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SEPARATION AND ESTIMATION OF MUSCLE SPINDLE AND TENSION RECEPTOR POPULATIONS BY VIBRATION OF THE BICEPS MUSCLE IN THE FROG

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INTRODUCTION

The spinal cord of the frog has been used as a model system to investigate force-field primitives (22). It is our hypothesis that proprioception plays an important role in the organization and regulation of primitives (21, 22). However, the role of proprioception in motor control in the frog has been controversial. Although frog spindles have been analyzed carefully in many regards, some aspects of the proprioceptive organization in amphibia are still not well understood (30). To use muscle vibration as a tool to examine proprioceptive control of primitives in reflex behaviors we needed a deeper understanding of the responses of spindles and golgi tendon organ (GTO) receptors in the frog in vivo when subject to muscle vibration.

Longitudinal vibration of muscles has commonly been used as a tool to specifically activate muscle spindles and to examine the feedback effects due to muscle spindle activation in a variety of animals (4, 7, 8, 9, 11, 39, 43). Muscle vibration has also been used in reduced frog preparations to activate and entrain muscle spindles (14, 27, 29, 36, 37;). Here we tested how muscle vibration affected muscle spindle firing in spinal frog and examined how our parameters of vibration affected GTO receptor firing. In mammals, it is known that vibration may activate GTO receptors in addition to muscle spindles if the amplitude of the vibration is increased or if the background tension of the muscle is increased (6, 7). In the frog, GTO receptors were first identified in the sartorius muscle (17). Their vibration response in frogs is not well examined. The proportions of types of muscle spindles and GTO receptors will determine the types of feedback regulation available (6, 7, 13, 34, 35), but these proportions are not well characterized in the frog. Thus, the data here are an important foundation for studies of proprioceptive control of primitives in the frog.

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METHODS

Surgical preparation.

To examine the effects of muscle vibration on muscle spindles and GTO receptors in the spinal frog, we chose to vibrate the biceps (iliofibularis) muscle. Thebiceps muscle spindles had interesting and potentially important firing patterns during hindlimb wiping (Kargo, Rome and Giszter, submitted). The hindlimb was immobilized at the ankle, and the distal tendon of biceps was detached from the tibia. Care was taken not to disturb the interface between the muscle belly and tendon, where most tension receptors are believed to reside (16, 17). Fascia between biceps and adjacent muscles were removed, and biceps was covered with a petroleum jelly-mineral oil mix. A small hook was placed through the distal tendon of biceps and was tightly secured into a 3.5 inch, 8 mega-ohm speaker which was mounted on a separate platform from the air table on which the frog and other apparatus was arranged. All transmission of speaker vibration to the limb was thus through the hook attachment system.

Muscle vibration.

The speaker, to which the tendon was attached, was driven sinusoidally at different frequencies by a function generator. We monitored the muscle length changes imposed by vibration or by muscle contraction using an optical position sensor (Optotrak, Northern Digital Inc., Waterloo, Ontario). Two infrared emitting diodes were placed on the distal, detached tendon of biceps and on its proximal, attachment site at the hip. 3-D position data of the diodes were sampled at 1 kHz and stored on computer using Northern Digital software. The straight-line distance between the diodes was calculated off-line in S-Plus to determine the longitudinal muscle length changes in biceps. Using a binocular microscope, we confirmed visually that movement outside of the longitudinal axis of the muscle was minimal (< 20 um). The extent of longitudinal vibration was controlled to achieve fixed amplitudes across all frequencies applied. Single-unit or compound action potential responses of muscle spindles and presumptive GTO receptors were recorded during the vibration.

Afferent identification and recording.

