Magnitude of Oscillations in the Response of Ia Muscle Spindle Endings Under a Static γ Stimulation of Increasing Frequency

S. S. Schäfer, B. Berkelmann, and F. Dadfar
Department of Neurophysiology (OE 4230), Hannover Medical School, D-30625 Hannover, Germany

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Schäfer, S. S., B. Berkelmann, and F. Dadfar. Magnitude of oscillations in the response of Ia muscle spindle endings under a static γ stimulation of increasing frequency. J Neurophysiol 89: 1748–1760, 2003; 10.1152/jn.00952.2002. Under static γ stimulations, Ia afferents may discharge in a highly irregular way or may be driven. However, the genesis of the highly irregular form of discharge is unclear. We offer an interpretation of irregular discharge behavior. Twenty-three primary (Ia) muscle spindle afferents from the tibial anterior muscle of the cat were subjected to static γ stimulation, the stimulation frequency increasing linearly from 2 to 110/s. In addition, 17 of the spindle afferents were subjected to two different prestretch values of the muscle while the static γ fiber was now subjected to constant frequency stimulation at five different stimulation frequencies ranging from 9.4 to 95/s. The responses of the Ia afferents to the static γ stimulation were presented through discharge patterns that were constructed by the frequencygram method and were subjected to computer analysis, by means of which the Ia responses were evaluated quantitatively. Two groups of static γ stimulations were identified. The first group of γ stimulations leads in the Ia response to highly irregular discharging within a broad discharge band. This highly irregular discharging resolves into regular oscillatory responses of large magnitude occurring in the rhythm of the γ stimuli. According to this observation, the highly irregular discharges result from the fact that the Ia afferent generates more than one action potential per γ stimulus. The second group of γ stimulation leads in the Ia response either to driving of the action potentials in the rhythm of the γ stimulation frequency or of submultiples of it or to irregular discharging within a smaller discharge band. Under the latter conditions, oscillatory Ia responses of small magnitude occurring in the rhythm of the γ stimuli are proved to be generated by the Ia afferents. The results are explained in terms of the strength of contraction of the polar parts and the resulting stretch of the sensory parts of the intrafusal muscle fibers that are responsible.

INTRODUCTION

Static γ fibers innervate the chain or the bag₂ intrafusal muscle fibers or both types of muscle fiber simultaneously via collaterals. The contraction properties of the two kinds of muscle fiber under the stimulation of static γ fibers have been characterized from the direct observation of isolated living muscle spindles (Bessou and Pagès 1975; Boyd 1976, 1980). The chain fibers were found to have a high contraction velocity and consequently a high fusion frequency (~ 100 stimuli per second) and considerable oscillatory length changes of the sensory part during unfused contractions. The contraction velocity of the bag₂ fibers was smaller. Fusion of their contractions occurred at lower stimulation frequencies (~50/s). Only small oscillations of their sensory part were described during unfused contractions. Their contraction strength was found to be higher. It was observed that the sensory parts underwent large length changes during the fused contraction.

The contraction properties of the two kinds of intrafusal muscle fiber led to typical effects that could be read from the Ia afferent discharge frequency. A static γ fiber innervating only chain fibers led to an entrainment of the primary ending at the stimulation frequency or a submultiple of it (1:1 driving, 1:2 driving, etc.) over a certain range of frequencies as a consequence of the unfused tetanus of the rapidly contracting chain fibers. If only bag₂ fibers were innervated, driving was rarely observed. Instead, the mean Ia discharge frequency characteristically increased, and simultaneously became more variable. Where there was co-activation of bag₂ and chain fibers, both the characteristic driving of the chain fibers and the discharge variability of the bag₂ fibers were manifest in the Ia firing. Additionally, it was possible to observe driving up to higher frequencies than those produced by chain fibers alone in combination with very irregular discharging over a particular range of stimulation frequencies (Banks 1991, 1994; Boyd 1986; Boyd and Ward 1982; Boyd et al. 1985; Celichowski et al. 1994). The studies described in the preceding text demonstrate that the occurrence of Ia driving at the stimulation frequency or a submultiple of it is explained by the unfused oscillatory contractions of the chain fibers. By contrast, the explanation for the appearance of the highly variable Ia discharging associated with bag₂ fiber contraction is less clear. Matthews and Stein (1969) suggest that the high variability shown by Ia discharges elicited by static γ stimulation is largely due to unfused contractions of the intrafusal fibers. Dickson et al. (1993) distinguish between driven and nondriven firing only to identify chain fiber contractions on the basis of the Ia discharge frequency. However, Celichowski et al. (1994) interpret the variable and irregular Ia discharges as being a consequence of the high number of impulses generated by the Ia afferent without oscillation of the innervated intrafusal muscle fibers at that frequency. Scheepstra et al. (1995) interpret the variable and irregular Ia discharging that occurs under static γ stimulation as being a consequence of chaotic processes taking place at the action potential generating site.

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In this investigation, our aim is to analyze the variable and irregular way in which Ia afferents discharge under static γ stimulation. The analysis leads us to the conclusion that the irregular discharges are based on oscillatory Ia responses. Thus both the driving behavior and the irregular discharges are consequences of oscillatory contractions of the intrafusal muscle fibers. Driving is an oscillatory Ia response of small magnitude and the irregular discharging an oscillatory Ia response of large magnitude. The magnitude of the oscillatory response is interpreted in terms of the strength of the contraction of the polar parts and the resulting stretch of the sensory parts of the intrafusal muscle fibers concerned.

**Methods**

**Surgery**

The experiments were performed on muscle spindles from the tibialis anterior muscle of cats (2–4 kg in weight) that had been anesthetized with pentobarbital sodium (initial dose: 45 mg/kg iv; continuation of anesthesia: 5 mg/h iv). The procedure of the operation, the stretching of the muscle, and the recording of the discharge patterns have been described (Holm et al. 1981). The results of this present investigation are derived from 23 Ia afferents (conduction velocity: 75–100 m/s) investigated under the stimulation of 19 static γ fibers (conduction velocity: 16–38 m/s; 18 cats).

