

It is obvious that there can be no reversal of rhythm in the higher-threshold pulmonary stretch fibres. In view of this difference in the behaviour of low- and higher-threshold fibres at low temperatures it was considered necessary to get an estimate of the relative number of low- and higher-threshold fibres. This was done by recording impulses in every pulmonary stretch fibre isolated at random in two cats breathing spontaneously. In the first cat out of thirty-eight fibres, sixteen (42 per cent) were higher-threshold fibres and twenty-two (58 per cent) low-threshold fibres. In the

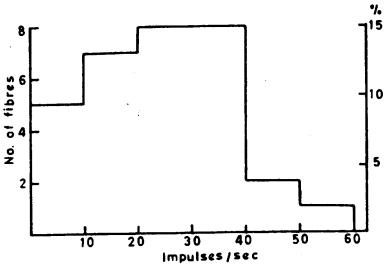

FIG. 5. Frequency distribution (ordinates) of the pre-inspiratory frequency of discharge (abscissa) in thirty-one low-threshold pulmonary stretch fibres sampled at random. The ordinate on the right gives the percentage values expressed as a percentage of all (53 in the present sample) pulmonary stretch fibres (low- and higher-threshold). Note that the fibres with a pre-inspiratory frequency of discharge less than 30 impulses/sec. constitute about 35 per cent of all pulmonary stretch fibres.

second cat, out of twenty-two fibres, the figures were respectively nine (41 per cent) and thirteen (59 per cent). In view of the similar results obtained in these two cats no further experiments of this sort were done. It can be concluded that roughly about 60 per cent of the pulmonary stretch fibres are low-threshold ones and about 40 per cent higher-threshold ones. These relative values apply to the prevailing experimental conditions, such as position of the cat and amount of tone in the respiratory muscles, *i.e.* functional residual capacity which determine the amount of activity during the respiratory pause. In the present experiments the cat was positioned on its back.

The low-threshold group includes some fibres with a perceptible but inconspicuous cardiac rhythm which was abolished during inspiration or inflation of the lungs. Pulmonary fibres with a prominent cardiac rhythm (which are relatively rare) that persists during inflation or inspiration [Bianconi and Green, 1959] were excluded.

Conduction Velocities. – There is no difference in the conduction velocities of the two groups of fibres as shown by the distribution of their conduction velocities and the overlap of the two in fig. 4. This figure has been plotted from thirty-four fibres of each group. Moreover, the mean conduction velocity of the higher-threshold fibres, which is 37 m/sec. (range 14–58; S.E. 1·8) is similar to the mean conduction velocity of the low-threshold fibres, which is 39 m/sec. (range 22–54; S.E. 1·4).

Pre-inspiratory Frequency of Discharge in Low-threshold Fibres. – It is important to have an estimate of the total discharge in low-threshold pulmonary stretch fibres reaching the respiratory centre during the respiratory pause. For making this estimate, only the fibres isolated at random in the two cats mentioned above were used. In each fibre, the frequency of discharge just before a spontaneous inspiration, was determined by counting the number of impulses in 0·5 sec. The results so obtained are shown in fig. 5, which gives the frequency distribution of low-threshold fibres with various pre-inspiratory frequencies of discharge in thirty-one fibres isolated at random. Fig. 5 shows that about 35 per cent of all pulmonary stretch fibres have a pre-inspiratory discharge frequency of less than 30 impulses/sec. This information is of value for interpreting the reflex effects of inflation of the lungs observed at low temperatures.

Reflex Responses. – After making the observations on the reversal of the rhythmic pattern of discharge described above (figs. 2 and 3), it was conjectured that the reversal of the inflation reflex (*i.e.* Head's paradoxical reflex) was probably due to this reversal of the respiratory rhythm in low-threshold fibres. The following experiments on reflex respiratory responses were therefore designed to mimic the conditions obtaining during natural stimulation. Accordingly, low frequency repetitive stimulation was applied at 10–20 stimuli/sec. to correspond to the pre-inspiratory discharge, and this was followed by high frequency stimulation at 100–200/sec. to correspond to the discharge during inflation of the lungs.

