HABITUATION OF EXTEROCEPTIVE SUPPRESSION AND OF EXTEROCEPTIVE REFLEXES IN MAN AS INFLUENCED BY VOLUNTARY CONTRACTION

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(Accepted September 15th, 1975)

SUMMARY

Habituation kinetics were found to vary considerably in different polysynaptic pathways of the brain stem in man. The exteroceptive reflex of the digastric muscle habituates markedly, even for stimuli repeated at 1-min intervals. The second component of the blink reflex habituates for intervals below about 8 sec, but this can largely be prevented by steady voluntary contraction of the muscle. On the other hand the exteroceptive suppressions of the masseter muscle only disclose slight habituation of their late component ES₂ and no habituation of the early component ES₁. This does not appear to be affected by voluntary activation since the suppressive effects present the same pattern in relaxed masseter muscles tested by proprioceptive reflex activation. Exteroceptive reflexes and exteroceptive suppressions of similar latencies disclose genuine and important differences in their habituation kinetics.

INTRODUCTION

Habituation or reversible muscle response decrement as a result of repeated stimulation is a prominent feature of the reflexes tested in animals, except for the monosynaptic tendon reflexes and it is supposed to occur in the course of transmission through interneuronal pathways^{14,17}. Polysynaptic reflexes elicited by exteroceptive stimuli (exteroceptive reflexes, abbreviated ER) are markedly susceptible to habituation in man, for example the abdominal reflexes⁵, the blink reflexes¹⁵ and the biceps femoris reflexes⁷. By contrast, exteroceptive suppressions (ES) appeared to disclose little, if any, habituation^{2,3,19}. This raises a question namely because the late component of ES has been shown to involve a polysynaptic pathway³ and should therefore be expected to present habituation.

It must be pointed out that ES are generally tested in man on voluntarily contracted muscles since a background of activity is required to demonstrate the inhibitory effect. The apparent contrast in the habituation features of ER and ES could therefore be thought to result from the respective experimental conditions used, and namely from the voluntary influence on the interneuronal pathways involved in ES. Lundberg and Voorhoeve¹¹ have indeed demonstrated pyramidal excitatory effects in cat spinal interneurons of various reflex arcs, including those activated from the skin⁹⁻¹¹. The present paper investigates habituation effects of ER and ES, with and without voluntary innervation of the tested muscles. It emphasizes the differential susceptibility to habituation of various brain stem reflex pathways in man.

MATERIAL AND METHODS

Fifteen normal unpaid volunteers of either sex, between 20 and 28 years old, with no signs as history of neurological disease were submitted to one or several recording sessions. They received no sedation. The general produces were similar to those described previously³. Electromyographical (EMG) potentials were recorded with unvarnished 0.3 mm diameter stainless steel needles inserted subcutaneously over appropriate muscles (belly-tendon recording): masseter, digastric or lower part of orbicularis oculi muscles. The potentials were displayed on a 565 Tektronix cathode ray oscilloscope. They were also electronically rectified and digitized (9 bits accuracy, 200 μ sec bin width) and averaged with a 1074 Nicolet computer. The zero reference for the write-out was obtained by automatically short-circuiting the input for the last 30 msec of the computer sweep³. When necessary, the EMG potentials elicited by a tendon tap were rectified and integrated with a home made circuit involving a Philbrick n° 470501 V/F converter. Activation of various exteroceptive inputs was done by delivering square electrical pulses of 0.5 msec through stainless steel needles inserted in the skin or through a pair of platinum wires 0.5 mm apart applied to the upper or lower lip mucosa. The stimulus intensity was monitored with a current probe throughout.