**γ stimulation and stretching**

The isolation and stimulation of the γ fibers were performed according to the procedure described by Matthews (1962). A γ fiber was identified by stimulating the ventral root filament concerned and recording the action potential at the peripheral nerve. To identify a γ stimulation as static, the two discharge patterns obtained for a single Ia afferent under a ramp-and-hold stretch with and without γ stimulation were compared (Matthews 1962).

To obtain the responses of the Ia afferents under static γ stimulation, the tibial anterior muscle was prestretched by 3 mm in 9 of a total of 18 experiments and by 9 mm in the remaining 9 experiments. The minimal physiological length of the tibial anterior muscle was 110–130 mm, depending on the weight of the cat. It was measured under total plantar extension of the ankle and was defined as a prestretch of 0 mm. Under the given prestretch the γ fiber was stimulated at a frequency increasing linearly from 2 to 110/s, the increase being effected within 5 s in six experiments, within 6 s in a further six experiments, and within 7 s in a further six experiments. To verify the Ia afferent response, each train of stimuli was repeated 15 times with a 7-s interval between successive trains. The Ia responses to the last 14 of the 15 trains were superimposed to obtain a discharge pattern. The stimulator had an internal basic frequency of 2 Hz. The linear increase in the stimulation frequency was initiated by an external gate. The first stimulus was however not given at a frequency of exactly 2 Hz; rather, it might occur up to 30 ms earlier or later. As a result, the frequency of the first stimulus ranged from 1.9 to 2.1 Hz and continued to increase with the same rate linearly from then onward; in consequence of which, the stimuli of the successively performed trains of linearly increasing frequencies do not coincide when subsequently superimposed.

In 14 of the 18 experiments, the effect of the static γ fibers (14 γ fibers) on the discharge frequency of the Ia afferent concerned (17 Ia afferents) was tested by stimulating the single static γ fiber at five different and constant stimulation frequencies—9.4, 28.8, 48.2, 77.6, and 95/s—while the Ia afferent’s response was recorded. The stimulation at each frequency was repeated 15 times. The last 14 Ia responses were afterward superimposed to obtain one discharge pattern. This is the procedure for the construction of frequencygrams described by Bessou et al. (1968a,b). The effect of each γ stimulation frequency on the response of the Ia afferent was tested under two length values of the muscle: on the one hand, the same prestretch value was used in each case for the recording of the Ia response as under the ramp frequency stimulation, and on the other hand, that length of the muscle increased by 7 mm. The first length is called the initial length and the second length the increased length. The change from the initial length to the increased length was performed by a ramp stretch (ramp rate 10 mm/s). The increased length was kept constant for 3 s before the muscle was released again. The γ stimulation started 3 s before the ramp and stopped 3 s after the release of the muscle. The interval between consecutive stimulations was 7 s. The results of this investigation are based exclusively on the Ia responses generated by the Ia afferents when at the initial length and at the increased length.

**Discharge patterns**

During each experiment, the length and the tension of the muscle, the triggering impulse, the γ stimulus impulses and the action potentials of one or two Ia afferents were recorded in parallel on an analog tape recorder. The length, the tension, and the triggering impulse were digitized off-line by means of an analog/digital converter (rate per channel: 10,000/s). The action potentials and the stimuli impulses were digitized at the speed of the clock of the computer (Intel 8254; rate per channel: ~6.7 × 10^7/s). The computer used was IBM AT compatible. Discharge patterns were obtained by superimposing on each other the responses of the same Ia afferent recorded under each set of parameters, omitting the response to the first of repeated stimulations.

**Evaluation of the magnitude of the oscillations in the Ia afferent response to a static γ stimulation**

Figure 1A shows a Ia discharge pattern obtained under a ramp-and-hold stretch performed during a static γ stimulation. The Ia afferent responds to both stimuli simultaneously. However, only the oscillatory responses occurring under the initial length, i.e., during the 500 ms before the ramp, and under the increased length, i.e., during the last 500 ms before the release, were of interest for this paper. To obtain objective information about the oscillatory Ia responses free of distortion from the underlying ramp-and-hold stretch and about their magnitude, a specific evaluation was necessary that enabled us, on the one hand, to eliminate the response to the ramp-and-hold stretch and, on the other hand, to determine the frequency and the magnitude of the oscillatory responses objectively and quantitatively. A method which fulfills both conditions is used and described in this section.

The frequency behavior of the transients of the overall Ia...
afferent response to the ramp-and-hold stretch overlaid by the response to the \( \gamma \) stimuli was determined with the aid of the fast Fourier routine. The resultant frequency spectrum obtained from the discharge pattern of Fig. 1C is shown in B. The high direct component at the frequency of 0 Hz represents the offset of the mean discharge frequency in the discharge pattern of Fig. 1A. The frequencies in the range >0 up to 8 Hz have somewhat elevated amplitudes, of a similar level to those in Fig. 1B. They represent the frequencies of the ramp-and-hold stretch. The somewhat elevated amplitudes at some higher frequencies (between 40 and 50 and 65 and 75 Hz) indicate those frequencies at which the discharge frequency is scattered around its mean value due to the variability of the occurrence of the action potentials.

The oscillatory responses induced by the \( \gamma \) stimuli that can be recognized by visual inspection of Fig. 1A are represented in the frequency spectrum of B by the basic frequency of the oscillatory responses and its integral multiples, each of which shows an increased amplitude. This is depicted in the panels of Fig. 2. In Fig. 2A, oscillatory responses are given whose mean discharge frequency is uninfluenced by the response to the underlying ramp stretch, i.e., the last 1,000 ms of the discharge pattern of Fig. 1A. Figure 2B shows the frequency spectrum of the Ia response of A. The high direct component at the frequency of 0 Hz corresponds to the offset that is apparent in the Ia response of Fig. 2A. This interpretation is verified by subtracting the offset (i.e., the direct component in imp/s) from the discharge frequency of each action potential of Fig. 2A. From this procedure Fig. 2C is derived in which the Ia responses oscillate around the discharge frequency of 0 imp/s without being offset. In the frequency spectrum of Fig. 2C, which is given in Fig. 2D, only the basic frequency of the oscillatory responses and its integral multiples remain, each of them.

**FIG. 1.** The response of an Ia afferent to a ramp-and-hold stretch with and without static \( \gamma \) stimulation and its analysis. A: 14 superimpositions. C: 4 superimpositions. The overall Ia afferent response, ramp rate: 10 mm/s. A: \( \gamma \) stimulation frequency: 9.4 stimuli/s. C: without \( \gamma \) stimulation. B and D: frequency spectrum of the Ia afferent response; in B of the discharge pattern of A and in D of that of C.

