

Position Sensitivity of Human Muscle Spindles: Single Afferent and Population Representations

PAUL J. CORDO,¹ CARMEN FLORES-VIEIRA,^{1,2} SABINE M. P. VERSCHUEREN,³ J. TIMOTHY INGLIS,⁴ AND VICTOR GURFINKEL¹

¹Neurological Sciences Institute, Oregon Health & Science University, Beaverton, Oregon 97006; ²Department of Neurology, Psychiatry, and Medical Psychology, University of São Paulo, 3900 Ribeirão Preto, Brazil; ³Department of Kinesiology, Katholieke Universiteit Leuven, 3000 Leuven, Belgium; and ⁴School of Human Kinetics, Brain Research Centre, The University of British Columbia, Vancouver, British Columbia V6T 1Z1, Canada

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Cordo, Paul J., Carmen Flores-Vieira, Sabine M. P. Verschueren, J. Timothy Inglis, and Victor Gurfinkel. Position sensitivity of human muscle spindles: single afferent and population representations. *J Neurophysiol* 87: 1186–1195, 2002; 10.1152/jn.00393.2001. The representation of joint position at rest and during movement was investigated in 44 muscle spindle primary afferents originating from the extensor carpi radialis brevis (ECRb) and extensor digitorum (ED) of normal human subjects. Position sensitivity was estimated for each afferent, and 43 of 44 were position sensitive. In each trial, six sequential ramp-and-hold movements (2–6°, 2°/s, total 24°) flexed the relaxed wrist, beginning from the angle at which the afferent was just recruited. Joint position was represented by three specific features of afferent firing patterns: the steady-state firing rate during the 4-s hold period between ramps, the initial burst at the beginning of each ramp, and the ramp increase in firing rate later in the movement. The position sensitivity of the initial burst (1.27 ± 0.90 pps/°, mean \pm SD) was several times higher than that of the hold period (0.40 ± 0.30 pps/°) and not different from that of the ramp increase in firing rate (1.36 ± 0.68 pps/°). The wrist position sensitivities of ECRb and ED afferents were equivalent, as were their recruitment angles and angular ranges of position sensitivity. Muscle spindle afferents, both individually and as a population, were shown to represent static joint position via the hold rate and the initial burst. Afferents were recruited over the entire 110° range of wrist positions investigated; however, the angular range over which each feature represented joint position was extremely limited ($\approx 15^\circ$). The population response, based on the summed activity of the 43 afferents, was monotonically related to joint position, and it was strongly influenced by the afferent recruitment pattern, but less so by the position sensitivities of the individual afferents.

INTRODUCTION

Among the variables attributed to the sense of proprioception, joint position is the most fundamental, in part because other variables can potentially be derived from joint position. Because proprioception plays an important role in the control of posture and movement, sensory receptors, such as muscle spindles, must provide the CNS with information about joint position (e.g., Burgess et al. 1982; Gandevia and Burke 1992; Matthews 1982; McCloskey 1978), and this information needs

to be appropriately precise for the CNS to control the intended motor task. For example, the precision requirements for movement are likely to be higher than those for the maintenance of posture.

A number of previous studies have examined how joint position, or the related variable muscle length, is represented in the firing patterns of individual proprioceptive afferents (e.g., Burgess et al. 1982; Edin and Johansson 1995; Harvey and Matthews 1961; Houk et al. 1981; Hulliger et al. 1985; Lennerstrand 1968; Matthews and Stein 1969; Vallbo 1974), although much less is known about how afferent populations represent joint position (cf. Botterman and Eldred 1982; Vallbo 1974). Under static or quasi-static conditions, individual muscle spindles have been shown to represent position by their steady-state firing rates (e.g., Botterman and Eldred 1982; Granit and Homma 1959; Harvey and Matthews 1961; Lennerstrand 1968; Vallbo 1974; Wei et al. 1986), but the static position sensitivities of human muscle spindles, at least, appear to be relatively weak. For example, in human muscle spindle Ia afferents, static position sensitivity has been reported to be ≤ 0.18 pps/° and even lower in group II afferents (Vallbo 1974).

During movement, the firing patterns of individual muscle spindles are more complex, increasing and decreasing as a nonlinear function of joint position. For example, during ramp-and-hold lengthening, a muscle spindle first produces a brief, high-frequency burst (“initial burst”), followed by a pause and then a gradual increase in firing rate. The peak firing rate of the initial burst has been suggested to be position-dependent (Houk et al. 1981; Lennerstrand 1968), although the nature of this dependence has not been systematically investigated. After the pause following the initial burst, the firing rate increases monotonically (“ramp increase”) as a function of position (e.g., Grill and Hallett 1995; Houk et al. 1981; Lennerstrand 1968; Matthews 1963). The position sensitivity of the ramp increase has not been quantified for human muscle spindles; however, in the decerebrate cat, it has been reported to be roughly twice that of static position sensitivity (Houk et al. 1981), consistent with

Address for reprint requests: P. J. Cordo, Neurological Sciences Institute, Oregon Health & Science University, 505 NW 185th Ave., Beaverton, OR 97006 (E-mail: cordop@ohsu.edu).

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the supposition that position sensitivity should be higher during movement than during the maintenance of posture.

The picture that emerges from previous studies, mostly performed with animals, is that individual muscle spindles represent position differently at rest and during movement. At rest, position appears to be represented by the steady-state firing rate ("hold rate") of these muscle spindles, and during receptor lengthening, it is represented by the ramp increase, possibly with some contribution from the initial burst. However, because most reported recordings of muscle spindles have been made one at a time over a limited range of muscle length, it is unclear how the population of receptors in a muscle, or synergistic group of muscles, represents position over the entire range of joint motion.

The study reported in this paper examined the relationship between joint position and firing rate (i.e., "position sensitivity") for the hold rate, the initial burst, and the ramp increase in a sample of human muscle spindle primary afferents. We quantified, for each afferent and each feature of the firing pattern, the recruitment angle, the position sensitivity, and the angular range of position sensitivity. A focus of the analysis was to determine whether any differences existed in position sensitivities for these three position-dependent features. The position sensitivity of the population was estimated from the summed firing patterns of the individual afferents in our sample, and the relative influences of afferent recruitment and firing pattern on the population response were compared. A preliminary report of this study was published as an abstract (Cordo et al. 2000).

METHODS

A total of 44 muscle spindle afferents were recorded in 18 experimental sessions involving 16 human subjects (ages 25–46) with no history of neuromuscular disorders. Prior to each experimental session, the subject provided informed consent according to procedures established by the Oregon Health & Science University Institutional Review Board. The activity of muscle spindle afferents originating from extensor digitorum (ED) and extensor carpi radialis brevis (ECRb) was recorded from the radial nerve of the right arm. Throughout the experimental session, the subject remained as relaxed as possible while the wrist was flexed with a staircase sequence of ramp-and-hold movements. We quantified the firing behavior of muscle spindle afferents during the hold period, at movement onset, and during the ramp change in position.