With low frequency stimulation (10–20/sec.) respiratory inhibition occurred at all temperatures down to about 7° C. (fig. 6) although below 10° C. the inhibition was reduced a little, especially when the frequency used was 20/sec. On increasing the frequency of stimulation suddenly from 10–20/sec. to 100–200/sec. the inhibitory reflex effect was clearly increased at all temperatures down to about 16–18° C. (fig. 6). Lowering the temperature below 16–18° C. gradually reduced the added inhibitory effect of high frequency stimulation applied in this manner until a temperature was reached, usually about 14° C., when no change was produced by it. Below 14° C. there was reversal of the response, *i.e.* high frequency stimulation now tended to reverse the effect of *low* frequency stimulation. This effect was best obtained between

9 and 11° C. in all three cats. A typical experiment is shown in fig. 6. At about 11° C. the reversed response was much reduced except in one cat in which it was visible at 15° C.

In the present results the effects of high frequency stimulation have been evaluated against the background of low frequency stimulation (fig. 6). The responses of the former in isolation were not studied because this would amount to evaluating the resulting responses in relation to the unknown (but

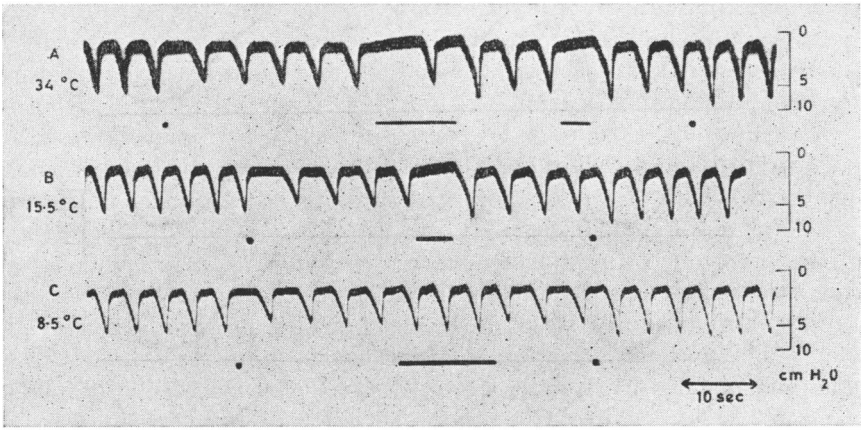

FIG. 6. Reversal of inhibitory reflex. The beginning of each of the three records shows the control respiratory movements (I.P.P.) with both vagi cut and without any added stimulus. At the first signal in each record, repetitive stimulation at 10/sec. of the central end of the right vagus was begun. At the next signal the frequency of stimulation was suddenly increased to 100/sec. This relatively high frequency stimulation lasted as long as the signal. At the end of this signal the frequency of stimulation was put back to 10/sec. Finally, at the last signal, the 10/sec. stimulation was turned off. In A, at 34° C., high frequency stimulation was applied for a second time at the third signal. B, shows that the inhibitory effect produced by high frequency stimulation at 15·5° C. was no less than that in A. In C, the reflex response to high frequency stimulation is reversed. This corresponds to Head's paradoxical reflex. Note that application of 10/sec. stimulation at first signal at each temperature causes inhibition of respiration, and its withdrawal at the last signal results in return of respiration to normal.

possible) injury discharges arising at the cut central end of the vagus. In the present experiments, the injury discharges, if present, have been, as it were, excluded by making them a common factor in the respective responses to low- and high-frequency stimulation. This should be kept in mind when comparing the present results with those of earlier workers, *e.g.* Hammouda and Wilson [1935 *a*]. Comparison with their results would be inappropriate because they [Hammouda and Wilson, 1935 *a*] studied the effect of repetitive stimulation of one vagus while the other was intact.

Results similar to those described above were observed on application of superimposed high frequency stimulation during a single breath (fig. 7). In this experiment repetitive stimulation at 15/sec. was applied continuously. This caused respiratory inhibition of the kind shown in fig. 6 with low frequency stimulation (not shown in fig. 7). Application of superimposed high

frequency stimulation at 200/sec. once again reversed this inhibitory effect of low-frequency stimulation at 11° C. (fig. 7C). Comparing fig. 7B with 7C it is possible to conclude that in this experiment the added inhibitory effect of high frequency stimulation (fig. 7A and 7B) or reversal would be absent at about 11·5° C.; such behaviour would be interpreted as block of the Hering Breuer inflation reflex.