**FIG. 2.** The response of the Ia afferent of Fig. 1 to the static \( \gamma \) stimulation during the last 1,000 ms of the plateau of Fig. 1A and its analysis. A and C: the response of the Ia afferent to the static \( \gamma \) stimulation (14 superimpositions); C after elimination of the offset. B and D: frequency spectrum of the Ia afferent response; in B of the discharge pattern of A and in D of that of C.
An analysis of the frequency spectrum of Fig. 1B shows that the responses of the Ia afferent to the γ stimuli can be obtained if the frequencies of the frequency spectrum which characterize the offset and the ramp stretch—the frequencies <8 Hz—are reduced to an amplitude of 0 imp/s. Transposing the remaining frequencies of the frequency spectrum back into the time dimension produces the response of the Ia afferent to the γ stimuli. The resulting oscillatory responses are shown by the dots in Fig. 3.

Of interest for this investigation are the frequency and the amplitude of the oscillatory responses induced by the γ stimuli. The frequency of the oscillatory responses corresponds to the basic frequency of the frequency spectrum. In Fig. 1B, for example, the basic frequency is the first frequency of elevated magnitude in the frequency spectrum beyond the direct component and the slightly elevated frequencies representing the ramp-and-hold stretch. In RESULTS, the basic frequency will be compared with the stimulation frequency.

To arrive at a qualitative determination of the amplitude, i.e., the modulation depth of the oscillatory responses induced by the γ stimuli, a spline function with $s = 100$ was inserted into the discharge pattern of the oscillatory responses. For a better demonstration of this procedure, eight oscillations occurring at the end of the plateau of Fig. 3B are shown in A against an enlarged time scale. The spline function is given by the fine line in Fig. 3A. A spline function describes the shortest distance between the values available. One can see from the spline function that none of the oscillatory responses is sinusoidal. Thus to determine the maximum and minimum of each oscillatory response the frequency spectrum of the spline function of each oscillatory response was determined by a fast Fourier transformation. The basic frequency obtained from the frequency spectrum of the fast Fourier transformation describes the sinusoidal function that deviates the least from the spline function and is given as a thicker line in Fig. 3A. The maximum, the minimum, and the zero point of each oscillatory response were determined from its sinusoidal function. In Fig. 3B, the sinusoidal function calculated for each oscillatory response is shown by the oscillating line only during the two spans of time that are of interest for this investigation, i.e., under the initial and increased length. During these two spans of time, the upper, middle and lower lines join the maxima, the zero points, and the minima, respectively, of the oscillatory responses as determined from their sinusoidal functions. The magnitude of an oscillatory response is the difference between the maximum and the minimum of its sinusoidal function.

The validity of fitting a sinusoidal function to the oscillatory Ia responses obtained after the elimination of the underlying ramp-and-hold stretch needs to be explained. An oscillatory Ia response exists if the discharge frequency increases from a minimum to a maximum and declines again to a minimum within the interval between two consecutive γ stimuli as is the case in each of the responses in Fig. 3A or in the panels designated with 1 in Figs. 6 and 9. To determine the maximum and the minimum of a single oscillation as a numerical value, an averaging procedure is necessary by which the values available from a single oscillatory response are afforded equal weight. The fitting of a sinusoidal function to each oscillatory response is such an averaging procedure which enables us to define quantitatively a maximum and a minimum of an oscillatory response.

The interpretation of 1:1 driving as an oscillatory response also requires particular explanation. The state of 1:1 driving exists if the Ia afferent generates one action potential per γ stimulus in a train of γ stimuli. However, we use the superimposition technique according to Bessou et al. (1968a,b). This implies that under the condition of 1:1 driving, as many action potentials exist per γ stimulus as there have been stimulation repetitions performed. As a consequence, all details of the Ia response to a single γ stimulus are depicted. Thus a further analysis of the Ia response to a single γ stimulus can be made.

1:1 driving may be combined with phase-locking of the action potential, i.e., with the occurrence of the action potential at a fixed phase between two consecutive γ stimuli or at a fixed distance relative to the first of the two stimuli. The same fixed distance must occur in each of the 14 repetitions of the train of γ stimuli. The consequence of such 1:1 driving with phase-locking of the action potential is that the discharge frequency in impulses per second corresponds exactly, without any deviation, to the stimulation frequency in stimuli per second. In our experiment, 1:1 driving with phase-locking of the action potential is observed in the case of only one Ia afferent. Figure 4 shows an example of 1:1 driving without phase-locking of the action potentials. A gives the response of a Ia afferent under the increased length and under a γ stimulation frequency of 28.8/s

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**FIG. 3.** Evaluations of the response of the discharge pattern of Fig. 1A to the γ stimuli obtained after elimination of the response to the ramp-and-hold stretch. Dots, discharge frequency. A: section from the pattern of B. Fine line, the spline function calculated from the dots; thick line, the sinusoidal function calculated from the spline function of each oscillatory response. B: the 2 periods of the response after elimination of the ramp-and-hold stretch being further evaluated in this investigation are accentuated. Oscillating line, sinusoidal function of each oscillatory response; upper, middle, and lower fine lines, maxima, 0 points, and minima of the oscillatory responses determined from their sinusoidal functions. Horizontal bars, mean maxima and minima of the oscillations determined within the period of the initial length and the increased length. 1, beginning; 2, end of the ramp; 3, end of the plateau of the originally underlying ramp-and-hold stretch.
presented in compressed scales. In Fig. 4B, a section of A is depicted given in enlarged scales. The Ia afferent responds to each $\gamma$ stimulus with one action potential during each of the 14 repetitions. However, the latency between two consecutive action potentials is not identical as between one repetition of the train of $\gamma$ stimuli and another but only similar. Thus the cluster of discharge frequency dots belonging to one $\gamma$ stimulus extends along the $y$ axis. Consequently, the Ia response corresponds to the definition of an oscillatory Ia response even when the action potentials are 1:1 driven within the rhythm of the $\gamma$ stimuli. To demonstrate this, the spline function is inserted into Fig. 4B. In general, the spline function rises from the minimum of one cluster of dots to the maximum of the following cluster. Thus the dot of a cluster having the highest discharge frequency is the maximum of that oscillatory response. On both sides of this maximum, the spline function shows lower discharge frequencies, so that the maximum is flanked by a minimum on both sides. Thus the discharge frequency rises from a minimum to a maximum and then passes over to a minimum again between two consecutive $\gamma$ stimuli. The difference between the maximum and the minimum is small and so, therefore, is the magnitude of the oscillatory response. Our evaluation method also produces the same depiction as in the preceding description of 1:1 driving as an oscillatory response. Figure 4C shows the response of the Ia afferent of A after elimination of the underlying ramp-and-hold stretch. Figure 4D, giving the same section of the Ia afferent response as in B, shows the result of our evaluation method. The dots represent the Ia response, the oscillatory line shows the sinusoidal function calculated from the discharge frequency dots of an oscillatory response of Fig. 4D. The three horizontal lines join the maxima, the zero points, and the minima of the consecutive sinusoidal functions, respectively. It can be seen that our evaluation procedure calculates the magnitude of the oscillatory response as being small if the Ia action potentials are driven within the rhythm of the $\gamma$ stimuli.