RESULTS

Exteroceptive reflex (ER) of the digastric muscle. Preliminary observations showed that an ER discharge could only be recorded from the human digastric muscle when slightly painful stimuli (4 mA or more) were delivered rather infrequently to the lip mucosa. After a period of rest of 15 min, a consistent reflex was obtained and its latency varied between 60 and 75 msec (Fig. 1). The duration of the reflex discharge ranged from 70 to 100 msec. The reflex involved both right and left digastric muscles when the stimulus was applied to the lip mucosa on one side. When the same stimulus was repeated at 1-sec intervals, the digastric reflex decreased very rapidly in size with little, if any, change in latency. The reduction involved first and foremost the later part of the EMG discharge (Fig. 1A). After a period of rest of 15 min, the reflex recovered fairly well to its control level (Fig. 1B). Repetition of the same stimulus at 5-sec inter-

Fig. 1. Electromyograms of the digastric muscle reflex elicited by electrical pulses of 10 mA, 0.5 msec to the contralateral upper lip mucosa. The rank of each reflex in any series is indicated on the left of each oscilloscope sweep. Series at intervals of 1 sec (A), of 5 sec (B) and of 1 min (C). A period of rest of 15 min occurred between each series.

vals produced an habituation effect which developed somewhat more progressively. When a similar series was elicited at intervals of 1 min, the habituation was still present, though considerably reduced and more progressive (Fig. 1C).

Exteroceptive suppressions (ES) of the masseter muscle. A slightly painful stimulus to the lip mucosa elicits 2 successive suppressions (ES_1 and ES_2) in the maintained voluntary activity of the masseter^{3,18-20}. In previous experiments the stimuli were generally delivered at 1/sec and the question arises whether any habituation occurred under such conditions. Fig. 2A shows a series of single sweeps illustrating ES_1 and ES_2 for stimuli at 20, 5 or 1-sec intervals, each series being separated by a period of rest of 5 min. ES_1 maintained the same features throughout each series while ES_2 disclosed definite habituation at 1-sec intervals and a slight habituation at 5-sec intervals. At 20-sec intervals, ES_2 was apparently not reduced. The averaging of 32 consecutive sweeps triggered at various rates proved useful to study the changes in ES pattern which actually varied among the subjects (Fig. 2B-D). The size and duration of ES_2 increased significantly for intervals of 20 sec, compared to intervals of 5 sec and even more so of 1 sec. ES_1 was not similarly affected and its pattern, which differed in the various subjects, was maintained at the various rates. In 2 subjects, ES_2 failed to be detected at 1-sec intervals but it was present at the longer intervals (Fig.

Fig. 2. Exteroceptive suppressions ES_1 and ES_2 (black arrows) elicited in the masseter muscle by electrical stimuli (empty arrows) to the contralateral upper lip mucosa at intervals of 20 sec (left column), 5 sec (middle column) and 1 sec (right column). The series are separated by a period of rest of 5 min. A: oscillograms from masseter muscle during steady voluntary contraction, male subject of 22 years; stimuli of 10 mA, 0.5 msec. The rank of each sweep in the series is indicated. B: same experiment with data displayed as average write-outs of sweeps 1–32. The line below each trace represents the computer level for zero input. C: same display in another male subject of 21 years; stimuli of 6 mA. D: female subject of 21 years; stimuli of 12 mA.

2D). Cumulative decrements of ES_2 , but not of ES_1 , were observed when several series of 64 stimuli at 1/sec were delivered to the lip mucosa.

Habituation of the blink reflex. Habituation of the second component of the blink reflex^{4,13,15} is much more important than that seen for ES_2 in the masseter muscle (Fig. 2) and the question arises whether the steady voluntary contraction used in the latter experiments to provide background EMG activities for demonstrating the suppressions might not have affected the habituation. The supraorbital nerve was stimulated on one side and the blink reflex was recorded the lower part of the orbicularis oculi muscle of the other side; this minimized electrical artifacts and also allowed to record only the second component without any preceding short-latency component, the latter being only ipsilateral to the stimulus¹⁵. EMGs of the second components were rectified and averaged for groups of 4 successive stimuli in a series at 20-sec intervals (Fig. 3A). The integrated activities present the usual latency of about

Fig. 3. Blink reflexes elicited by stimuli of 8 mA to the contralateral supraorbital nerve. Rectified and averaged EMGs for groups of 4 successive reflexes (rank indicated above the write-outs). A: series at intervals of 20 sec. B and C: series at intervals of 5 sec (notice the reduced amplification which is indicated in arbitrary units). D and E: series at intervals of 1 sec. In A, B and D, the orbicularis muscle is relaxed. In C and E, it is maintained in steady voluntary contraction. Horizontal calibration in msec.

