

## Information About Peripheral Events Conveyed to the Cerebellum Via the Climbing Fiber System in the Decerebrate Cat\*

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**Summary.** Discharges of Purkinje cells (PCs) with simple (SS) and complex spikes (CS) in the  $c_1$ -zone of lobule Vc of the anterior lobe of the cerebellar cortex were analyzed in the decerebrate cat during a passive movement of the cat forepaw. The CS of the PC responded differentially and/or proportionally to the position of the extremity, amplitude of the movement, velocity and acceleration. Inphase and outphase responses of the climbing fiber (CF) system to sinusoidal movements could depend on the position of the extremity within the operational range. From these results we deduce that peripheral events can be signalled by the CF system. The possible function of the interaction between the two inputs at the PC level is discussed.

**Key words:** Passive movements – Cerebellar cortex – Climbing fiber input – Purkinje cells

In a previous study (Rubia and Kolb 1978) the sensory feedback from a passive movement of the cat forepaw was investigated. It was found that some complex spike (CS) discharges of Purkinje cells (PCs) appeared similar to mossy fiber (MF) and granular cell (GrC) discharges. This led to the conclusion that both cerebellar inputs [(MF) and climbing fiber (CF)] were able to signal peripheral events.

Since the careful studies of Thach (1967), Larson et al. (1969a, b) and Oscarsson (1968, 1969), the CF system has been considered poorly organized from a topographical standpoint mainly because of the large convergence on single olivary neurons. In addition,

the CF system did not appear very discriminative in the transmission of peripheral events, since it was difficult to evoke CSs in PCs by using natural stimulation. Oscarsson concluded that since the CF system showed weak effects on natural stimulation and since the neurons of the spino-olivocerebellar paths were strongly activated by stimulation of descending paths (from motor cortex and mesencephalon), this system provides the cerebellum with information about intended movements rather than sensory feedback coming from actual limb displacement. The latter process is considered to be more a function of the MF system (Oscarsson, 1967).

This opinion was considerably supported by the work done by Thach (1968) on awake monkeys in which the CS of the PC did not show any relationship to a movement consisting of rapidly alternating flexions and extensions of the arm. In a later study, Thach (1970) was able to show that the CSs changed their discharge frequency in relation to a signal-initiated but not to a self-paced rapidly alternating movement.

On the other hand, several studies in the literature show that the CF system can respond to adequate stimulation of cutaneous receptors, muscle stretch or teleceptive stimulation (Eccles et al. 1972c, 1972d; Leicht et al. 1973; Ishikawa et al. 1972a, b; Maekawa and Simpson 1972; Simpson and Alley 1974).

More recently, Rushmer et al. (1976) reported extremely sensitive CS responses to less than 100  $\mu$ m displacements of the cat forepaw. This information appeared to be independent of the quality, amplitude and direction of the movement. Therefore, they ascribed the role of an "event detector" to the CF system, signalling a touching of the foot, or its lifting during locomotion. Furthermore, the CF system would function to signal "status", rather than "intended" events.

\* Preliminary results were reported at the 47<sup>th</sup> meeting of the Deutsche Physiologische Gesellschaft in Regensburg (Kolb and Rubia, 1976) and at the XXVII<sup>th</sup> International Congress of Physiological Sciences in Paris (Rubia and Kolb, 1977)  
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Because of the strong convergence of descending and ascending information at single olivary neurons (Sedgwick and Williams 1966, 1967), the inferior olive could be one site at which information about "intended" and "ongoing" movements is cancelled if both signals are equal according to the "Reafferenz" hypothesis (von Holst and Mittelstaedt 1950). If both signals are not equal, the olivary cell would inform the cerebellum about the error in the performance of the movement. This implies that the inferior olive, and therefore the PCs, should receive precise information about the movement via the CF system and that this information could be fully detected only in the absence of descending influences from higher motor centers.

This study will present evidence of precise signaling by the CF system of changes in movement parameters in the decerebrate cat, a preparation in which descending information is absent.

## Methods

The surgery and recording methods have been described elsewhere (Rubia and Kolb 1978).