A further property of 1:1 driving needs to be considered; 1:1 driving means that only one action potential per $\gamma$ stimulus is generated. It is known that the amplitude of a sine cannot be mathematically defined if only one value of the sine is known. However, we use the superimposition technique. Under the condition of a sufficient number of superimposed Ia responses, all details of an Ia response are depicted. This implies that the magnitude of the oscillatory response can be evaluated. By contrast, if a train of $\gamma$ stimuli is performed only once and the Ia afferent responds with 1:1 driving then in fact only one action potential per $\gamma$ stimulus exists. Under this condition, no statement can be made about the magnitude of the oscillatory Ia response.

The magnitude (maximum minus minimum) of the oscillatory responses fluctuates. To obtain the magnitude of a representative oscillation under one $\gamma$ stimulation frequency, a mean magnitude of oscillation was determined within the two spans of time of interest, i.e., under the initial length during the last 500 ms before the beginning of the ramp and under the increased length during the last 500 ms before the release. The mean maximum and the mean minimum of the oscillations during these two spans of time are shown by horizontal lines in Fig. 3B.

**RESULTS**

**First group of static $\gamma$ stimulations leading to oscillations in the Ia discharge frequency of large magnitude**

The discharge frequencies of 23 Ia afferents were recorded under the stimulation of a static $\gamma$ fiber at a linearly increasing frequency. A first group of static $\gamma$ stimulations, namely those activating 10 different Ia fibers, led in the response of the Ia fibers to a cloud of discharge frequency dots whose mean discharge frequency increased with the linearly increasing stimulation frequency and whose minimum discharge frequency was higher than or equal to the stimulation frequency. Figure 5 shows a representative example. The dots represent the Ia discharge frequency, the fine diagonal line gives the frequency of the $\gamma$ stimuli. One can see that discharging is affected in a highly irregular way. The minimum discharge frequency is higher than the stimulation frequency between ~20 and 80 stimuli/s and beyond that roughly equal to the stimulation frequency. We supposed that oscillatory responses of the Ia afferent lay behind the irregular discharging. This assumption was tested under constant stimulation frequencies. We chose a constant $\gamma$ stimulation frequency because we could then determine the magnitude of the oscillatory responses with the fast Fourier routine as described in METHODS.

Figure 6 shows sections of the discharge pattern of the Ia afferent of Fig. 5 under stimulation frequencies of 9.4, 48.2, and 77.6/s. In Fig. 6, A–C the discharge frequency is given during the two spans of time of the initial and increased length. Under a constant stimulation frequency of 9.4/s (Fig. 6A), the Ia afferent responds with fairly large oscillatory discharge frequency changes occurring in the same rhythm as the $\gamma$
stimuli. The spline function ($s = 100$) calculated from the discharge frequency is given in Fig. 6A in the section obtained under the increased length. In this section, the minima of the oscillatory responses are higher than the stimulation frequency. This means that during the 14 $\gamma$ stimulation repetitions, the Ia afferent regularly generates more than one action potential per $\gamma$ stimulus. (Under this condition, the minimum discharge frequency is higher than the stimulation frequency; the maximum of the discharge frequency cannot be predicted because the distance between the multiple action potentials per $\gamma$ stimulus is not known.) In the discharge pattern of Fig. 5, recorded under a ramp frequency stimulation, the stimulation frequencies for which Fig. 6 shows sections of the discharge pattern are marked by vertical lines. At a stimulation frequency of 9.4/s, the Ia response in Fig. 5 is very similar to that in Fig. 6A obtained under the increased length: the minima of the discharge frequency are higher than the stimulation frequency and the maxima reach high values.

In the two discharge pattern sections shown in Fig. 6, B (48.2 stimuli/s) and C (77.6 stimuli/s), only highly irregular Ia discharging can be seen. Because of the compressed time scale, no oscillatory discharge frequency changes can be recognized. However, when the time scale is enlarged as in Fig. 6, B1 and C1, the oscillatory Ia responses occurring in the rhythm of the stimulation frequency can easily be recognized. The spline function ($s = 100$) calculated from the discharge frequency dots is inserted in both panels. In Fig. 6B1, the minima of the oscillations are higher than 48.2 imp/s. This means that in each of the 14 superimposed patterns the Ia fiber generates more than one action potential per $\gamma$ stimulus. In Fig. 6C1, by contrast, the minima of the oscillatory responses lie at $\sim 80$ imp/s. Here the Ia fiber generates only one action potential per $\gamma$ stimulus in some of the 14 stimulation repetitions. Thus the minimum discharge frequency is equal to the stimulation frequency. However, in other repetitions more than one action potential per $\gamma$ stimulus is generated so that the maxima of the oscillatory responses are higher than the stimulation frequency.