To identify single afferent units from biceps in several preparations, we recorded single units directly from the biceps muscle nerve. The biceps muscle nerve was exposed from its entry points to the muscle and its fusion to the sciatic nerve. The freed portion of the nerve was pinned onto a wax platform using minuten pins as used in insects (3). Single units were recorded from teased and cut filaments of the muscle nerve using suction electrodes (A-M Systems). The large majority of the muscle nerve was left intact. Within the opened vertebral canal, ventral roots 8 and/or 9 were placed on bipolar hook electrodes and were stimulated at low levels (.1-.2 V) to evoke contraction of the biceps muscle. Muscle spindles were initially identified by a clear pause in tonic firing rates upon muscle contraction and by increased discharges in response to direct palpation of the exposed muscle belly and in response to muscle lengthening. Presumptive GTO receptors were identified by an increased discharge upon muscle contraction and by low tonic firing rates (< 1 Hz), even at relatively extended in vivo muscle lengths. After this initial identification and categorization, behavior of the units in response to vibration were examined. Single unit recordings of presumptive muscle spindles and GTO receptors were made from the exposed biceps muscle nerve as the muscle was vibrated.

In several frogs, cut-end recordings (using suction electrodes) were performed from small fascicles teased from the dorsal roots. The dorsal root fascicles contained several to many units that responded to BI muscle contraction and to vibration.

In several more frogs cut end suction electrode recordings from the entirety of the dorsal roots were made to examine compound action potentials of large populations of afferents from the muscle.

RESULTS

Unit identification and categorization.

Identified biceps units could be categorized into spindles or GTOs based on their response profiles to ventral root stimulation, muscle stimulation and muscle vibration.

In Figure 1A, the response of an identified biceps muscle spindle to muscle vibration is shown. The vibrator drove sinusoidal length changes of the biceps muscle of ~ 150 μm. In the single unit recordings of passive muscle, muscle vibration effectively entrained identified muscle spindles (1:1) over a range of frequencies from 20 to 110 Hz. At frequencies of 10 Hz and below, muscle spindles often fired two spikes per cycle. The efficacy of muscle spindle entrainment was reduced at frequencies of 120 Hz or above (1:2 or 1:3 entrainment). Figure 1B shows a muscle spindle and a GTO afferents' firing patterns and the biceps muscle length in response to stimulation of ventral root IX. The muscle spindle showed a pause in firing with ventral root driven muscle contraction while the GTO was recruited to fire a few spikes. When 80 Hz muscle vibration and muscle contraction were combined, the contraction did not improve the efficacy of entrainment, and most spindles actually reduced firing below perfect entrainment (or 1:1 firing with vibration). In contrast, GTO firing was accelerated: Over the first 100 ms of vibration (where the ventral root had not been stimulated yet) a GTO shown was entrained to a subharmonic of the applied 80 Hz vibration. That is, it fired at 40 Hz or 1 spike for every 2 cycles of vibration (1:2 ratio). However, when muscle contraction was superimposed on the vibration, the presumptive GTO receptor was entrained 1:1 (and in some cases fired 2 spikes per 1 vibration cycle or at a 2:1 ratio).

Controlling the muscle spindle and Golgi tendon populations of a muscle with vibration.

To improve our direct control over spindle and GTO firing we used curarization of the target muscle. This was necessary in order to eliminate both intrafusal and extrafusal contractions. We found this manipulation provided us fuller control of the activity of the receptor population in a given muscle. Following selective curarization of a muscle we were able to precisely control the firing of spindle and tendon organs since both (1) the tension induced double firings of tendon organs and (2) the intrafusal muscle fiber induced spindle firings described above were eliminated by this means. The remainder of this paper focusses on responses of spindles and GTOs in such curarized muscle preparations.

Population activity:modulation of wave amplitude and phasing of spindle and GTO populations with vibration frequency.

In several frogs, cut-end recordings (using suction electrodes) were performed from small fascicles teased from the dorsal roots. Such fascicles contained several to many units that responded to BI muscle contraction and to vibration. During a single cycle of biceps vibration, there were two sequential and partly overlapping