### Stimulation

The cat's left forelimb was fixed onto a mechanical device and the forepaw was moved around the wrist joint (see Fig. 1A) following a time function which was calculated by a digital computer and stored in its memory (Nicolet MED-80 System). During data recording, this movement function was scanned by the processor in steps of 5 ms which were fixed by the binwidth used. This signal was given as a set point to an electronic feedback system which controlled the position of the cat forepaw by a DC-motor.

Most of the movements were ramp functions; multiple ramp and sinusoidal functions were also used. The parameters of all functions could be varied in a wide range. The movements started from the lower position  $\varphi_1$  and went in the plantar-dorsal direction (positive direction) to the upper position  $\varphi_{II}$  and back (Fig. 1A).

### Data Analysis

The spikes of the cerebellar units were compared with two different level discriminators, in order to separate CSs from SSs. A logic circuit was used to make sure that wavelets of CS activity were not recorded as SSs. The computer was used on-line to obtain simultaneously Peri-Stimulus Time Histograms (PSTH) and dot rasters with a binwidth of 5 ms. The binwidth was changed off-line up to 40 ms. To achieve an objective criterion of whether a unit responded to a movement or not, we compared the probabilities of unit discharge during four characteristic sections of the ramp movement: 500 ms before the two dynamic phases of the movement and during the dynamic phases themselves. The 150 ms after each dynamic section of the ramp movement were also included in this evaluation in order to account for responses to the acceleration at the end of the dynamic phases. To evaluate the average probability of unit discharge during a certain movement section, the latter was subdivided into time intervals of 0.5 ms. This small

interval was chosen so that not more than one spike could occur during that time. The probability in percentage was estimated from:

$$p(t_s, T_i) = \frac{c(t_s) \cdot 100}{n \cdot T_s/t_i}$$

where:

$t_s$  = duration of a specific movement section

$t_i$  = 0.5 ms = time interval

$c(t_s)$  = number of counts during a certain movement section for  $n$  stimulations

$n$  = number of stimulations.

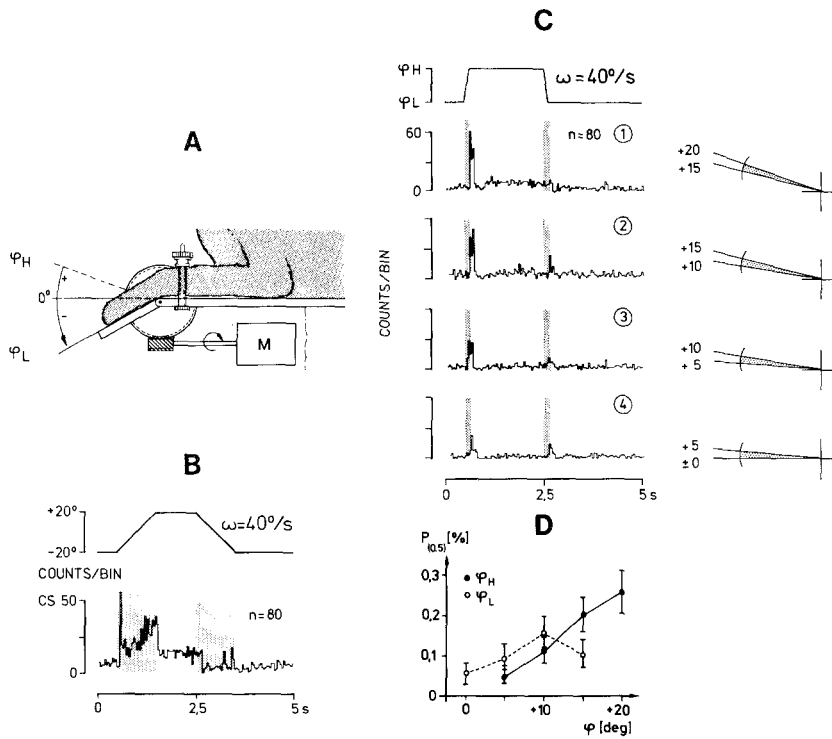
The 95% confidence limits were also calculated. Units were rejected if the probability of discharge during the characteristic sections did not differ significantly from one section to another.