The characteristics of the oscillatory responses described from Fig. 6, B1 and C1, can also be found in Fig. 5 under ramp frequency stimulation at the respective stimulation frequencies. At the stimulation frequency of 48.2/s the lowest discharge frequency of the broad, irregular discharge band is higher than the stimulation frequency, whereas the maximum discharge frequency is similar in height to Fig. 6B1. At the stimulation frequency of 77.6/s, the lowest discharge frequency is at the level of the stimulation frequency while the maximum discharge frequency reaches values like those in Fig. 6C1. Under a constant $\gamma$ stimulation frequency, we can demonstrate, by using an appropriate time scale and a sufficient number of superimpositions for the presentation, that there are oscillatory responses underlying the irregular appearance of Ia discharges.

In Fig. 6C1, obtained under 77.6 stimuli/s, the oscillatory responses of the Ia afferent delineated by the spline function ($s = 100$) are quite uneven. The reason for these uneven responses is the small number of repetitions, namely only 14. As a consequence, only a small number of discharge frequency dots fall into one oscillatory Ia response at this high-stimulation frequency. Theoretically, if an even oscillatory response is to be obtained, the number of repetitions should be at least as high as the expected oscillation frequency (Bessou et al. 1968a). However, it was not possible to increase the number of repetitions per experiment. The protocol of the experiment was already so long that any further extension would have involved the danger that fatigue of the spindle would lead to unfavorable Ia responses being recorded.

In Fig. 6, right, the same periods of the Ia response are shown as on left. Figure 6, D–F, shows the oscillations after a sinusoidal function has been fitted to the oscillations of the Ia responses obtained after the elimination of the offset and the ramp stretch of the original discharge frequencies. Figure 6, E1 and F1, show the oscillations selected from the span of time under the increased length on an enlarged time scale. The maxima, minima, and zero points of the sinusoidal oscillations are each joined by a fine line so that the oscillation’s magnitude are defined quantitatively.

Under the increased length, Fig. 6D gives an example showing that the fitting of a sinusoidal function to the oscillatory Ia response is an averaging process that gives equal weight to all the available values. The minimum of each of the oscillatory responses is characterized by a large number of values, whereas at their peaks there are only a small number of values. Thus the fitted sinusoidal function would give excessive weight to the small number of peak values if the maxima of the sinusoidal function were higher.

The fine horizontal lines in Fig. 6, D–F, show the mean magnitude of the oscillatory responses under the stimulation frequency concerned within the two spans of time depicted. It can be seen that the magnitude of the oscillations is largest at the stimulation frequency of 48.2/s and smaller at the lower and higher stimulation frequencies. Moreover the magnitude is enhanced under the increased muscle length. In Fig. 7, in which the magnitudes of oscillation of eight Ia afferents are averaged, these observations are generalized. It was only possible to include the effects of 8 $\gamma$ stimulations in the average, because only 8 of the 10 $\gamma$ stimuli of the first group were tested under constant $\gamma$ stimulation frequencies. Figure 7 gives the mean result. The magnitude of the oscillations determined under the increased length attains its highest value at a stimu-
lation frequency of 29/s and then declines to give only small values at 95/s. At all stimulation frequencies ≤77.6/s, the magnitude of the oscillations determined under the initial length is smaller than that determined under the increased length. Only at 95/s is the magnitude of oscillation equally large during both periods of time. The magnitude determined under the initial length does not attain its highest value until the stimulation frequency reaches 48/s and is still very small at 29/s. The high difference in the magnitude of oscillation determined during the two periods at a stimulation frequency of 29/s results from the fact that under the increased length, the Ia afferents respond with large oscillations, whereas under the initial length, as a consequence of the small stretch, the Ia afferents generate oscillatory responses of only small magnitude because various Ia afferents are driven in a 1:1 rhythm with the γ stimuli. The prestretch of the muscle under which...
the effect of a γ stimulation on the magnitude of oscillation of the Ia afferent was tested was 9 mm for five and 3 mm for three of the eight γ stimulations.

The frequency of the oscillatory responses can be determined quantitatively by the basic frequency of the frequency spectrum, this being the first frequency of elevated magnitude beyond the frequencies of the offset and the ramp stretch (Figs. 1B or 2D). In Fig. 6, left, the frequency spectrum’s basic frequency is given in the time dimension by the sinusoidal function that has been fitted to the oscillations of the Ia response. To be able to test whether the frequency of the oscillatory responses is equal to the stimulation frequency, the basic frequency is compared with the γ stimulation frequency. The investigation shows that under each of the five γ stimulation frequencies, the basic frequency of the 8 Ia afferents corresponds to the γ stimulation frequency. Thus in all instances the Ia discharge frequency oscillates in the rhythm of the γ stimuli of the first group. Moreover, on a compressed time scale, the discharges of the Ia afferents under the increased muscle length form a broad discharge band whose width roughly corresponds to the magnitude of the Ia oscillation. In no instance is 1:1 driving of the Ia action potentials in the rhythm of the stimulation frequency or submultiples of it observed under the increased muscle length.

Second group of static γ stimulations leading to oscillations of small magnitude in the Ia discharge frequency

Thirteen Ia afferents respond to the static γ stimulation of linearly increasing stimulation frequency with one action potential per γ stimulus (driving) until a specific stimulation frequency is reached. Beyond that frequency the discharge frequency settles at a constant level. Although the discharge patterns under linearly increasing stimulation frequencies have the same qualitative appearance, they differ quantitatively, dividing into two subgroups. In 4 of the 13 afferents—the first subgroup of this second group, an example is given in Fig. 8A—the discharge frequency shows 1:1 driving in a non-phase locked manner up to a stimulation frequency of ~45/s. Beyond that stimulation frequency, the discharge frequency becomes very irregular and stops increasing beyond ~80/s. In 9 of the 13 afferents—the second subgroup of this second group, an example shown in Fig. 8B—the initial driving period is more pronounced before the discharge frequency settles at a constant level in a moderately broad discharge band beyond ~80/s, and—as is typical of the second subgroup—develops then a second lower discharge band whose minimum discharge frequency corresponds to 1:2 driving.