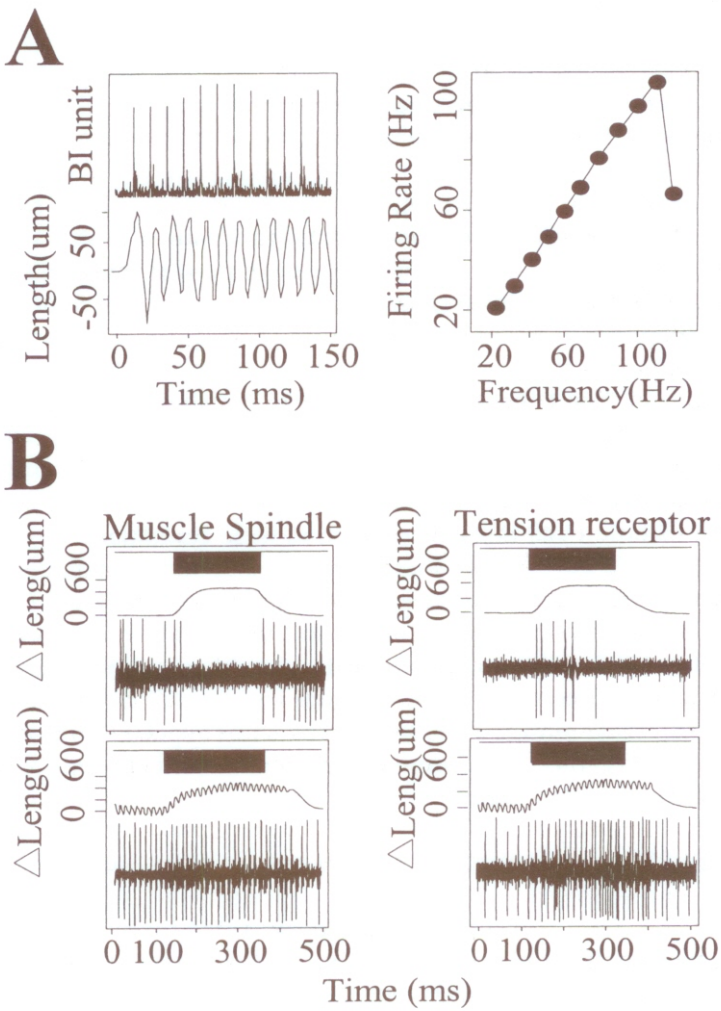

Fig. 1. - *BI afferents responded in one of two ways to muscle vibration and muscle contraction.* A (left panel): a BI muscle spindle (top row) is recorded during longitudinal vibration of the resting BI (bottom row is length of BI). Each oscillation, at a frequency of 80 Hz and amplitude of ~ 150 um, resulted in a single action potential. This unit was thus effectively entrained 1:1 to the vibration frequency from 20 Hz up to 110 Hz (right panel). B: the firing patterns of a presumptive muscle spindle and GTO receptor are shown in the left and right columns respectively. In the top row of each column, ventral root 9 was stimulated to evoke BI muscle contraction (black box marks period of stimulation; BI muscle length is shown below stimulation). In the bottom row of each column, the effect of BI muscle contraction is superimposed on the effect of background 80 Hz BI vibration. BI muscle spindles had higher tonic firing rates and exhibited a pause in firing with muscle contraction (top-left). GTO receptors had low tonic firing rates and exhibited an increase in firing with contraction (top right). Muscle spindle firing rates were entrained 1:1 by vibration and not noticeably altered with contraction (bottom left). The GTO receptor was less effectively entrained (1 action potential every 2 vibration cycles; bottom right, for the first 100 ms). However, when vibration was superimposed on a background muscle contraction the receptor was entrained to fire one (and even 2) action potentials to a single vibration cycle (bottom right, 100-400 ms).

waves of evoked activity in these small fiber populations. In Figure 2A, we show the averaged responses of a dorsal root fascicle to a single cycle of vibration at 40 Hz and 90 Hz. Averages of 200 cycles were constructed.In the recording shown, the first wave of vibration-evoked activity was smaller than the second wave. However, in most recordings the first wave was larger. The first wave represents the discharge of the frog muscle spindles, the fastest conducting afferents activated by vibration. Based on the conduction velocity measurements of (16, 17, 42) muscle spindles form the fastest conducting population of frog muscle afferents (~ 20-30 m/sec). The second peak were thought to be GTO receptors. At higher frequencies of vibration (i.e. moving e.g. from 40 to 90 Hz), the delay between the first peak of activity and the second peak of activity was reduced.