Experimental set-up and recording

The subject sat in a comfortable seat with the right arm on a table surface and the elbow resting on a foam cushion that rotated freely. The forearm was wedged in a U-shaped cuff. The fingers were inserted into a D-shaped handle, with the fingers and thumb wrapped around the handle (thumb at the top) and taped in place. The shoulder was abducted 60°, the elbow at 150°, and the wrist midway between supination and pronation. Beneath the table surface, a hydraulic actuator controlled the angular position of the wrist.

Afferent recordings were obtained from identified muscle spindle afferents originating in ED ($n = 13$) and ECRb ($n = 31$) using microneurographic procedures (Gandevia and Hales 1997; Hagbarth and Vallbo 1969). All 44 afferents responded to wrist flexion. An epoxy-insulated, tungsten microelectrode with a 0.25-mm shaft diameter and 5- μm tip was manually inserted through the skin of the upper arm into the radial nerve. To obtain a single afferent recording, the experimenter repositioned the microelectrode, guided by the amplified

nerve recording (audio and visual output) during sinusoidal wrist rotation (2 Hz, 2–4° peak to peak) and/or manual percussion of the dorsal forearm.

Muscle spindle afferents were identified based on a series of standardized procedures. The receptive field of the afferent was identified first through manual probing of the tendon and skin of the hand and forearm. Muscle spindles typically have two distinct receptive fields, one located over the muscle belly (1–3 cm in diameter) and another where the tendon crosses the wrist. Compression of a receptive field accelerates the firing rate, and release abruptly silences the afferent. Attempts were made to activate the afferent with passive joint rotation and localized voluntary contraction.

If all of these preliminary tests were positive for an afferent, it was tentatively classified a muscle spindle, and one to three trials were conducted on it with computer-controlled joint rotations. A trial consisted of one staircase sequence of wrist rotations. About 10% of the reported afferents were identified solely based on these preliminary tests (Table 1). If the recording remained stable for at least three trials, the appropriate tendon and the muscle receptive fields were then vibrated at 70 pps with a hand-held vibrator. If the afferent was not driven by vibration at either site with $\geq 2:1$ ratio, the afferent was discarded. Following a successful vibration test, additional trials were run.

After 8 to 12 trials, the muscle nerve was electrically stimulated with the voltage increasing to maximum contraction levels (Burke et al. 1987). The resulting muscle twitches usually caused us to lose the recording prior to reaching a maximal contraction, so twitch tests were used only to exclude tendon organ afferents ($n = 1$), which fire on the rising phase of twitches (Matthews 1933). No attempt was made to distinguish muscle spindle groups Ia and II afferents. However, the sample described in the following text consists principally, or exclusively, of muscle spindle Ia afferents because of their larger axon diameters and vibration sensitivities (Brown et al. 1967).

Although the subject attempted to remain relaxed, occasional reflex or voluntary contractions occurred, which might have led to thixotropic changes in the afferent response (Gregory et al. 1988). Therefore, the receptor was "reset" after each trial by briskly tapping the skin over its receptive field, to elicit four to five intense bursts of activity.

Wrist position, wrist force, EMG, and the nerve recording were digitized and stored on a computer. The wrist angle (Fig. 1C) was transduced by a potentiometer and recorded at 500 samples/s. By convention, a wrist angle of 0° represents a straight line between the hand and forearm, with flexion positions as positive and extension positions as negative. The raw electromyographic (EMG) activity of ED and ECRb (Fig. 1D) was recorded (Myotrace, Noraxon) with pairs of surface electrodes (Blue Sensor, Medicotest), spaced 4 cm center to center, parallel to the direction of muscle fibers, and digitized at 2,000 samples/s. These EMG recordings were amplified (4,000 times) and band-pass filtered (16–500 Hz). The nerve recording (Fig. 1B) was amplified (10,000–20,000 times), band-pass filtered (0.5–10 kHz), and digitized at 25,000 samples/s. Wrist force was measured by semiconductor strain gauges mounted to the wrist cuff, ~2 cm proximal to the wrist joint and digitized at 500 samples/s. All signals were processed by a data acquisition system (Micro1401, Cambridge Electronic Devices) prior to storage on a computer. Single-unit discrimination from the nerve recording was performed off-line.

Experimental procedures

Once a recording was acquired, the wrist was set as close as possible to the threshold angle for that afferent. If the afferent could not be silenced by wrist extension, the joint was set as close as possible to the position where the firing rate increased during the first ramp in a sequence. For ~30% of the afferents tested, additional starting positions were used, to evaluate the behavior of the afferent over a wide range of joint angles.

TABLE 1. Afferent recruitment angles and position sensitivities

Subject	Muscle	Trials, <i>n</i>	Recruitment Angle, °	Hold Rate		Initial Burst	
				Sensitivity, pps/°	Sensitivity range, °	Sensitivity, pps/°	Sensitivity range, °
VD	ECR	5	5	0.64	12	1.07	>24
	ECR	4	-16	0.33	12	0.9	12
DL	ECR	2	<-31	0.48	12	1.83	12
	ECR	2	<-31	0.38	8	2.3	8
SBI	ED _I	3	-1	1.32	6	1.18	16
	ECR	10	-1	0.5	14	1.27	14
MB	ED _M	5	4	0.61	12	1.88	8
	ED _M	3	4	0.93	4	3.4	4
	ECR	2	-17	0.3	18	NS	
	ECR	1	14	NS		1.48	>24
KB	ED _M	2	0	0.30	12	4.15	4
	ECR	3	-9	0.35	12	0.29	12
	ECR	2	-10	0.38	>33	0.82	>24
CS1	ECR	6	36	0.57	>19	0.9	>19
GK1	ED _M	7	23	NS		0.63	>24
	ECR	4	27	0.13	12	1.45	8
GG	ECR	4	<10	0.48	8	1.61	8
	ECR	1	<0	0.77	7	2.5	7
HE	ED _R	2	-10	0.42	>24	0.54	>24
	ECR	6	-10	NS		0.593	>20
WT	ECR	1	<-45	0.22	>24	0.44	>24
	ECR	5	-15	1.5	3	2.25	7
	ECR	3	0	0.18	17	1.2	8
	ECR	5	-6	0.32	12	0.53	>16
SS	ECR	11	<-20	0.48	20	0.85	20
	ECR	2	-13	0.5	9	1.52	9
	ECR	7	-4	0.13	4	0.88	15
SR	ED _M	2	0	0.68	4	2.98	8
	ECR	2	7	0.32	15	1.18	13
	ECR	2	0	NS		NS	
	ECR	1	<0	0.15	>24	0.17	>24
CS2	ED _I	2	<1	0.158	>24	1.77	12
CV	ED _I	2	<2	0.285	>24	0.334	24
	ECR	6	<0	0.24	>24	0.4	15
BP	ECR	3	8	0.282	>24	0.34	>24
GK2	ED _L	6	<-31	0.29	10	1.255	8
	ED _L	3	<-31	0.24	19	0.81	15
	ED _R	6	-10	0.39	9	0.62	>20
	ED _I	4	-14	0.6	16	1.47	16
SD	ECR	10	-10	0.37	16	1	20
	ECR	1	-9	0.3	9	1.02	>24
	ECR	8	<-15	0.28	>20	0.51	>24
	ECR	13	<-15	0.2	>24	2.1	9
	ECR	9	<-28	0.21	20	2.78	8

I, index; M, middle; R, ring; L, little.