The responses of 10 of the 13 Ia afferents of the second group were investigated under a constant γ stimulation frequency. Of these 10 Ia afferents, 3 belong to the first and 7 to the second subgroups; and here too, the two subgroups differ to some extent in the behavior of the discharge frequency in their discharge patterns. Figure 9, A–D, depicts discharge patterns of a Ia afferent under the γ stimulation of Fig. 8A, i.e., patterns of the first subgroup. At a γ stimulation frequency of 9.4/s (Fig. 9A), the mean discharge frequency is >9.4imp/s, so that the Ia afferent generates more than one action potential per γ stimulus. Both at the initial length and at the increased length oscillatory discharge frequency changes can be observed occurring in the rhythm of the stimulation frequency. The oscillatory responses are of small magnitude. In the discharge pattern obtained under 48.2 stimuli/s (Fig. 9B), the Ia afferent discharges irregularly at an elevated level. But when presented on an enlarged time scale as in Fig. 9B1, in which a section of Fig. 9B is given under the initial length, the irregular discharging resolves into recognizable regular oscillatory responses in the rhythm of the γ stimuli. However, the magnitude of the Ia oscillations is only small compared with that of the first group (Fig. 6). Figure 9, E–H, shows discharge patterns under the γ stimulation of Fig. 8B, i.e., patterns of the second subgroup. Under the γ stimulation frequency of 9.4/s (Fig. 9E), the discharge frequency is driven at the initial length and develops oscillations of slightly elevated magnitude at the increased length, each in the rhythm of the γ stimuli. Under the stimulation frequency of 48.2/s (Fig. 9F), the discharge frequency is driven in a non-phase locked manner. The magnitude of the oscillatory Ia responses in Fig. 9F1, a section from Fig. 9F at
the increased muscle length, verifies the low magnitude of the oscillatory responses occurring in the rhythm of the \( \gamma \) stimuli. Thus under the higher stimulation frequencies, the responses of the Ia afferents to the \( \gamma \) stimuli are characterized by undulating oscillatory responses in the first subgroup and by driving in the second subgroup. However, in both subgroups the magnitude of the oscillatory responses is small. This is quantified in Fig. 9, right.

These panels show the magnitude of the oscillations in the discharge frequency after the elimination of the offset from the original discharge patterns of Fig. 9, left. The oscillations in the discharge patterns of the first subgroup, i.e., in Fig. 9, C and D, are of slightly elevated magnitude compared with those of the second subgroup, i.e., in Fig. 9, G and H, except under the increased length in Fig. 9G. The difference in magnitude between the oscillations of the two subgroups results from the fact that the discharge frequency of the second subgroup is typically driven or subdriven in the rhythm of the \( \gamma \) stimuli.

Figures 10, A and B, generalize the observations concerning the magnitude of the oscillatory responses of the two sub-
groups of the second group. Figure 10A shows the mean magnitude of oscillation calculated from three Ia afferents of the first subgroup and B that calculated from seven Ia afferents of the second subgroup, each tested at the five constant γ stimulation frequencies determined under the initial and increased lengths. In both subgroups, the magnitude of oscillation determined under the initial length is very low and more or less independent of the stimulation frequency, whereas under the increased length, the magnitude of oscillation at stimulation frequencies of 28.8 and 48.2/s is slightly higher in the first than in the second subgroup. This difference is not significant (P > 0.05), and results from the driving behavior of the second subgroup as compared with the undulating oscillatory Ia responses of the first subgroup. However, it is evident that the responses of both subgroups of the second group are of low magnitude as compared with those of the first group.

Furthermore, Fig. 10, C and D, illustrates additional features characterizing the two subgroups of the second group under constant frequency stimulation. First a test was made of the extent to which the frequency of the oscillatory responses is equal to the stimulation frequency. The frequency of the oscillatory responses is determined quantitatively by the basic frequency of the frequency spectrum. The γ axis of Fig. 10, C and D, shows the extent to which the two frequencies are equal, each column depicting this in respect of one Ia afferent. Figure 10C shows the results from the three Ia afferents tested under the γ stimulations of the first subgroup. With one Ia afferent, the two frequencies are equal up to the maximum stimulation frequency of 95/s, but with the remaining two, this is only the case ≤48.2/s, although they were tested ≤95/s (as is indicated by the parts of the 2 columns shown by broken lines). At stimulation frequencies of 77.6 and 95/s, these two Ia afferents discharge in an irregular way and in a comparatively small discharging band without oscillatory responses in the rhythm of the γ stimuli. Figure 10D represents the results obtained from the seven Ia afferents tested under the γ stimulations of the second subgroup. With all of them, the frequency of the oscillatory responses is equal to the stimulation frequency up to the maximum stimulation frequency tested, although for the two first Ia afferents of Fig. 10D this is only 77.6/s. The second feature examined is the way the Ia afferents’ discharge frequencies oscillate in the rhythm of the γ stimuli. This is read from the discharge frequency under increased length and is indicated in each column. The undulating lines represent oscillatory Ia responses given by a number of action potentials per oscillation (as in Fig. 9, A, B, and E, under increased length). The extent of these lines indicates the stimulation frequencies at which this kind of undulating Ia oscillatory response was observed. The dotted part of each column represents those stimulation frequencies at which the Ia response is characterized by driving or subdriving. Thus the discharge behavior of all the three Ia afferents of the first subgroup (Fig. 10C) is characterized by undulating oscillatory Ia responses, whereas six of the seven Ia afferents of the second subgroup develop driving or subdriving under the higher stimulation frequencies. The seventh Ia afferent also demonstrates driving and subdriving behavior but only under ramp frequency stimulation. Thus the seven Ia afferents of the second subgroup develop driving or subdriving behavior, whereas the three Ia afferents of the first subgroup are characterized by nondriving behavior.

Statistical difference between the magnitudes of oscillation of the first and second group of static γ stimulations

The oscillatory responses of the Ia afferents to the γ stimuli of the first group of static γ stimulations are of large magnitude and of small magnitude if the static γ fibers of the second group, irrespective of the subgroup, are stimulated. However, only at the increased length could a significant difference [P < 0.01 (t-test)] be observed in the magnitude of oscillation under the γ stimulations of the second subgroup and of the first group at the stimulation frequencies of 28.8, 48.2, and 77.6/s. We suppose that a significant difference in the magnitude of oscillation as between the first and the second group of γ stimulations would be found more frequently if the number of individual values available for each group were larger. To increase the number of values, we developed an enlarged significant test. We used the individual values of one group available under each of the five stimulation frequencies to calculate a single mean value per group. A comparison of the enlarged mean values of the first group and of the two subgroups of the second group shows that the magnitude of oscillation is significantly larger under γ stimulations of the first group than...
under either of the two subgroups of the second group, with $P < 0.01$ ($t$-test) at both the initial and the increased length, whereas it is not significantly different between the two subgroups of the second group at either the initial or the increased length.