The decreased latency between the first and second waves of activity at higher frequencies of vibration resulted from an increased delay of the first wave relative to peak muscle length, rather than from any shifting of the second wave relative to peak muscle length. This is shown in Figure 2B. Histograms of the times of peak afferent activity, relative to muscle length are shown for vibration at 40 Hz and 90 Hz. The peak of both evoked waves of activity occurred after peak muscle length. At frequencies of 10 Hz and below, not used here, evoked muscle spindle activity occurs instead on during increasing arm muscle length (23, 37). We tested a range of higher frequencies. The latency between the peak muscle length and the second wave of activity was constant at all frequencies of vibration (see triangles in Figure 2C). The peak firing rate of frog muscle spindles to vibration is around 150 Hz or less, i.e. there is a minimum 6 msec latency between evoked waves of muscle spindle activity (14, 33, 37). Thus, the small latency seen here (~ 1.2 to 2.8 msec), strongly supports the idea that the two waves represent different receptor afferent populations. In addition, only a single receptor afferent of uniform conduction velocity (~ 20-25 m/sec) innervates frog muscle spindles, i.e. there is no division into group Ia and II afferents as in mammals (14, 16, 17). The first wave, representing muscle spindle activity shifted relative to peak muscle length while the second population of afferents (or GTO activity) remained in a fixed relationship to muscle length. In frog sartorius, GTO receptors have a conduction velocity of 8-12 m/sec (17). The second wave represents the GTO receptor population which locks to a different phase of muscle vibration.

Population activity:muscle spindle:tension receptor ratio estimation.

Dorsal root recordings at different holding lengths of the BI muscle also show two distinct populations of afferents are recruited by biceps vibration as described above. In addition, the dorsal root recordings provide an initial rough estimate of the relative proportions of muscle spindles to GTO receptors in BI muscle.

In Figure 3, responses of averaged compound action potentials (CAPs) recorded from the entire eighth and ninth dorsal roots in response to a single cycle of vibration are shown for different holding lengths of BI muscle. At short muscle lengths vibration did not activate the GTO wave of afferents in the CAP. In contrast, the first wave of spindle afferents contributing to the CAP was activated at the shortest hold-