The wrist was rotated with one of three sequences of six ramp-and-hold movements, with a velocity of 2°/s (e.g., Fig. 1C). The ramp distances were 4-4-4-4-4-4° (*sequence A*), 6-3-4-2-5-4° (*sequence B*), and 4-2-6-5-3-4° (*sequence C*). The hold period between the ramps lasted 4 s. The initial 18 afferents were tested with *sequence A* only, but *sequences B* and *C* were subsequently added to the protocol to determine whether the ramp increase in firing rate was sensitive to ramp amplitude. With *sequence A*, the position sensitivities of only the hold period and the initial burst could be determined. All three ramp sequences had a net displacement of 24° and a net duration of 45 s, the only difference being the distance moved during successive ramps.

The ramp sequence was designed for efficient data collection because recordings frequently could be held for a very limited period, and the ramp sequence allowed usable data to be acquired in a single trial. In each ramp-and-hold movement within the sequence, the wrist was rotated at 2°/s, to provide a ramp duration long enough to identify discrete components of the firing response, but to restrict the overall

distance of rotation during the sequence to 24°, which was important for maintaining recording stability. While 2°/s is relatively slow ($\approx 0.2\%$ resting length/s in ECRb), the observed afferent firing patterns resembled those seen in higher velocity movements (e.g., Grill and Hallett 1995; Kakuda and Nagaoka 1998).

During data acquisition, the subjects were asked to relax the right arm completely (e.g., Fig. 1D), and the raw EMG signal was displayed at high gain on an oscilloscope to provide visual feedback. In a few subjects, weak contractions ($\approx \pm 20 \mu\text{V}$) were seen in EMG recordings, but these always opposed the movement rather than assisting it. A resting noise level of $\pm 5 \mu\text{V}$ was typical for raw EMG recordings.

Data analysis

Data analysis focused on the quantitative measurement of afferent firing patterns and the correlation of these patterns with joint position. Afferent recordings were prepared for analysis by measuring the time of occurrence of each nerve spike and converting the interspike

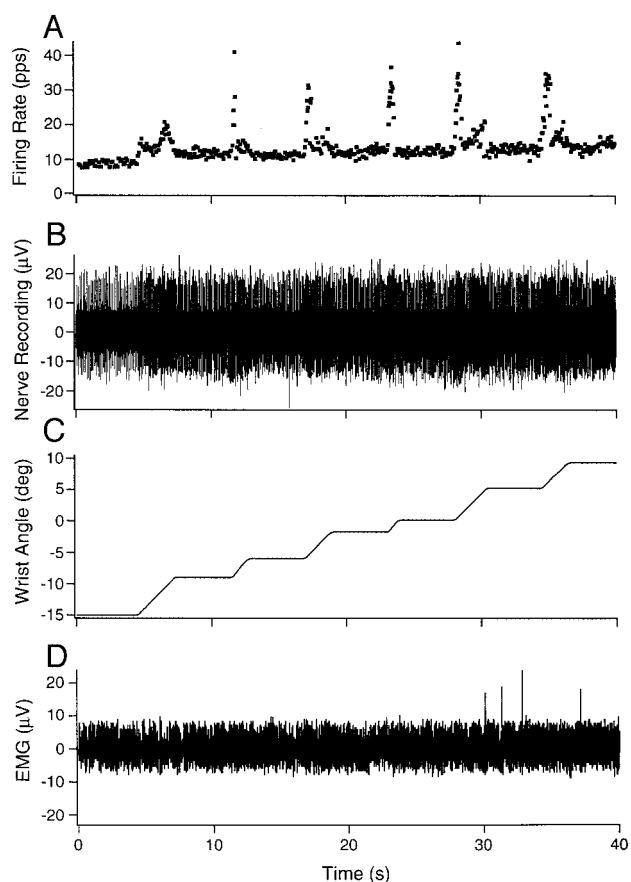


FIG. 1. Data recorded during each ramp sequence. From top to bottom: instantaneous afferent firing rate, raw nerve recording, wrist angle (ramp sequence B), and electromyographic (EMG) activity of the muscle of origin (ECRb).

intervals to instantaneous firing rate, indexed to the beginning of the relevant interval.

Three discrete features in afferent firing patterns were measured: the “hold rate,” “initial burst,” and “ramp increase,” as illustrated in Fig. 2 with data from a representative afferent. The *hold rate* was defined as the average firing rate during the portion of the hold period 2–0.5 s prior to the onset of each ramp, that is, beginning 2 s after the end of the preceding ramp. The *initial burst* was defined as the average rate of the three shortest interspike intervals occurring during the interval from movement onset to the minimum in firing rate (left-most dashed box). The time that the peak occurred (0.50 ± 0.16 s) was defined as the beginning of the shortest interspike interval during the initial burst, shown in Fig. 2 as the circled data point. The error bars labeled “P” show the grand mean time (± 1 SD) of the initial burst peak, and the error bars labeled “M” show the grand mean time (± 1 SD) of the minimum in firing rate (circled data point; 0.89 ± 0.41 s). The example shown in Fig. 2 had a relatively late minimum. The mean times of the initial burst peak and the minimum were significantly different (paired *t*-test, $P < 0.0001$; $n = 44$). The *ramp increase* was defined as the average rate of the three shortest interspike intervals near the end of the ramp just before the movement began to decelerate (i.e., right-most dashed box). The peak rate was measured rather than the slope of the relationship between firing rate and joint angle because the relatively short movements used in this study usually produced too few spikes for a slope measurement.

The position sensitivities of the hold rate, initial burst, and ramp increase were defined as the slope of linear regression of the firing rate versus joint position. Unlike the position sensitivities of the hold rate and initial burst, the position sensitivity of the ramp increase was

based on the *change* in firing rate relative to the preceding hold rate, and the joint position was based on the *change* in position (i.e., the distance) moved during the individual ramp. In almost all afferents, position sensitivity based on the change in rate was better correlated with distance than was the absolute rate with absolute joint position.