**DISCUSSION**

We describe two groups of static $\gamma$ stimulations. The $\gamma$ stimulations of the first group elicit oscillatory Ia responses of large magnitude, those of the second group responses of small magnitude. First we follow up the question as to which kind of intrafusal muscle fiber has contracted under the $\gamma$ stimulations of the first and of the second group, respectively. Celichowski et al. (1994) elaborate characteristic features read from the discharge frequency of the Ia afferents under the stimulation of static $\gamma$ fibers from which the kind of intrafusal muscle fiber contracting in the individual case can be identified (Emonet-Dénand et al. 1997). The former authors elaborate the characteristic features under a constant $\gamma$ stimulation of $30/s$ from cross-correlograms constructed during ramp frequency stimulation and during constant frequency stimulation of $100/s$ and by visual inspection of the discharge frequency under ramp frequency stimulation.

If the bag$_2$ and chain fibers are innervated simultaneously, the discharge frequency generally elicits very irregular discharges under ramp frequency stimulation and increases in a broad discharge band (Boyd 1986; Boyd and Ward 1982; Celichowski et al. 1994). Under a stimulation frequency of $30/s$, the Ia afferent discharges in a broad irregular discharge band whose minimum is higher in impulses per second than the stimulation frequency in stimuli per second. Under a stimulation frequency of $100/s$ significant peaks are observed in the respective cross-correlograms, which are a characteristic feature of a bag$_2$-chain contraction. We refer to these descriptions to identify bag$_2$-chain fiber contractions taking place under our $\gamma$ stimulations; we did not, however, construct cross-correlograms ourselves.

Under $\gamma$ stimulation of the first group, the bag$_2$ and chain fibers should as a rule contract simultaneously. Under ramp frequency stimulation, the Ia afferents generate very irregular discharges, and the discharge frequency increases in a broad discharge band (Fig. 5). Under a stimulation frequency of $30/s$, the irregular and very broad discharge band has a minimum that is clearly above the stimulation frequency. In two cases, admittedly, the minimum discharge frequency is only at just the same level as the stimulation frequency even though the irregular discharge band is indeed very broad. In these two cases, it could be that there is a contraction of the bundle of chain fibers only.

Under the $\gamma$ stimulations of the second group, we assume bag$_2$ or chain fiber contractions. Chain fiber contractions are best identified by the presence of driving of the action potentials in a 1:1 rhythm with the $\gamma$ stimulation frequency or submultiples of it (Boyd 1980, 1986; Boyd and Ward 1982; Boyd et al. 1977, 1979; Dickson et al. 1993). Thus seven of the $\gamma$ stimulations of the second group—i.e., the second subgroup—induce chain fiber contractions, identified by the discharge frequency being driven in the rhythm of the stimulation frequency or in submultiples of it, under constant stimulation frequency or ramp frequency stimulation (Fig. 10D). By contrast, in the case of bag$_2$ fiber contractions, driving of the discharge frequency is a rarity and occurs only very occasionally. Instead, irregular discharging is often observed (Boyd 1981, 1986) or else regular discharging under ramp and under constant frequency stimulation (Figs. 8A and 9B), so that we postulate bag$_2$ fiber contractions under these $\gamma$ stimulations.

The frequency of the oscillatory responses is determined quantitatively, under our evaluation method, by the basic frequency of the frequency spectrum. The frequency of the oscillatory responses is the same as the stimulation frequency under the $\gamma$ stimulation of the first group, in each instance up to a stimulation frequency of $95/s$. Under the $\gamma$ stimulations of the second group, the equality of the frequency of oscillation and the $\gamma$ stimulation frequency extends $\leq 77.6$ and $95/s$, respectively under each of the seven $\gamma$ stimulations to which chain fiber contractions are ascribed. Under the three $\gamma$ stimulations where bag$_2$ fiber contractions are postulated to take place, this equality extends in one case $\leq 95/s$ and in the remaining two instances $\leq 48.2/s$. This means that in the case of bag$_2$ fiber contractions as well, the discharge frequency oscillates in the rhythm of the $\gamma$ stimuli (Fig. 9, A and B1). Oscillatory responses in the rhythm of the $\gamma$ stimuli are regularly demonstrated at $\leq 48.2/s$ under bag$_2$ fiber contraction, but $\leq 95/s$ (Fig. 10B) under chain fiber contraction. This reflects the contraction velocity, which is slower for bag$_2$ fibers than for chain fibers (Boyd 1976), so that the fusion frequency ought to be reached at a lower range of stimulation frequencies under bag$_2$ (50/s) than under chain fiber contraction (100–150/s).

The aim of this elaboration on the kind of intrafusal muscle fiber contracting under the $\gamma$ stimulations of the first and second group is to explain the appearance of oscillatory responses of large and of small magnitude in terms of their mechanical properties. It is true that the Ia responses may depend on the properties of the transducer or on the mechanical properties of the intrafusal muscle fibers or both. But we suppose that the oscillatory responses depend mainly on the mechanical properties of the intrafusal muscle fibers in the range of stimulation frequencies we used.

The reasons why the oscillatory Ia responses to the individual $\gamma$ stimuli are significantly larger under $\gamma$ stimulations of the first than of the second group will now be discussed. The magnitude of the oscillatory Ia responses depends on two parameters: the degree of stretch of the sensory Ia endings and the number of sensory Ia endings being stretched. These two parameters define the overall receptor potential that initiates the action potential sequence at the action potential generating site and whose discharge frequency is recorded in our experiments.