37 msec and their size did not vary systematically for the 5 successive groups compared. However a strong habituation was observed in the series at 5-sec intervals (Fig. 3B) and even more in the series at 1-sec intervals (Fig. 3D). When the series were repeated while the subject maintained a constant, moderately strong, voluntary occlusion of the eyes, the blink reflexes presented an increased size and disclosed very little habituation (Figs. 3C and E, 4A and B). Notice that the voluntary EMG activities were also rectified and integrated, which resulted in an upward shift of the write-outs with respect to the computer base line (see methods).

The steady voluntary activation obviously increased the ER (Fig. 4A₁ and B₁) but this was not a sufficient explanation for the relative lack of habituation under such conditions. Indeed when the exteroceptive stimulus was made stronger so as to elicit a larger blink reflex roughly matching the one in Fig. 4B₁, but in a relaxed muscle (Fig. 4C₁), the habituation at 1/sec proceeded at about the same rate (Fig. 4A and B).

Exteroceptive suppression (ES) of the masseter reflex. In view of the above findings on the blink reflex, the study of ES of masseter motoneurons was replicated in the absence of any steady voluntary contraction, by comparing the masseter tendon

Fig. 4. Series of blink reflexes elicited by stimuli of 8 (A and B) or 15 (C) mA to the contralateral supraorbital nerve. The rank of successive sweeps is indicated. In B, the subject maintains a steady voluntary contraction of the tested muscle.

reflexes elicited by a tap on the chin, with and without preceding stimulation of the lip mucosa³. Since proprioceptive reflexes are only stable when elicited at intervals of at least 5 sec¹², the procedure was to have every fifth lip mucosa stimulus (at 1/sec) followed at a chosen interval by a tap on the chin. Groups of 10 such masseter reflexes at a chosen interval after the exteroceptive stimulus were rectified and averaged (Fig. 5B), and compared with alternate groups of 10 masseter reflexes elicited also at 5-sec intervals, but without preceding lip mucosa stimulation (Fig. 5A). Such precautions are necessary in view of the known fluctuations in tendon reflexes¹². Fig. 5C shows a control ES recorded on a background of voluntary EMG activity at the beginning of the session. The same test carried out at the end of the same session, after about 7 runs of 60 lip mucosa stimuli at 1/sec (Fig. 5E) showed a similar ES₁ while ES₂ was slightly reduced through cumulative habituation. The suppression of masseter reflexes (Fig. 5D) presented a fairly consistent time course. Habituation effects were looked for by comparing the maximum suppressions for the first and for the last (crosses) runs carried out in the session: the amount of tendon reflex suppression was found identical for ES₁ but slightly reduced for ES₂. Thus the pattern of ES₁ and ES₂ and the small habituation of ES₂ were not significantly different in the absence of voluntary contraction of the tested muscle.

Fig. 5. ES of masseter muscle elicited by electrical pulses of 10 mA at 1/sec delivered to the lip mucosa. C and D: ES of steady voluntary EMG activity, at the beginning (C) and at the end (E) of the session. B and D: ES of the masseter monosynaptic reflex tested in the relaxed muscle. A: control groups of 10 (averaged) reflexes without preceding exteroceptive stimulation at the interval indicated on the abscissa (see text). The horizontal time calibration for the averaged reflexes in A and B is half that indicated on the abscissa for the intervals. D: group of ES of masseter reflex. Crosses represent applications at intervals of 30 and 70 msec at the end of the session which illustrates the slight habituation of ES₂ at 70 msec.