For both the hold period and initial burst, the angular region of position sensitivity was determined with an algorithm that defined up to three regions, based on all trials recorded from a given afferent (see Fig. 3). The central (“intermediate”) region was the angular range over which the particular feature of the firing pattern was position sensitive. At more extended angles (“early region”) in some afferents, activity was present, but the feature did not change in amplitude in response to further changes in joint position. At more flexed angles (“late region”), the maximum firing rate of the initial burst or ramp increase of most afferents reached a plateau. The algorithm was an iterative, straight-line fitting procedure in which points were excluded from the intermediate region if they significantly reduced the sensitivity in the intermediate region, while at the same time, they did not make the slope of the early or late regions statistically significant. The *range* of position sensitivity was not determined for the ramp increase, as the distances traveled during the ramps ($2\text{--}6^\circ$) were limited. Differences in the occurrence of the three regions of position sensitivity were evaluated with the χ^2 test. The significance of regression slopes was determined with the *F* test. Significant differences between samples of data were evaluated with paired *t*-tests and ANOVA. The level of significance was defined as $P < 0.05$.

To determine whether the position sensitivities of muscle spindles were better related to joint position or to muscle length, muscle length

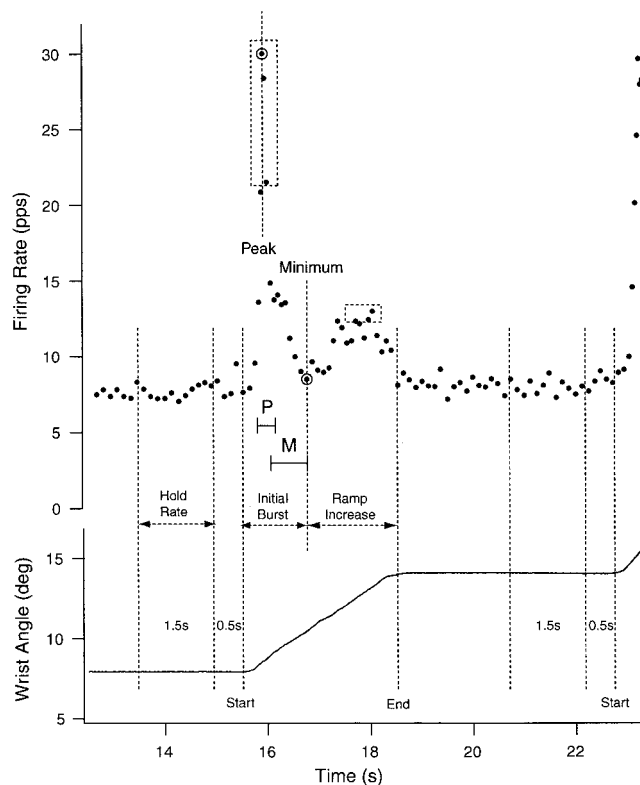


FIG. 2. Quantitative analysis of afferent responses. The instantaneous firing rate of an afferent response (top) to a single ramp-and-hold movement of the wrist (bottom) is shown for a portion of a ramp sequence. Measured variables include the hold rate, initial burst, and ramp. The error bars labeled “P” represent the mean ± 1 SD time of the initial burst (circled data point) for all 44 afferents. The error bars labeled “M” represent the mean ± 1 SD time of the minimum (circled data point) for all 44 afferents. The values of the initial burst and ramp increase were based on the mean firing rate of the shortest three interspike intervals (dashed boxes).

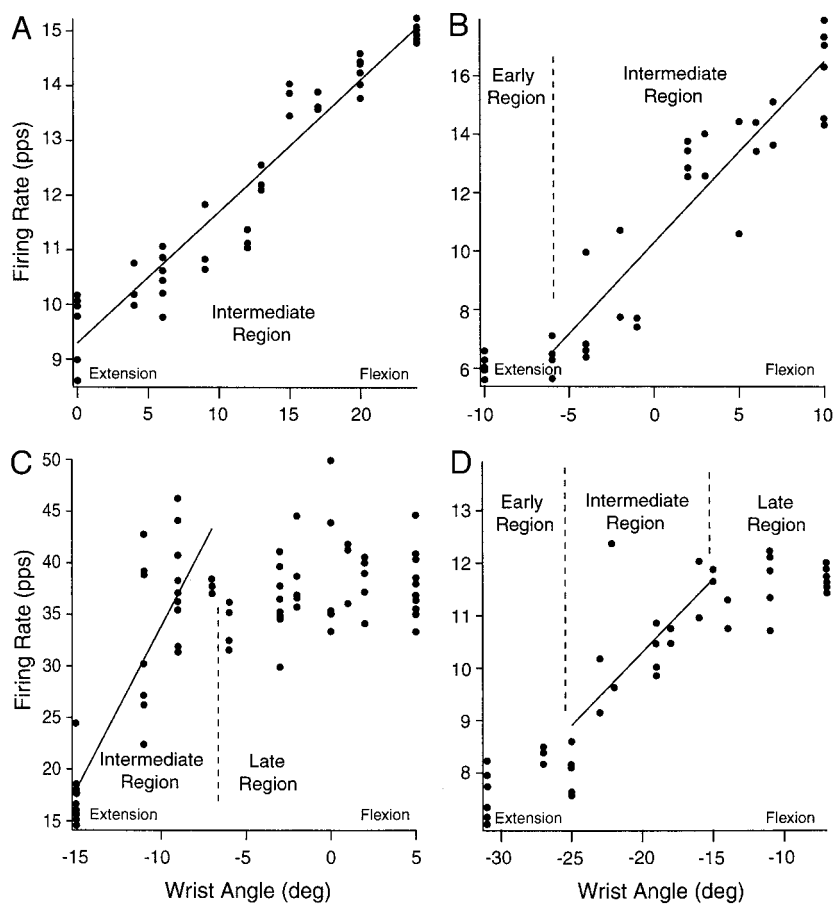


FIG. 3. Position sensitivities of individual afferents. The firing rate during the hold period (A and D) and the initial burst (B and C) is plotted versus wrist position. The muscle of origin, regression slope, and number of trials were: for A, ECRb, $m = 0.24$ pps/ $^{\circ}$, $n = 6$; for B, extensor digitorum (ED), $m = 0.62$ pps/ $^{\circ}$, $n = 6$; for C, ECRb, $m = 2.10$ pps/ $^{\circ}$, $n = 5$; and for D, ED, $m = 0.29$ pps/ $^{\circ}$, $n = 6$. Regression slopes in the early and late regions were not significant.

was estimated from ECRb moment arm data (Loren et al. 1996) and ECRb length measurements from our subjects. With the wrist in the neutral position, the length of ECRb from the origin to the wrist was estimated at 26 cm, and the length from the wrist to its insertion was estimated at 2.5 cm, for a total muscle length of 28.5 cm. For joint angles in the extension direction, muscle length was estimated with the sum-of-sines equation. For flexion angles, the tendon was assumed to wrap around a spherical wrist joint of 2.5-cm radius. Muscle length was found to decrease slightly as the wrist rotated from -50° to -30° extension and then to increase through intermediate to flexed joint angles at ≈ 1 cm/ 30° (i.e., $333 \mu\text{m}/^{\circ}$). Above 30° flexion, the muscle lengthened more slowly. At intermediate joint angles, a 6° wrist rotation corresponded to a 2-mm change in ECRb length, $<1\%$ of its resting length. As ED is anatomically similar to ECRb, the lengths of ED and ECRb are likely to have similar relationships to wrist angle.

