

THE RESPONSE OF CHELONIAN MUSCLE SPINDLES TO MECHANICAL STIMULATION

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SUMMARY. Single unit recordings have been made from the muscle spindles of the extensor digitorum brevis I muscle of the chelonian *emys orbicularis*. The responses to ramp-type mechanical stretches (up to 5 mm s^{-1} velocity and up to 1.6 mm extension) were compared to those of spindles from other groups. It is found that the spindles have lower rates of firing than those from the other groups with the exception of the snake spindles. Generally the spindles behaved like the secondary ending of mammalian spindles or the tonic type of snake spindle in terms of their response to the velocity of stretch. The results are consistent with the view that the tonic response arises from intrafusal muscle fibres in which the sensory region has a structure which is fairly uniform and similar to that of the polar regions and not interrupted by accumulations of nuclei.

Recent morphological studies (1,2) on chelonian muscle spindles have shown that there are striking differences when they are compared to spindles of other groups. In particular, the equatorial region contains no fluid space and the connective tissue layers of this region wrap closely around the intrafusal fibres and the single sensory neuron. The intrafusal fibres contain no reticular zone or nuclear regions and the myofibrils extend throughout the region of sensory innervation. This paper is a preliminary report of an investigation to determine the physiological properties of chelonian spindles to mechanical stimulation.

METHODS

The information presented is based on studies on extensor digitorum brevis I muscles taken from *emys orbicularis*. Samples of muscle were subjected to light microscopical studies to ensure that there were no obvious qualitative

differences from spindles in *testudo graeca* as used in more detailed morphological studies. Physiological recordings were taken from the nerves of muscles that were subjected to controlled mechanical ramp stretches. Single units were obtained by splitting the nerve. The time intervals between successive action potentials were recorded in digital form for analysis by a CDC 1700-computer.

RESULTS

Computer print-out records of the instantaneous frequency of firing of single spindle units subjected to ramp stretches are presented in the figures. It is seen that for low velocity stretches the frequency of firing increases steadily during the upward slope of the ramp to reach a peak value at the point where the steady part of the ramp starts. For velocities above 4 mm s^{-1} there are very few impulses during this interval. The muscles were about 1 cm long and the stretches were limited to 1.6 mm. The peak frequency was about 20 impulses per sec for the highest velocities of stretch that were used (i.e. about 5 mm/s).

The frequency of firing began to decrease immediately at the start of the steady part of the ramp. For the faster ramp stretches one or two impulses of a relatively high frequency were seen at this point but generally over the steady part of the ramp the frequency of firing decayed in a reasonably exponential manner. If this part of the ramp is extended, the firing rate becomes steady but the final frequency is higher than that for the unstretched state. Fewer action potentials were seen during the downward slope of the ramp than during the upward slope. For ramp speeds greater than about 2.5 mm s^{-1} no impulses were seen during the downward slope and in such cases the spindle would be silent for up to five seconds after it had returned to its initial length. If the spindle was firing before the stretch was applied the pre-stretch firing rate was attained after about 20 seconds from the end of the ramp. For lower ramp speeds the rate of firing decreased steadily during the