DISCUSSION

As shown by Hoffmann and Tönnies⁶ the stimulation of the lip mucosa or gums elicits jaw opening which apparently involves mainly a reflex contraction of jaw-opening muscles in lower mammals¹, but an inhibition of jaw-closing muscles in man. The failure to record a digastric reflex reported by some²⁰ can now be ascribed to the use of too high a rate of activation (1/sec) since we found this reflex to be highly susceptible to habituation (Figs. 1 and 6). The digastric reflex decrement was rapid and profound even when many seconds were allowed between the successive stimuli.

The second component of the blink reflex⁸ elicited by electrical pulses to the supraorbital nerve shows prominent habituation^{4,15} the kinetics of which are however quite different since the reflex decrement only became appreciable when the intervals between stimuli were reduced below about 8 sec (Fig. 6). We found that steady voluntary occlusion of the eyes (contraction of the effector muscle: orbicularis oculi) not only augmented the reflex discharge, but also considerably reduced the susceptibility to habituation of the second component of the blink reflex (Fig. 3). This relative resistance to habituation during volition was not the result of mere reflex potentiation since other tests were carried out in which the muscle response disclosed marked habituation, even when it had been increased by stronger stimulation in the absence of voluntary contraction (Fig. 4).

These results must be related to the significant excitatory effects exerted by the pyramidal discharges on segmental interneurons, as directly demonstrated by micro-

Fig. 6. Different habituation kinetics of the digastric reflex (crosses), the second component of the blink reflex (circles), and ES_2 (dots) and ES_1 (triangles) of the masseter muscle of the same subject. Ordinate: percentage habituation obtained by dividing the mean amplitude of the 6th to 10th responses by the mean amplitude of the 1st to 5th responses in the same series. Abscissa: interval in sec between successive stimuli in each series.

physiological studies in the cat spinal cord^{10,11}. There is also recent evidence in man that the pyramidal system can influence the disynaptic reciprocal pathway¹⁶. In relation to the present discussion about brain stem mechanisms in man, a pyramidal effect of the kind shown by Lundberg and Voorhoeve¹¹ could account for the potentiation of the polysynaptic reflexes. However the reduction of susceptibility to habituation had not been hitherto demonstrated.

On the other hand, the exteroceptive suppressions proved much less susceptible to habituation. The early ES_1 component which has a latency of about 14 msec in the human masseter muscle shows virtually no habituation, up to about 3/sec. However the late ES_2 component shows definite habituation (Fig. 6) which involved predominantly the later part of ES_2 (Fig. 2). The pattern of ES during repetitive stimulation at intervals chosen between 1 and 20 sec was characteristic of an habituation process, with more rapid reduction in ES_2 at the higher rates (Fig. 2). In 2 of the subjects studied, ES_2 was even nearly completely eliminated through habituation during stimulation at 1/sec, while ES_1 was little affected (Fig. 2D). Prolonged repetitive stimulations during a session substantially reduced ES_2 in all the subjects and this effect proved slowly reversible after a period of rest which had to be as long as 1 h in the case of marked habituation. These features are consistent with classical habituation¹⁷. The different kinetics of habituation of ES_2 cannot be ascribed to the use of background voluntary contraction to show suppression since identical features were recorded when testing ES on masseter reflexes in the relaxed muscle (Fig. 5). It can thus be said that voluntary activation neither potentiated nor decreased ES_1 and ES_2 to any significant extent. The above results are also in line with the proposal that ES_2 involves a complex polysynaptic pathway³ which should thus be rather susceptible to habituation, while the earlier ES_1 involves a paucicynaptic mechanism rather resistant to habituation. Another suggestion arising from the data is that reflexes (digastric, second component of blink) or suppressions (ES_2 in masseter) which involve afferent

and efferent peripheral pathways of comparable lengths and which present latencies of a similar range of 40–65 msec can disclose considerable differences in their respective habituation kinetics (Fig. 6).

ACKNOWLEDGEMENTS

This research was supported by the Fonds de la Recherche Scientifique Medicale and the Muscular Dystrophy Association of America Inc.

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