RESULTS

Position sensitivity of individual afferents

In 40 (hold rate) or 42 (initial burst) of the 44 afferents investigated in this study, the relationship between afferent firing rate and joint position was significant. That is, the position sensitivities of these two features of the firing pattern had an *intermediate region*; however, most afferents also discharged in at least one region of the joint space where joint position did not influence the hold rate or initial burst (i.e., *early or late regions*). As shown in Fig. 3A, the influence of joint position on the hold rate of an ECRb afferent extended from the point of recruitment at 0° , to the most flexed joint position investigated in this afferent (24°). The relationship

between either the hold rate or the initial burst and joint position was linear over the entire angular range investigated in 6/13 ED afferents and in 11/30 ECRb afferents (Table 1), that is, this subset of relationships lacked early or late regions. The ED afferent described in Fig. 3B was recruited at -10° , but the initial burst did not respond to joint angle until the wrist was flexed to -6° , producing an early region. Early regions were found in a minority of afferents, in 4/13 ED afferents and 10/30 ECRb afferents (Table 1, " $<$ " for "recruitment angle"). In contrast, late regions for the hold rate or the initial burst were observed in a majority of afferents, 11/13 in ED and 22/31 in ECRb (Table 1, no " $>$ " for "sensitivity"), as shown for the initial burst of a single ECRb afferent in Fig. 3C. In this afferent, the intermediate region spanned only 8° , from -15° to -7° . Finally, some afferents had early, intermediate, and late regions, as illustrated in Fig. 3D for the hold rate of an ED afferent. Thus, all combinations were observed, but 43 of 44 muscle spindle afferents were position sensitive over some range of joint positions. A χ^2 analysis showed that there was no significant difference in the distribution of these regions in ED versus ECRb nor for hold rate versus initial burst.

Both ED and ECRb muscle spindles were recruited throughout the range of joint angles investigated, as shown in Fig. 4 (dashed lines, ED; solid lines, ECRb). The average firing rate of individual afferents is shown in Fig. 4A for the hold period and in Fig. 4B for the initial burst (note difference in vertical scales). In most afferents, the firing rate during the hold period and the initial burst increased with joint position to a maximum and then plateaued. While in some afferents, the plateau

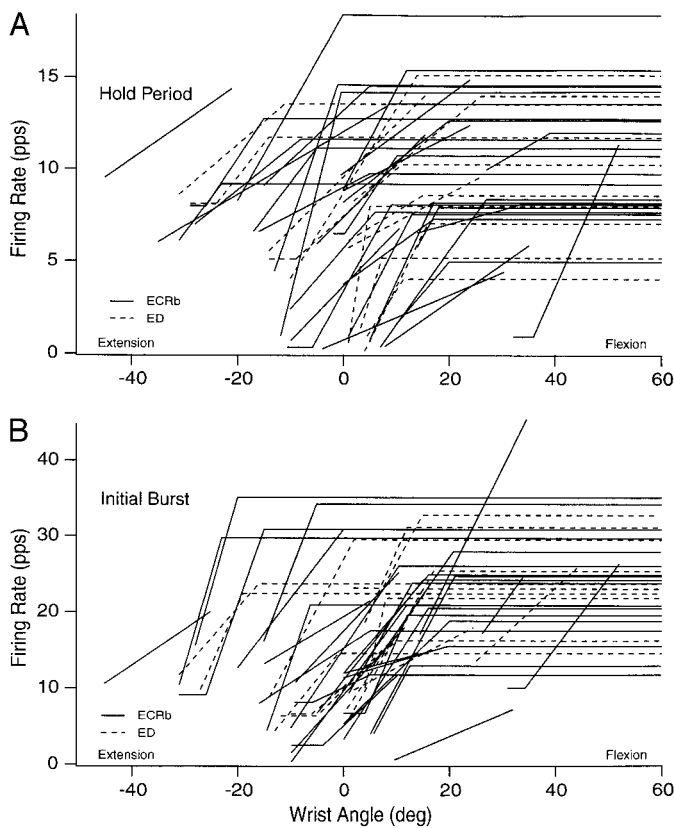


FIG. 4. Position sensitivities of all recorded afferents. Each line represents the average position sensitivity of a single afferent: in *A* for the hold period average rate, and in *B* for the initial burst rate. Dashed lines, afferents from ED. Note afferents without a plateau and decreasing overall firing rates in higher threshold afferents.

trended higher or lower, it is represented as a constant rate in Fig. 4 because its slope was not statistically significant from zero. For both the hold rate and the initial burst, the overall firing rates of afferents tended to decrease as a function of their recruitment angles.

A quantitative analysis of recruitment angles and angular ranges of position sensitivity is presented in Fig. 5, where the horizontal extent of each bar represents the intermediate region of an individual afferent. A dashed line to the right indicates that a plateau angle was not observed within the angular range investigated; □ represents afferents from ED and ■ afferents from ECRb. Assuming the position sensitivities that were not observed to plateau did so at the maximum rate recorded, the average angular range over which afferents showed position sensitivity was $14.9 \pm 7.2^\circ$ for the hold rate and $15.1 \pm 6.8^\circ$ for the initial burst. A disproportionately large number of afferents were recruited between -10° extension and $+10^\circ$ flexion, but afferent recruitment and position-sensitive responses were observed over the entire 110° range of wrist positions investigated. An ANOVA showed no significant difference in recruitment angles for ED and ECRb afferents ($F[1,37] = 0.0003, P = 0.99$).

Position sensitivity of the population

The population representation of position sensitivity was estimated from the sum of the individual afferent hold rates and initial bursts, as depicted in Fig. 6 by the “cumulative firing

rate.” The hold rates and initial bursts of all afferents in the population representation were assumed to plateau at the maximum recorded rate, if not at an observed rate. Note in Fig. 6 the difference in vertical scaling for the hold period representation (*A*) and the initial burst representation (*B*). The population response—the sum of the individual afferent responses—is shown by the dotted line. The population response increased slowly at extreme extension and flexion positions of the wrist and maximally in intermediate positions. The shape of the population response resembles that of the afferent recruitment pattern (Fig. 5). Plotted against muscle length (Fig. 6*A*, dashed line), the population response increased from 0 to 20% of maximum while the muscle shortened and then lengthened back to its starting length. Thus, at more extended wrist positions, the population response is more simply related to joint position than it is to muscle length.