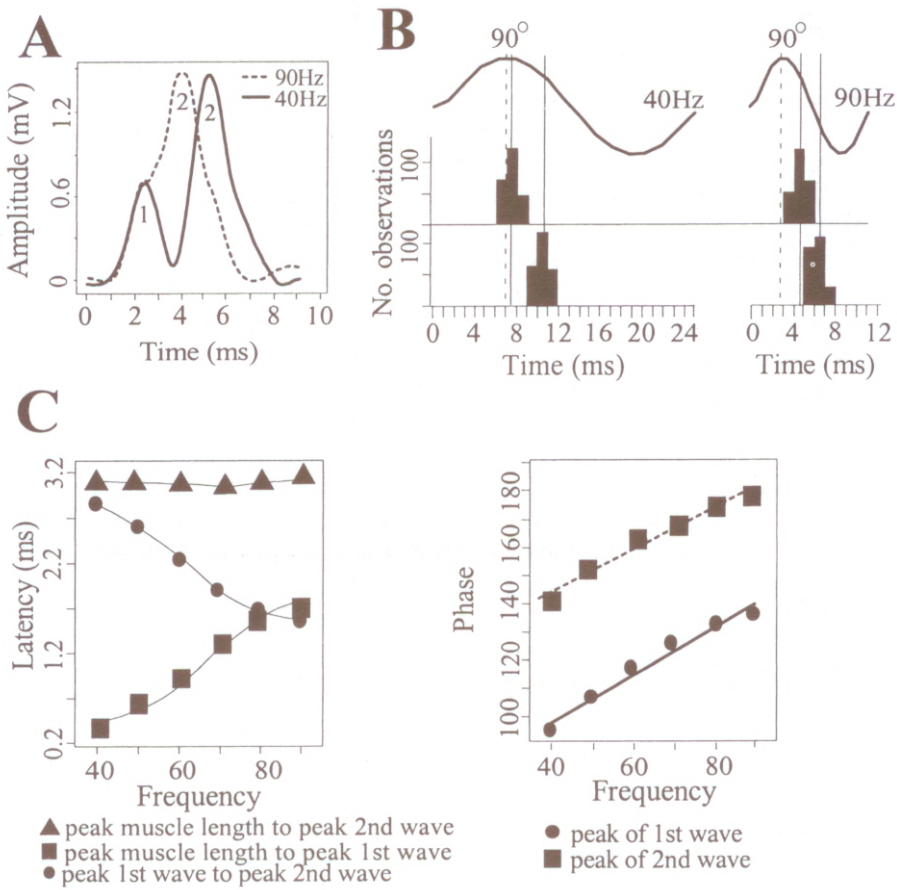

Fig. 2. - *The two populations of biceps (BI) afferents (muscle spindles and GTO receptors) responded differently to variations in vibration frequency.*
A: the left panel shows an averaged population recording from a fascicle from dorsal root 8 during a single cycle of BI vibration at 80 Hz (solid line) and at 40 Hz (dotted line). Recordings were rectified and 200 individual cycles were aligned and averaged at the peak of the first evoked wave of activity. Each vibration cycle activated a population of faster (muscle spindle) and slower conducting (GTO) afferents. At higher frequencies of vibration, activation of the second population of afferents was shifted relative to the first population. B: the relationship of the times of peak activity of the first and second waves to muscle length change for a single vibration cycle are shown at 40 Hz (left column) and at 90 Hz (right column). The top row shows the muscle length change for a single vibration cycle. The middle row shows a histogram of number of times the peak of the first wave occurred within 1 millisecond bins. 200 cycles (or observations) form the histogram. The first msbin starts at the onset of muscle lengthening. The bottom row shows a histogram of number of times the peak of the second wave occurred within a 1 ms bin, relative to the muscle length change. At 90 Hz, the latency between the peaks of the first and second waves of evoked activity was reduced. The peak of the first wave became shifted relative to peak muscle length (peak length marked by a dotted vertical line). The peak of the second wave was not shifted. C: at increasing frequencies of vibration the latency between peak muscle length and the peak of the first wave increased (squares), the latency between peak muscle length and the second peak of activity was constant (triangles), and the latency between the evoked activity peaks was decreased (circles). D: the phase relationship of the first and second waves of activity were different and both waves progressively increased phase with increasing vibration frequency. Phase was determined relative to the onset of muscle lengthening (i.e. if peaks occurred at the onset, the phase would be 0°).