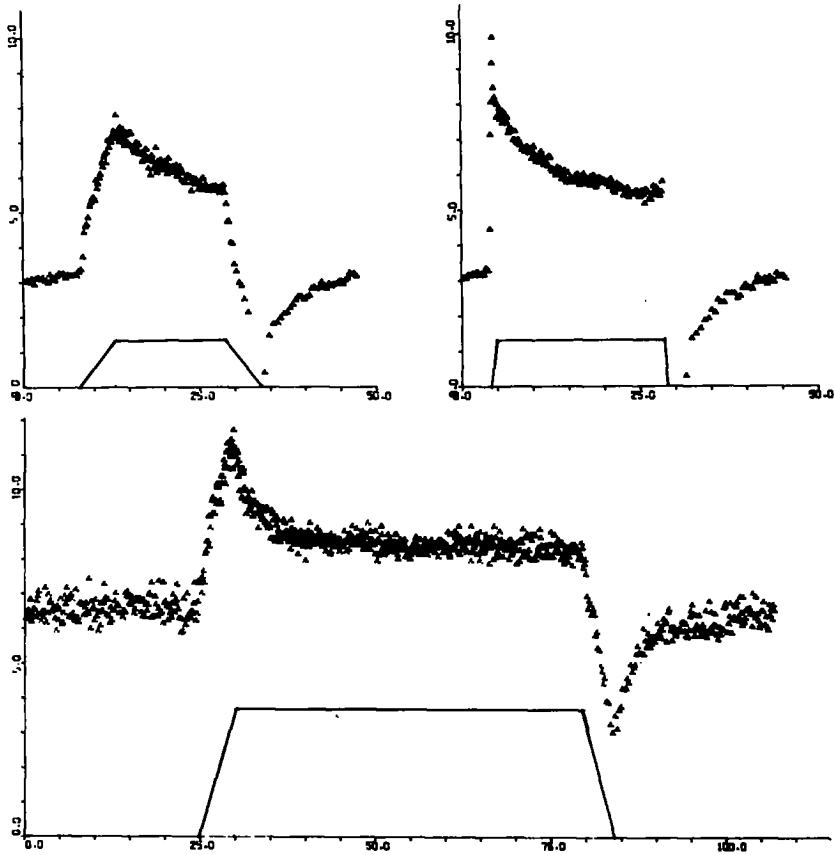


Fig. 1. Computer records of the frequency of firing of single spindle units in response to ramp stretches. Each point represents a single action potential. Its position on the horizontal axis (measured in seconds) is the time of its measurement. Its position on the vertical scale (measured in impulses per second) is the inverse of the time interval that has elapsed since the previous action potential. The upper two records are for the same spindle subjected to ramps of different speeds ($.27 \text{ mm s}^{-1}$ and 2.66 mm s^{-1}) but equal height 1.33 mm . The lower record is of another spindle subjected to a prolonged ramp of speed $.07 \text{ mm s}^{-1}$ and height $.36 \text{ mm}$. The ramps have been drawn on the graphs but their heights are not to scale.

downward slope to a frequency below the unstretched firing rate. After the ramp the frequency would rise steadily to attain the prestretch frequency after about twenty seconds.

DISCUSSION

The present results confirm the previously reported fact (3) that the tortoise spindle is slowly adapting and thus it has been found necessary to study the organ when subjected to ramp stretches of long duration. Further, in order to make comparisons with the spindles of other species, we have limited the range of stretch to within about 16% of the spindle length. It would appear that this range of stretch is below that used in previously reported studies (4).

The properties of the chelonian spindle can be compared to the frog spindle (5), the snake spindles (6) and the primary and secondary endings of the mammalian spindle (7) where ramp stretches of roughly the same magnitude and velocity in terms of the length of the spindle have been applied in the absence of stimulation of the motor nerves.

During the upward slope of the ramp stretches the chelonian spindle fires at a lower rate than the other spindles except for the snake spindle. In particular the pattern and magnitude of the frequency of firing of the 'tonic type' of snake spindle resembles that of the spindles used in the present study. That is to say that, provided the ramp slope is not too steep, there is a steady build-up of frequency which reaches its peak at the highest part of the ramp. This behaviour is qualitatively similar to that of the mammalian secondary ending except that such an ending has an overall higher frequency of firing than the chelonian spindle. No responses were seen which resembled the 'phasic type' of snake spindle in which there was a sudden change to a relatively high frequency at the onset of the stretch and which remained fairly constant during the upward part of the ramp.

The behaviour was also similar to the secondary ending and the tonic snake spindle during the steady part of the ramp stretch. No dramatic reduction in frequency was seen at the onset of this period as is characteristic of the phasic type of snake spindle, the primary ending of the mammalian spindle and, for higher velocities of stretch, in the frog spindle.

It would appear also that the present records are similar to those of the tonic spindles of the lizard (8) but the reported records for the latter seem to indicate that a proportionately higher degree of stretch was applied.

Most ramp stretches applied to muscle spindles have a duration of a few seconds. In the present case it was found necessary to extend the steady part of the ramp to obtain a reasonably steady firing rate. Comparisons with other spindles in this respect are not easy because of the paucity of comparable data. Also there is little data available on the behaviour of spindles during the downward slope of the ramp. For the lower ramp speeds the chelonian spindle behaves similarly to the secondary ending of the mammalian spindle where a steady decline in firing rate is observed rather than an abrupt cessation at the onset of the release. For the higher ramp speeds the absence of firing during the downward slope would be expected if very few or no impulses at all are seen during the corresponding upward slope. This is due to the short duration of the sloping part of the ramp in terms of the intervals between the action potentials rather than to a so-called dynamic response.

The present results do not suggest a function for the fluid filled capsule as found in other spindles or explain its absence in the chelonian spindle. The impression previously expressed (e.g. 8) that an intrafusal muscle fibre that has myofibrils and the absence of accumulations of nuclei in its sensory region exhibits a tonic response is strengthened by the present results. In other words, a uniformity of visco-elastic properties over the whole intrafusal fibre length would provide a static response to stretch. In the case of

the chelonian spindle this would mean that the close wrappings of connective tissue that comprise the capsule and seem to bind the intrafusal fibres together (1,2) would not contribute to a difference in physical properties of the fibres in this region as opposed to the polar regions.

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