To investigate how the position sensitivities of individual afferents contribute to the population representation, a second population representation was constructed that was based entirely on recruitment—once recruited, each afferent fired at its observed plateau (or estimated maximum) rate without any rate

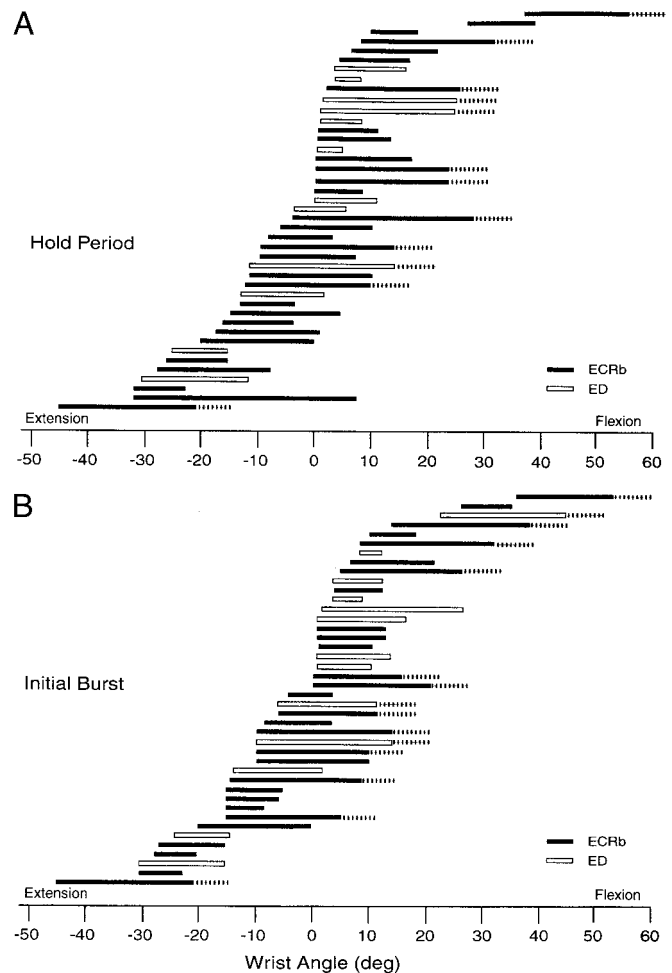


FIG. 5. Distribution of afferent recruitment angles. Each horizontal bar represents the angular range over which each afferent exhibited position sensitivity: in *A* for the hold period average rate and in *B* for the initial burst. □, ED afferents; ■, ECRb afferents. Dashed extensions to the right, possible continued regions of position sensitivity (i.e., a plateau in firing rate was not observed).

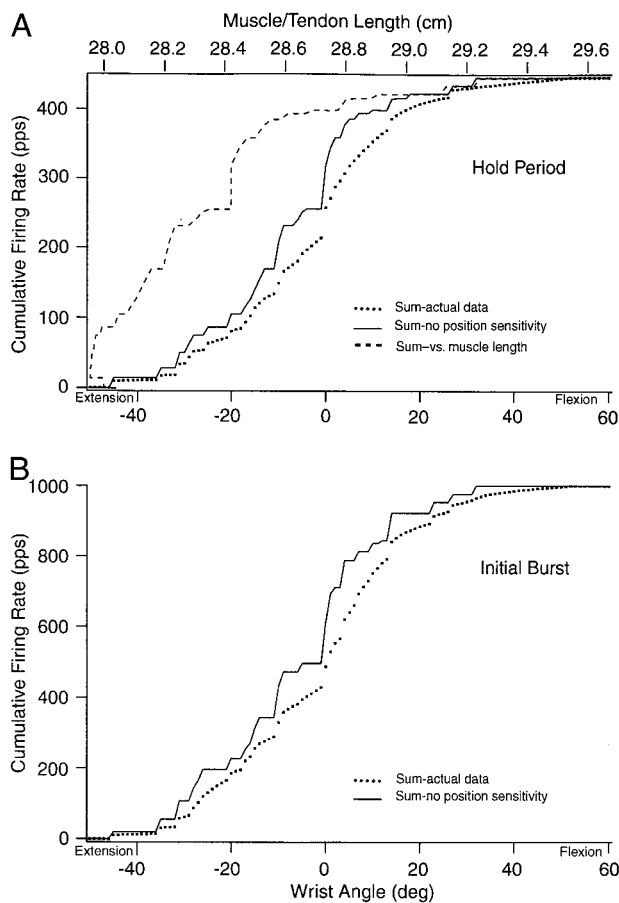


FIG. 6. Estimated population response. Each line represents the cumulative firing rate ($n = 44$), in *A* for the hold period, and in *B* for the initial burst. Traces include the cumulative sum of active afferents using the actual data (dotted line), cumulative sum with the data modified to remove position sensitivity from individual afferent responses (thin solid line), and cumulative sum plotted against muscle length (dashed line in *A*).

modulation. The solid lines in Fig. 6 illustrate the population response obtained when individual afferents lacked position sensitivity. Not surprisingly, this hypothetical "position-independent" population had a higher overall firing rate compared with the actual population, but the increase was small, and the shape of the population response did not change. Thus, the position sensitivities of individual afferents (e.g., Fig. 3) did not strongly influence the population response. "Position sensitivity" should not be equated with the stereotyped firing pattern of afferents to an individual ramp movement, for the sequence of hold rate, initial burst, and ramp increase allowed the population to represent several different analogs of position (see DISCUSSION).

Ramp increase in firing rate

Based on movement distance relative to the ramp starting position, the position sensitivity of the ramp increase was comparable to the position sensitivity of the initial burst. In our analysis of the ramp increase, significant regression slopes were observed in 16 of the 26 ED and ECRb afferents investigated with ramp sequences *B* and *C* (Fig. 7*A*). The average position sensitivity of the ramp increase was 1.36 ± 0.68 (SD) pps/ $^{\circ}$ ($n = 16$). The bar graph in Fig. 7*B* compares the average position sensitivities of the hold rate, initial burst, and ramp

increase. An ANOVA showed a significant effect of the response feature on the position sensitivity ($F[2,107] = 20.9$, $P < 0.0001$), and post hoc analysis (Scheffe) showed that the position sensitivities of the initial burst and ramp increase were significantly different from those of the hold period ($P < 0.0001$), but those of the initial burst and ramp increase were not significantly different from each other ($P = 0.62$).

Adequate stimulus for muscle spindles

A striking resemblance was found between the firing patterns of afferents and the passive resistance of the joint to rotation. In Fig. 8, the response of a representative afferent to a type-B ramp sequence is shown with the passive resistance (i.e., force) of the wrist. In this trial, the initial burst reached a plateau on the fourth ramp. With each ramp in the sequence (*C*), the resistance (*B*) rose abruptly, followed by a yield and then a slower rise in force. The resistance to the first ramp in the sequence was usually larger than the resistance to the 5 that followed probably because the resting period between trials was longer than the hold period between ramps (Hunt and Ottoson 1976). However, the peak firing rate of the first initial burst in the sequence was not correspondingly larger.