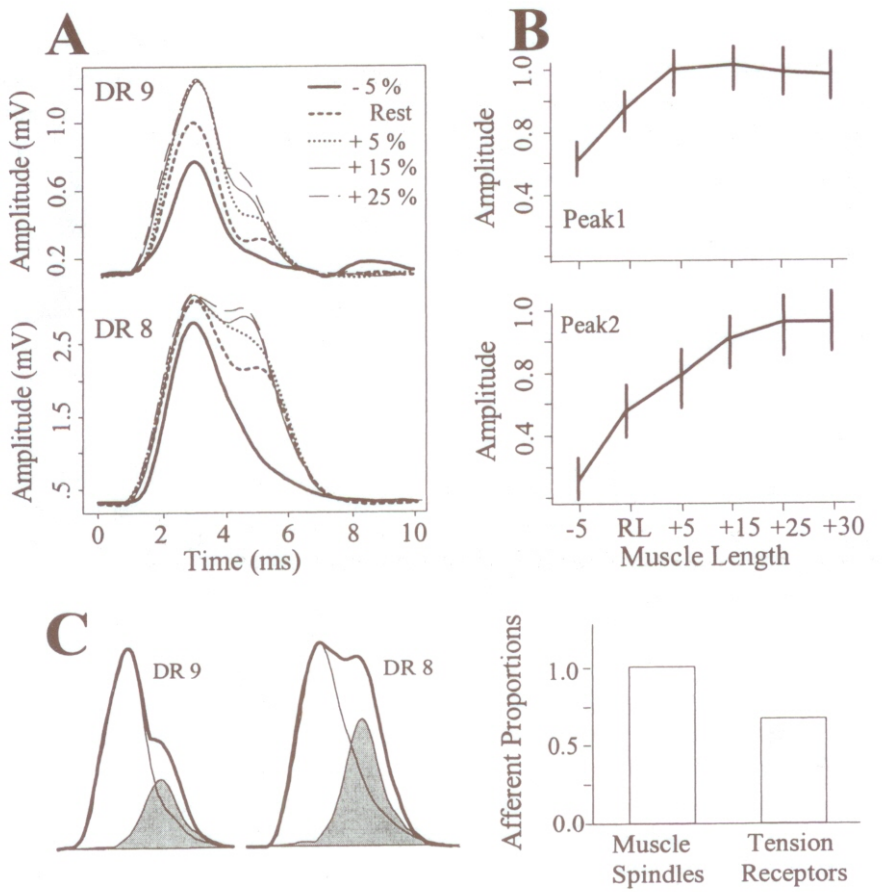

Fig. 3. - *The two populations of biceps (BI) afferents (muscle spindles and GTO receptors) responded differently to vibration when the holding length of biceps was varied.*
A: shows an averaged population recording from dorsal root 9 (top) and dorsal root 8 (bottom) during a single cycle of BI vibration at five different holding lengths (- 5% rest length – bold solid line, rest length – bold dashed line, + 5% rest length – bold dotted line, + 15% rest length – thin solid line, + 25% rest length – thin dashed line). Rest length for BI was determined at the limb configuration in which the hip angle was 0° relative to the mediolateral axis of the frog and internal knee angle was 90°. At progressively longer holding lengths, vibration activated a larger portion of both populations of afferents. B: the averaged peak amplitude of the first (spindle: top) and second waves (GTO: bottom) of evoked activity at the different holding lengths are shown for three frogs (standard deviations shown as vertical lines). For an individual frog, the amplitude of the two waves from each dorsal root were normalized to the peak amplitude of each respective wave. Data for each root and for the three frogs were then combined. The amplitude of the first wave saturated at lengths 5% greater than rest length. The amplitude of the second wave was relatively low at shorter holding lengths and saturated at 25% rest length. C: the averaged responses recorded from dorsal roots 8 and 9, at the longest holding length, are shown for a single frog (bold solid lines). Most if not all BI afferents forming each population were effectively activated and contributing to the displayed wave. In this frog, no responsive units were found in dorsal root 7. The shaded wave represents the wave contributed by the second population of afferents. This wave was obtained by subtracting the averaged response at the longest holding length from an amplitude-scaled version of the response at - 5% rest length (the thin solid line; at this rest length, the second wave was not apparent). Thus, unshaded thin-lined wave plus the shaded wave represent the voltage contributed by the two populations of afferents.

ing length. At increased holding lengths, the amplitude of both waves became enhanced as the muscle was tautened further. The increase in CAP amplitude represents a combination of two factors. Single units become more effectively entrained at longer holding lengths (1:1 firing), and new units are recruited by vibration at longer holding lengths. We found that there was a range of holding lengths at which the amplitude of the first wave saturated, and all spindles were entrained, while the amplitude of the second wave continued to increase (+ 8 and + 12 mm greater than rest length). The combined data for the frogs show these same trends (Fig. 3B). Both waves of the CAP became saturated at muscle lengths 25% greater than rest length.