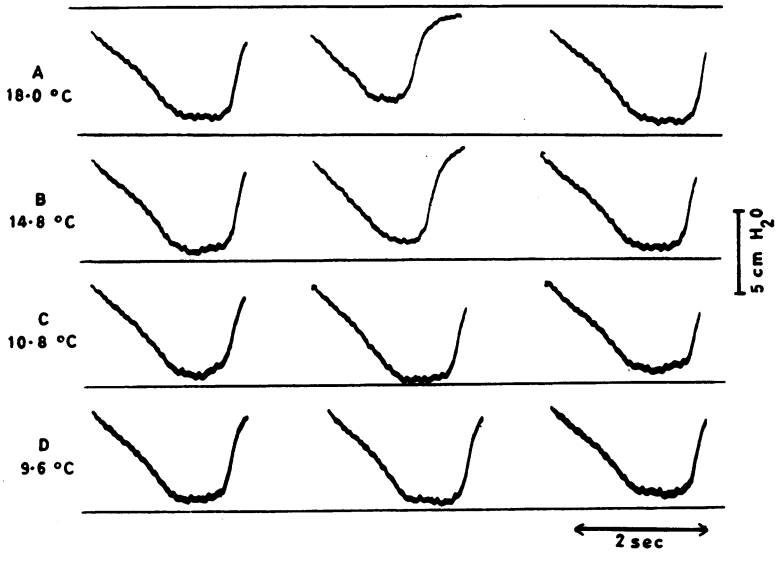

FIG. 7. Effect of high frequency stimulation (superimposed on low frequency stimulation) on a single breath as shown in records of intra-pleural pressure (inspiration downwards). Continuous repetitive stimulation at 15/sec. was started before the above records were taken. The 1st and 3rd series of sweeps in each set (A–D) show breaths in the presence of this low frequency stimulation. The middle series of sweeps show the breath with superimposed high frequency stimulation at 200/sec. that was applied at the beginning of each sweep; this stimulation lasted as long as the sweep. Note that the inhibitory effect (*i.e.* reduced amplitude of breath) of high frequency stimulation in A and B is reversed in C at 10·8° C. (Head's paradoxical reflex). This reversal is reduced at 9·6° C. in D. The calibration on the right is for the intrapleural pressure. The upper four horizontal dividing lines correspond to −1·0 cm. H_2O pressure for the respective traces.

The reversal of the inhibitory effect of high frequency stimulation at low temperatures shown in figs. 6 and 7 can be explained if the impulses reaching the respiratory centre during high frequency stimulation are less than those reaching it during low frequency stimulation alone. This is to be expected from what is already known about block of a high frequency discharge of impulses (Paintal, 1965 *b*) (*cf.* Discussion).

Maximum Transmissible Frequency through Cooled Vagus. – For the interpretation of reflex responses at different temperatures shown above (figs. 6 and 7), it is important to have information about the maximum frequency of discharge that can pass unblocked through a region of cooled nerve at different

temperatures and in fibres of different conduction velocities. This information is now available and is given in fig. 8. This figure is based on the knowledge that the maximum transmissible frequency of a train of impulses through a cooled stretch of nerve depends on the ARP after the second impulse or subsequent impulses [Paintal, 1965 *b*]. Therefore the peak frequency of discharge will be the reciprocal of the ARP after the second impulse.