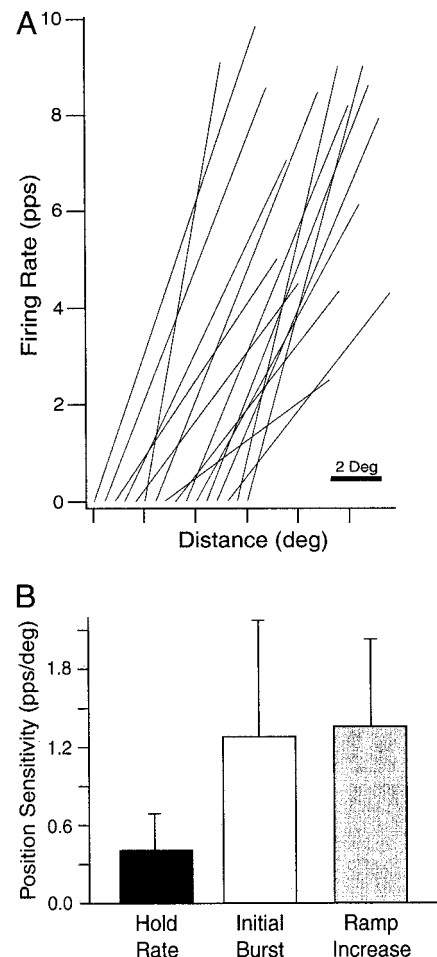


FIG. 7. Dynamic position sensitivity of ramp increase in firing rate. *A*: each line represents a significant linear regression of the change in rate during the ramp increase vs. movement distance for a single afferent. Regression lines are incrementally shifted by 0.4° for clarity. *B*: the average (± 1 SD) position sensitivity is compared for the hold period (0.40 ± 0.30 pps/ $^{\circ}$), initial burst (1.27 ± 0.90 pps/ $^{\circ}$), and ramp increase (1.36 ± 0.68 pps/ $^{\circ}$).

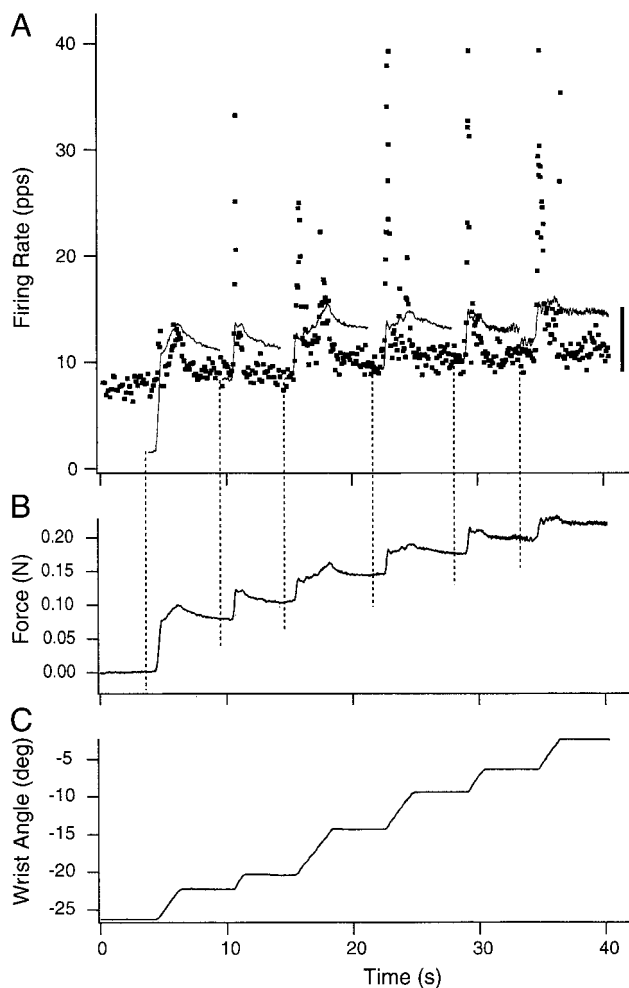


FIG. 8. Relation between joint force and afferent firing pattern. A: the response of an afferent to a type-C ramp sequence is shown for a single trial. In A, the torque record from B has been clipped 1 s before the start of each ramp (i.e., vertical dashed lines) and shifted vertically to align each torque segment with the corresponding part of the instantaneous frequency plot. The clipped torque records have been scaled vertically to match the firing rate plot, but horizontal scaling is unchanged.

To compare the joint resistance with the afferent firing pattern, clips of the wrist force record were superimposed onto the firing pattern in Fig. 8A. At the beginning of each ramp, a steep rise in resistance coincided with the initial burst. Subsequently, a force yield coincided with a sudden decrease in firing rate (i.e., the minimum); a slow increase in force paralleled the ramp increase in firing rate; and during the hold period following the ramp, a gradual decline in force was paralleled by a decline in the firing rate. Thus, the firing pattern of muscle spindles during individual ramp movements corresponds much more closely to the passive resistive force of the joint than it does to joint position. On the other hand, joint position is highly correlated with the parametric values of the hold period, initial burst, and ramp increase (i.e., Figs. 3 and 7 and Table 1).

DISCUSSION

Representation of position by single afferents

The responses of muscle spindle primary afferents to ramp-and-hold movement include three distinct features: the hold

rate, initial burst, and ramp increase. All three features were shown, in human muscle spindles, to represent joint position, although so far, this representation has been observed under limited circumstances.

Position sensitivity was measured, by necessity, during relatively slow joint rotations ($2^\circ/\text{s}$), but the same pattern of afferent firing—with all three features—has also been observed during faster movements (e.g., Grill and Hallett 1995; Kakuda and Nagoaka 1998). The joint rotations were imposed on a generally passive limb, not during active movement. In *active* movements, especially those with slow speeds, the antagonist muscles lengthen relatively passively. Therefore, the results obtained in our experiment with imposed movements should have relevance, at least, to slow active movements.

The hold rate of individual afferents had an average position sensitivity of $0.40 \text{ pps}/^\circ$, which, while relatively low, is considerably higher than the sensitivity previously reported by Vallbo (1974). This difference may be due to the limitation of position sensitivity measurement in the present study to just the range of joint angles over which the firing rate increased with joint angle. Nevertheless, the position sensitivity of the hold rate was several times lower than that of the initial burst and ramp increase, which suggests that position information during the maintenance of posture need not be as precise as during movement. Our estimates of position sensitivity should probably be regarded as upper limits, however, because experimental conditions were highly controlled to minimize thixotropy (Gregory et al. 1988), hysteresis (Burgess et al. 1982; Wei et al. 1986), and post-ramp adaptation (Crowe and Matthews 1964; Matthews 1963).

The initial burst had an average position sensitivity of $1.27 \text{ pps}/^\circ$, quite large, we believe, for a response feature as yet not clearly related in the literature to any particular movement variable. The initial burst, first described by Matthews (1963), was initially believed to signal acceleration (Shäfer and Henatsch 1966, 1967), but this was challenged by Lennerstrand and Thoden (1968). In the latter study, the authors remarked that the initial burst seemed to be sensitive to the “initial extension” of the muscle prior to an imposed movement (see also Houk et al. 1981, their Fig. 5A). Thus, there have been several suggestions that the initial burst is position sensitive, but a systematic investigation of this relationship has not been carried out, in humans or other animals.