As before the GTO (second) wave was activated at a constant latency relative to peak muscle length, while the first wave (spindles) shifted in latency. Both waves of the CAP were phaselocked to the sinusoid at differing but specific phases. To derive a measure and range for the relative proportions of biceps muscle spindles to GTO receptors from the CAPs recorded from the dorsal root, we used several assumptions. First, we assumed that muscle spindle and GTO receptor afferents were located in similar fascicles or in fascicles at a similar distance from the recording surfaces of the suction electrode. Second, following (12, 28, 41), we assumed the magnitude of an extracellularly recorded action potential from an axon depends on the conduction velocity (CV) of the axon raised to the 1.5; (i.e. $CV^{1.5} \propto$ extracellular voltage). We allowed that there could be a possible range of the correct exponent from 1 to 1.7. The conduction velocities of frog muscle spindles range from 20-25 m/sec, while those of GTO receptors range from 8-15 m/sec (16, 17). It is expected then, if the first and second waves of the CAP represent the extracellular potentials produced by a 'single' muscle spindle and a 'single' GTO receptor afferent respectively, that the recorded amplitude ratio of the first to the second waves would be 2.48:1 (muscle spindle CAP Voltage: GTO receptor CAP Voltage). We assumed that the compound action potential was a similarly weighted sum of the range of spindle and GTO fibers in the nerve roots (and see 10). The ratio of the amplitudes of the recorded first and second waves was in fact ~ 5:1 (when CAP recordings from both dorsal roots were summed). This suggests then that the relative proportions of muscle spindles to GTO receptors is ~ 2.02:1 (and not 1:1), or that there are roughly half as many GTO receptors as there are muscle spindles in the biceps muscle. These proportions of GTO receptors compared to spindles (40-60%) are somewhat lower than proportions typically seen in most mammalian limb muscles (60-80%; 18). Using the upper and lower bounds for spindle and GTO conduction velocity and the maximum and minimum CV to amplitude exponents (1 and 1.7) we obtained the upper and lower bounds for the ratios of spindle to GTOs based on CAP amplitude and our assumptions. These are from 1:1.2 to 4:1. The minimal proportion of GTOs to spindles in the frog is thus from our data likely to be 25%. The CAP analysis shows that GTOs are likely to be able to contribute significantly to setup and regulation of primitives. Further, the ratio of GTO receptors to spindle could approach that of mammals.

DISCUSSION

Our parameters of vibration activated muscle spindles efficiently over a range of frequencies. Selective activation of muscle spindles was demonstrated at relatively short holding lengths of the muscle, and therefore at low levels of background tension. GTO receptors were more effectively activated and entrained at longer holding lengths in curarized muscle or when vibration was superimposed on muscle contraction in non-curarized muscles.

Two waves of population activity were evoked with each cycle of vibration. The amplitude and phase relationship of the second, slower wave (the GTO receptor population) relative to the vibration cycle was modulated independently of the first wave of spindle activity. The two populations could be differentially recruited by imposing different levels of background muscle tension. Analysis of the compound action potential waves of population activity showed that in the biceps muscle the spindle to GTO receptor ratio is likely to be approximately 2:1. Thus, this study provides further evidence that several frog hindlimb muscles contain GTO receptors in addition to muscle spindles (16, 17) and shows that in some muscles, the spindle to GTO receptor ratio approaches mammalian ratios (15). Our data support use of muscle vibration in the frog as a tool to investigate how feedback pathways from identified muscle afferents regulates force-field primitives in the frog. Both GTO receptors and spindles are likely to contribute to the feedforward planning and feedback regulation of hindlimb behaviors both spinally and by descending controls (1, 13, 34, 38, 11, 21, 31, 33) and to the regulation of force-field primitives that compose reflex behaviors in the frog (22). Both receptor types can be experimentally controlled in spinalized frogs by imposing specific patterns of vibration and holding lengths in curarized muscles.

SUMMARY

Frog spinal cord reflex behaviors have been used to test the idea of spinal primitives. We have suggested a significant role for proprioception in regulation of primitives. However the in vivo behavior of spindle and golgi tendon receptors in frogs in response to vibration are not well described and the proportions of these proprioceptors are not established.

In this study, we examine the selectivity of muscle vibration in the spinal frog. The aim of the study was (1) to examine how hindlimb muscle spindles and GTO receptors are activated by muscle vibration and (2) to estimate the relative numbers of GTO receptors and spindle afferents in a selected muscle, for comparison with the mammal. Single muscle afferents from the biceps muscle were identified in the dorsal roots. These were tested in response to biceps vibration, intramuscular stimulation and biceps nerve stimulation. Biceps units were categorized into two types: First, spindle afferents which had a high conduction velocity (~ 20-30 m/s), responded reliably (were entrained 1:1) to muscle vibration, and exhibited distinct pauses to

shortening muscle contractions. Second, golgi tendon organ afferents, which had a lower conduction velocity (~ 10-20 m/s), responded less reliably to muscle vibration at physiologic muscle lengths, but responded more reliably at extended lengths or with background muscle contraction, and exhibited distinct bursts to shortening muscle contractions. Vibration responses of these units were tested with and without muscle curarization. Ensemble (suction electrode) recordings from the dorsal roots were used to provide rough estimates of the proportions of the two muscle afferent types.

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