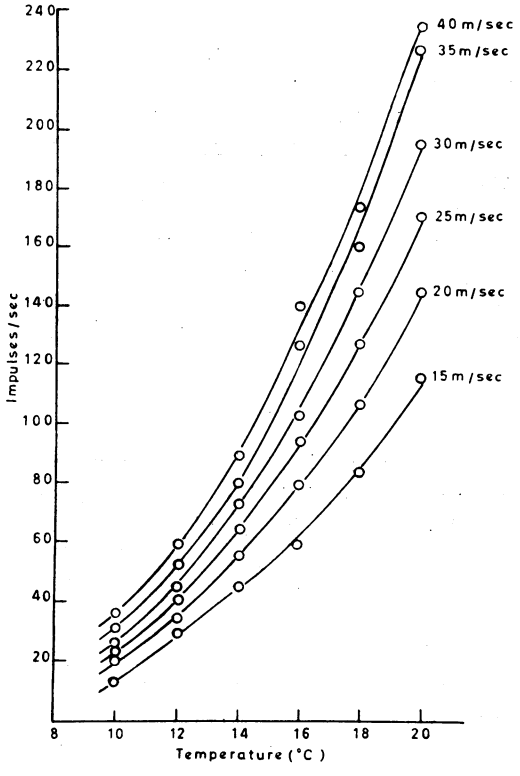

FIG. 8. Graphs showing the relation between maximum frequency of discharge of a brief train of impulses that can pass unblocked between 10 and 20° C. in fibres of different conduction velocities. The data for this figure were obtained from the results of an earlier investigation [Paintal, 1965 *b*].

The data for fig. 8 were obtained from fig. 8B and C of an earlier paper [Paintal, 1965 *b*] and also from some unpublished information connected with that figure (*i.e.* values at temperatures other than those shown in that paper). The blocking temperatures of the fibres ranged between 6·2 and 8·2° C. As a rough approximation it was assumed that the ARP after the second impulse was about 25 per cent greater than the ARP after the first impulse. This approximation was derived from the relative values of the ARP after the first and second impulses shown in fig. 6B and 8A of the earlier paper [Paintal, 1965 *b*]. In addition an arbitrary allowance of 5 per cent

was made for the likelihood that the ARP after the second impulse immediately after the ARP following the first impulse [*cf.* figs. 6B and 8A Paintal, 1965 *b*] would be a little greater than the ARP after the second impulse if a train of constant frequency is used for determining the ARP after the second impulse. This would result in the second impulse falling clearly after the ARP following the first impulse so that it would have recovered its amplitude to a greater extent [Paintal, 1966]; this would tend to reduce the ARP after this (second) impulse.

The results in fig. 8 pertain to the maximum transmissible frequency obtained with brief trains of stimuli lasting a fraction of a second. With longer trains the actual maximum transmissible frequency becomes a little less. Small fluctuations in temperature may be partly responsible for this. It should be remembered that the peak frequency will also depend on the blocking temperature of the fibres, the higher the blocking temperature, the lower the peak frequency for a particular temperature [*cf.* Paintal, 1965 *b*].

It should be noted that the peak frequencies shown in fig. 8 are different from the peak frequency relating to the first impulse interval [*cf.* fig. 9B in Paintal, 1965 *b*] which depends on the length of cooled nerve.

Discussion

It is now possible to give a suitable explanation for the reversal of the effect of high frequency stimulation at 9–11° C. Fig. 4 shows that the conduction velocities of most of the low-threshold pulmonary stretch fibres are above 30 msec. Fig. 8 shows that in such fibres a train of impulses at 30/sec. or less should pass through the cooled nerve at 10° C. without any of its impulses getting blocked. This is consistent with the fact that respiratory inhibition appears on application of stimuli at 10–20/sec. at 10° C. and disappears on its withdrawal (fig. 6). On now increasing the stimulation to 100–200/sec., the total number of impulses passing the cooled nerve will be considerably reduced because the discharge, as shown already [Paintal, 1965 *b*], is either blocked completely or reduced considerably. Therefore, since the total number of impulses passing the cooled region during high frequency stimulation will be less than that passing it during low frequency stimulation, it follows that reversal of the effect of high frequency stimulation must result, as has been consistently observed in the present experiments (fig. 6).

Mechanism Underlying Head's Paradoxical Reflex. – In view of (1) the results showing the reversal of the rhythmic pattern of discharge in low-threshold pulmonary stretch fibres (figs. 2 and 3) and (2) the mechanism responsible for the reversal of reflex effect of high-frequency stimulation outlined above, it follows that Head's paradoxical reflex must be due to the fact that at low temperatures of about 9 to 11° C., the discharge in pulmonary stretch fibres (taken as a whole) is less during inflation than before it.