A prerequisite for the initial burst to occur at the onset of a movement is a preceding period in which receptor length is constant. Both Lennerstrand and Thoden (1968) and Hunt and Ottoson (1976) demonstrated that it takes 4–6 s for the peak firing rate of the initial burst to recover completely from a preceding movement, although recovery begins almost immediately following the cessation of movement. Therefore, we used constant hold periods of 4 s to allow the initial burst to recover so that we would be measuring the initial burst while the receptor was in a consistent state from movement to movement in the ramp sequence.

The mechanism underlying the dependence of the initial burst on position probably relates to the length-tension properties of intrafusal muscle, in which actin filaments can overlap and obstruct cross-bridge binding when the muscle fibers are short (e.g., Gordon et al. 1966). During the hold period, slow turnover cross-bridges form over time to develop short-range stiffness, which is high relative to stiffness after significant

amounts of stretch. Thus, the external stiffness presented to the sensory region of the muscle spindle (Fig. 8) at the beginning of movement should depend on the initial length of extrafusal muscle, providing, of course, an adequate rest period. The region of short-range stiffness ($\approx 370 \mu\text{m}$)—as predicted by the initial burst duration (0.50 s) and the speed of movement over this period ($\approx 1.8^\circ/\text{s}$)—corresponds well to that previously measured in cat muscle spindles (Hasan and Houk 1975). The relatively long duration of the initial burst observed in the present experiment is, therefore, consistent with shorter initial bursts observed during faster movements.

The average position sensitivity of the ramp increase (1.36 pps/ $^\circ$) was not significantly different from that of the initial burst. We defined the ramp increase as the *change* in firing rate during the ramp rather than as the absolute rate, and we related this change in firing rate to the distance moved, rather than to the absolute joint angle, because the firing rate did not correlate as well with absolute joint position as it did with distance. In fact, the firing rate of the ramp increase appears to have been “reset” between ramps, as shown in Fig. 1. This resetting behavior contrasts with that observed by Houk et al. (1981) in decerebrate cats, in which the firing rate increased as a function of absolute joint position during the ramp increase. The relatively high position sensitivities of the ramp increase and the initial burst suggest that the precision of position information should be high during movement. The similar value of position sensitivity for the ramp increase and initial burst also raises the question whether the CNS might combine these two features to provide a high precision signal of absolute joint position during movement. Position sense at rest tends to drift (Paillard and Brouchon 1968; Wann and Ibrahim 1992), which might be mitigated by the initial burst, so that movements proceed from an accurately perceived initial position.

Representation of position by the afferent population

While 43/44 afferents were position sensitive, their range of position sensitivity was limited to an average of 15° . A complete representation of joint position, therefore, would require a population of afferents that has a continuous distribution of recruitment angles and ranges of position sensitivity (e.g., Milgram and Inbar 1976; Ray and Doetsch 1990). Indeed, such a distribution was observed when the average responses of all 43 afferents were combined into an estimate of the population response, although a disproportionately high concentration of afferents were position sensitive between -10° extension and $+10^\circ$ flexion. This uneven distribution of position sensitivities suggests that position sense should be more precise in intermediate joint positions, in contrast to the assertion of Wei et al. (1986) that the highest perceptual sensitivity should occur at extreme joint positions, although the manner in which the precision of position sense varies across the joint space has not yet been systematically tested.

The “strategy” of reconstructing the joint space from a large number of narrow position-sensitive zones probably requires each muscle to contain a greater number of afferents than it would require if all afferents fired were recruited at movement onset and modulated their firing rates in parallel over the entire range of motion. However, the dynamic range of human muscle spindles is relatively narrow ($\approx 10\text{--}30$ pps), so by distributing these dynamic ranges over narrow regions of the joint

space, the precision with which position is represented might be enhanced. Nevertheless, the population response simulated with position-insensitive afferents (Fig. 6, solid lines) suggests that the position code used by the CNS is primarily based on the pattern of afferent recruitment rather than the firing patterns of individual receptors.

Ultimately, the responses from individual and collective muscle spindles depend on the mechanical environment of these receptors, and this environment can be differentiated into *internal* and *external* components. The internal environment consists of the anatomical arrangement within each receptor (e.g., Banks and Stacey 1988; Boyd 1976), and the external environment consists of the mechanical properties of the immediate skeletal muscle region occupied by each afferent. The internal mechanical environment appears to be qualitatively consistent across the population of muscle spindles, as all 44 afferents investigated in this study responded to stretch with the same temporal sequence of the initial burst, minimum, and ramp increase. The origin of this sequence derives from the systematic variations in intrafusal muscle stiffness during stretch, as reflected in the passive resistance of the joint (Fig. 8) (see also Meyer-Lohman et al. 1974). Therefore, the external mechanical environment of receptors seems more likely to account for the observed differences in recruitment angles (Fig. 5) and firing rates (Fig. 4). The amount of local stretch produced by joint rotation in any particular muscle region should depend on the angle of pinnation of muscle fibers in the local compartment as well as the distance of the region from the rotating joint. Therefore, a parsimonious explanation for the different recruitment angles and overall firing rates of muscle spindles is that the muscle spindles are located in different parts of the muscle.

The complexity and the synchronization of afferent responses allow the population to represent independently multiple parameters, such as the starting position and distance of movement. However, as we used only one velocity in our study, it is unclear whether the initial burst and ramp increase are represented independently from velocity. In cat muscle spindles, at least, the initial burst (Hunt and Ottoson 1976) and ramp increase (e.g., Houk et al. 1981) are both velocity dependent. Velocity dependence would complicate the task for the CNS to decode joint position, but if an independent representation of velocity were available, it could be subtracted from the position signals. At this point we do not know whether or how velocity is represented by the human muscle spindle, so the elucidation of this question will require further work.

The study presented in this paper describes three novel findings in human muscle spindles. First, the peak firing rate of the initial burst represents the starting position of movement with a precision comparable to that of the ramp increase. Second, the range of joint angles over which the hold period and initial burst are position sensitive is limited to 15° , which strongly suggests that the human CNS uses a population code for joint position, both during posture and movement (see also Bergenheim et al. 2000; Roll et al. 2000; Verschueren et al. 1998). Third, the population representation of joint position is dominated by the recruitment pattern of afferents rather than by their individual firing patterns. These findings provide additional insight into the relationship between the peripheral representation of joint position and position perception, although a full description must incorporate the contributions of other

afferents, particularly the muscle spindle group II and skin afferents. Besides, an identified representation of position or other kinematic variable that is based on a conventional statistic might differ dramatically from the decoding algorithm used by the CNS. Further perceptual-motor testing is required to resolve this issue.

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