Under a $\gamma$ stimulation, the degree of stretch of the sensory endings of one intrafusal muscle fiber depends on the degree of contraction of its polar parts. In the frequency range of the unfused tetanus, the background force that increases continuously with the stimulation frequency is overlaid by rhythmic contractions. The magnitude of the rhythmic contractions decreases the nearer the stimulation frequency comes to the range of the fused tetanus. In the corresponding length, changes in the equatorial part the sensory Ia endings participate by responding with a corresponding receptor potential.
In respect of the $\gamma$ stimulations of the first group, we deduced that the bag$_2$ and chain fibers or the bundle of chain fibers contract. The number of intrafusal muscle fibers contracting is large and so also is the number of sensory endings experiencing a stretch and generating a receptor potential. Up to a stimulation frequency of $\leq 50$/s, the bag$_2$ and chain fibers should contract with an unfused tetanus (Fig. 10, C and D). In this range of frequencies, the bag$_2$ and chain fibers oscillate synchronously so that the receptor potential of the sensory endings of the oscillating intrafusal muscle fibers can add so that, as a consequence, the oscillatory Ia responses are of large magnitude. This interpretation correlates with the enhanced oscillation’s magnitude up to the stimulation frequencies of 48.2/s (Fig. 7). The magnitude of the oscillatory Ia responses diminishes again under stimulation at frequencies of 77.6 and 95/s. Under these stimulation frequencies in general, the bag$_2$ fibers will be in a state of fused tetanus (Fig. 10C). Thus the oscillatory depolarizations and repolarizations of the receptor potential are carried only by those chain fibers whose fusion frequency is $\sim 100$ stimuli/s. At the same time, the chain fibers are close to their fusion frequency so that the changes in the oscillatory force of their polar parts are only small, as are also, correspondingly, the length changes of their sensory endings.

We deduced that the bag$_2$ fiber or the chain fibers contract under $\gamma$ stimulations of the second group. We observe only small oscillatory Ia responses (Fig. 10, A and B). This is best explained if only a small number of sensory endings undergo an elongation as is the case if only the bag$_2$ or only one or at most two of the chain fibers are innervated and if the $\gamma$ fiber reaches only one pole as seems not infrequently to be the case (Boyd 1986; Dickson et al. 1993). If only one pole contracts, the force of the contracting pole will predominantly stretch the passive pole and only to a lesser degree the equatorial part (Boyd 1976). Moreover, if only a small number of sensory endings perform oscillatory length changes, the oscillatory Ia responses will be of small magnitude because the overall receptor potential is small.

Consideration needs to be given to the presumption that the muscle spindles are slack under $\gamma$ stimulations of the second group and tight under those of the first group (Proske et al. 1993). We can exclude this presumption because we choose as the initial length a degree of prestretch of the muscle at which each Ia afferent generates an initial peak at the beginning of a ramp-and-hold stretch. This test was performed with the passive spindle. However, a Ia afferent generates an initial peak only if the spindle is tight. Thus the spindles of the second group of $\gamma$ stimulations were not in a slack state when investigated.

An enhanced stretch of the equatorial part was induced experimentally by increasing the stretch of the muscle by 7 mm. The enhanced stretch caused the Ia afferent to respond to the $\gamma$ stimuli with oscillatory responses of increased magnitude (Figs. 7 and 10, A and B). This could be the result of an increased contraction force as the consequence of an increased sarcomere length induced by the enhanced stretch. This effect seems to be more successful under the $\gamma$ stimulations of the first group than under those of the second. We assume that this difference between the two groups is a consequence of the number of poles contracting, and thus increasing their contraction force, as a result of the increased sarcomere length. The effect of the increased contraction force on the overall receptor potential of the sensory spirals is higher where there is a larger number of innervated poles, as is the case under stimulations of the first group, than where only one or at most two poles enhance their contraction force, as under stimulations of the second group.

We describe two groups of $\gamma$ stimulation. These two groups do not correspond to two groups of $\gamma$ fibers. Rather, we believe that one $\gamma$ fiber will produce a first group effect on one Ia afferent and a second group effect on another, depending on the number of static intrafusal muscle fibers that the static $\gamma$ fiber innervates in the single spindle and by this as well on the number of sensory Ia endings experiencing an elongation.

To observe large oscillatory Ia responses, the technique has to be used of superimposing Ia responses recorded under a particular number of stimulations performed one after another (Bessou et al. 1968a,b). The Ia afferent responds to each repetition of the stimulation with an action potential sequence whose discharge frequency is a reflection of the intrafusal sensory length changes. However, within the sequence, under each repetition, the action potentials are displaced in respect of time. As a result, each repetition adds some further detail of the stimulus to the Ia response. Consequently, all the details of the Ia response to the stimulation are delineated in the discharge pattern obtained after superimposing the Ia responses to the various stimulation repetitions (Awiszus 1988). However, different author groups performed each $\gamma$ stimulation only once. Under these circumstances, large oscillatory Ia responses present themselves as irregular discharging (Celichowski 1994), as biasing (Banks 1991) or as nondriven firing (Dickson et al. 1993). These descriptions result from the fact that where the Ia afferent generates more than one action potential per oscillation (as in Figs. 6C1 or 9B1), the individual action potentials are not in general generated in any definite time relationship to the $\gamma$ stimuli. It is thus not possible to identify Ia action potentials occurring in the rhythm of the $\gamma$ stimuli. By contrast, driven action potentials that are phase locked or nearly phase locked to the $\gamma$ stimuli can be identified even if a $\gamma$ stimulation is performed only once. This seems to be the main reason why driven action potentials were interpreted as the only possible Ia response to intrafusal oscillatory contractions. In fact, however, driven action potentials is only one of the possible Ia responses to intrafusal oscillatory contractions. Banks (1991) observes driving in the discharge frequency of the Ia afferent under low-stimulation frequencies of a static $\gamma$ fiber. The author interprets the driven Ia firing as indicating chain fiber contractions. The Ia firing changes to irregular discharging under high-stimulation frequencies. This kind of Ia discharge is interpreted as being a consequence of the bag$_2$ fiber contracting together with the chain fibers. However, Banks (1991), like Celichowski et al. (1994), can less easily explain how the chain fiber driving is suppressed by a concomitant bag$_2$ fiber contraction. Our interpretation of this observation is straightforward. Under low-stimulation frequency, the background tension of the polar parts is low, the stretch of the sensory part induced by the low background tension is small so that the Ia sensitivity to the overlaid oscillatory contractions is still low, so the Ia afferent responds with oscillatory responses of small magnitude, i.e., with driving. Under high-stimulation frequencies, the effect of each of the factors enumerated is high. The Ia afferent is able to respond with oscillations of large magnitude, which without further
analysis appear to be irregular discharging. Thus the oscillatory response of the Ia afferent changes from one of small magnitude to one of large magnitude.

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