The Hering Breuer reflex will be abolished when the input during inflation is the same as that before inflation. At what temperature this occurs must vary from experiment to experiment just as Head's paradoxical reflex

[Widdicombe, 1954 *b*], and so it is not surprising that the inflation reflex is sometimes abolished before Head's reflex and sometimes at a lower temperature than Head's reflex [Widdicombe, 1954 *b*] (see also fig. 9).

In view of these considerations, it is also possible to provide an explanation for the inhibitory reflex that appears after Head's paradoxical reflex is blocked [Widdicombe, 1954 *b*]. This reflex response at low temperatures (of about 6° C.) might well be due to the passage of a relatively greater number of impulses during inflation than before inflation. However, there are non-medullated fibres that can be stimulated briefly by large inflations of the

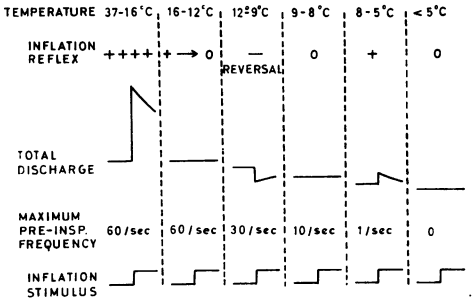

FIG. 9. Schematic diagram summarizing the changes in the inflation reflex with fall in temperature. The total discharge (series of curves in the middle) relates to the total discharge in both low- and higher-threshold pulmonary stretch fibres; these curves show schematically the discharge before and during inflation of the lungs. Between 16 and 12° C. the inflation reflex is either weak (+) or is absent (0). Between 12 and 9° C. there is reversal in the discharge which is accompanied by a reversal of the reflex (Head's paradoxical reflex). Below about 8° C. the inflation reflex reappears but it is weak and short-lived [*cf.* Widdicombe, 1954 *b*]. Note that the maximum pre-inspiratory frequency of discharge between 37 and 16° C. is 60 impulses/sec. because this is about the highest frequency of discharge in the low-threshold pulmonary stretch fibres (fig. 5).

lungs [Coleridge *et al.*, 1965; Paintal, unpublished observations] and these must be kept in mind even though their rôle in the production of the reflex is likely to be small owing to their inconstant responses and the fact that they are stimulated only by hyperinflation of the lungs.

Thus the variations in the relative amount of discharge of impulses (in the two groups of pulmonary stretch fibres) before and during inflation can account for the entire series of reflex responses to inflation between normal body temperature and 5° C. when block of conduction in all medullated nerve fibres is nearly complete [Paintal, 1965 *a*]. These series of responses are summarized schematically in fig. 9. Between 37 and 16° C., because the total discharge in pulmonary stretch fibres is greater during inflation than before it, there results a strong inhibitory reflex. Between 16 and 12° C., the inflation reflex is suppressed because the total discharge is the same before as during inflation. On lowering the temperature still further, there is reversal of the inflation reflex (Head's paradoxical reflex) between 12 and 9° C. Just below 9° C. inflation once again produces no effect because, once again, the total discharge during inflation is the same as that before inflation. Thereafter, between 8 and 5° C., the inflation reflex reappears, because even though the total discharge is greatly reduced at this temperature, it is, nevertheless greater during inflation than before inflation, since the total number of fibres active during inflation is more than that active before inflation.

Finally, below 5° C. all reflex responses are abolished because of complete block in the fibres. An appreciable overlap in the ranges of temperature shown in fig. 9 is to be expected because of variations in experimental conditions from one animal to the next.

In the assessment of the discharge passing a cold block it must be remembered that as far as discharge frequencies greater than the maximum transmissible frequency is concerned, the discharge emerging through the block does not follow any fixed rule, partly owing to the variations and uncertainty about the behaviour of the transition zone. Thus it is not rare for a relatively low frequency (albeit greater than the maximum transmissible frequency) to be completely blocked while allowing some impulses of a still higher frequency train of impulses to pass through [*cf.* fig. 13 in Paintal, 1965 *b*]. As demonstrated recently, this is due to the production of abortive spikes during the ARP [Paintal, 1966].

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