## Results

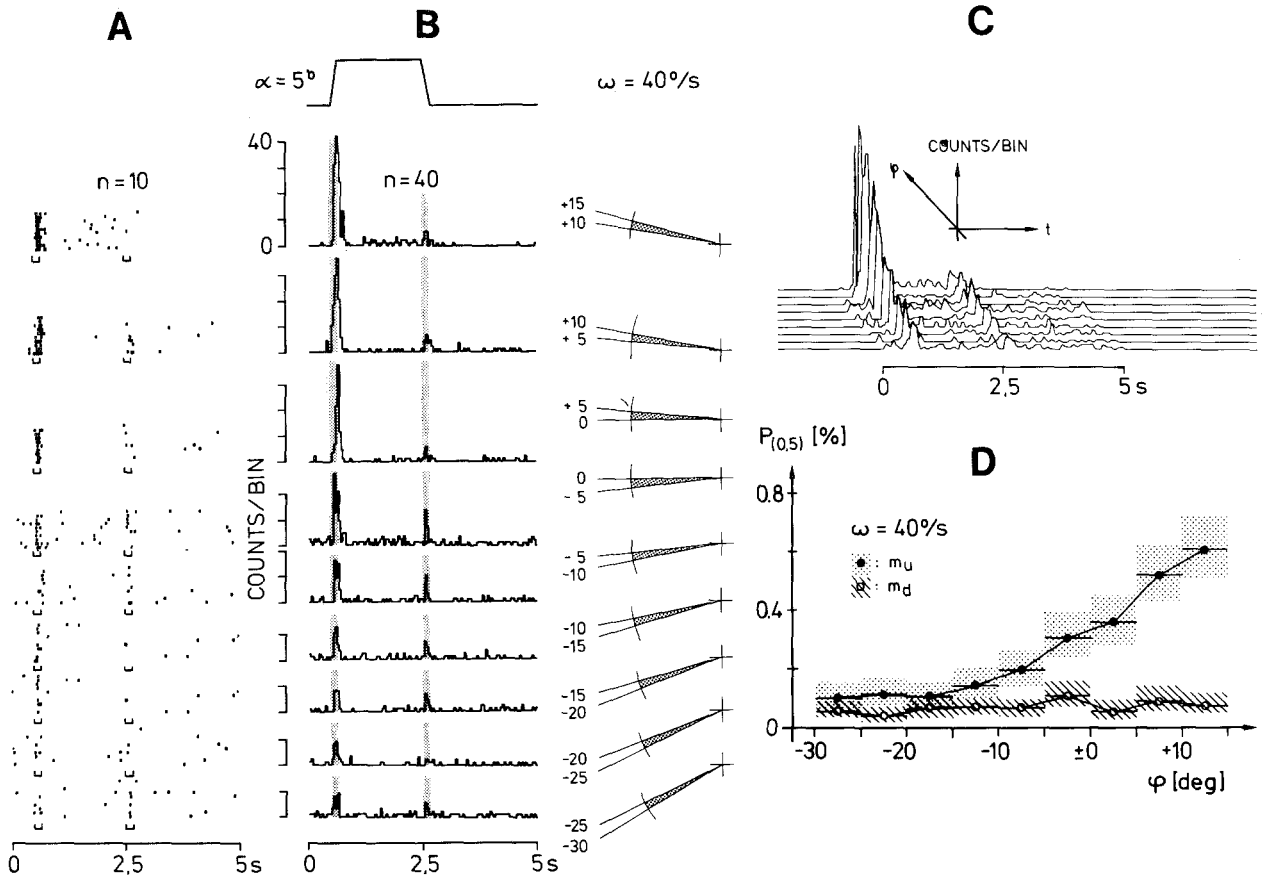
Every movement can be considered as being composed of both static (position) and dynamic parameters (velocity, acceleration and higher derivatives). To discover whether a relationship exists between the above mentioned parameters of a movement and the PC complex spike discharges, we examined the firing pattern of PCs during different types of movement. In addition, the parameters of these movements were varied to verify that the CF system carried information which was related to these changes. We recorded from 423 PCs; 35% of these cells showed significant differences between the characteristic sections of the movement.

### Position-related Responses

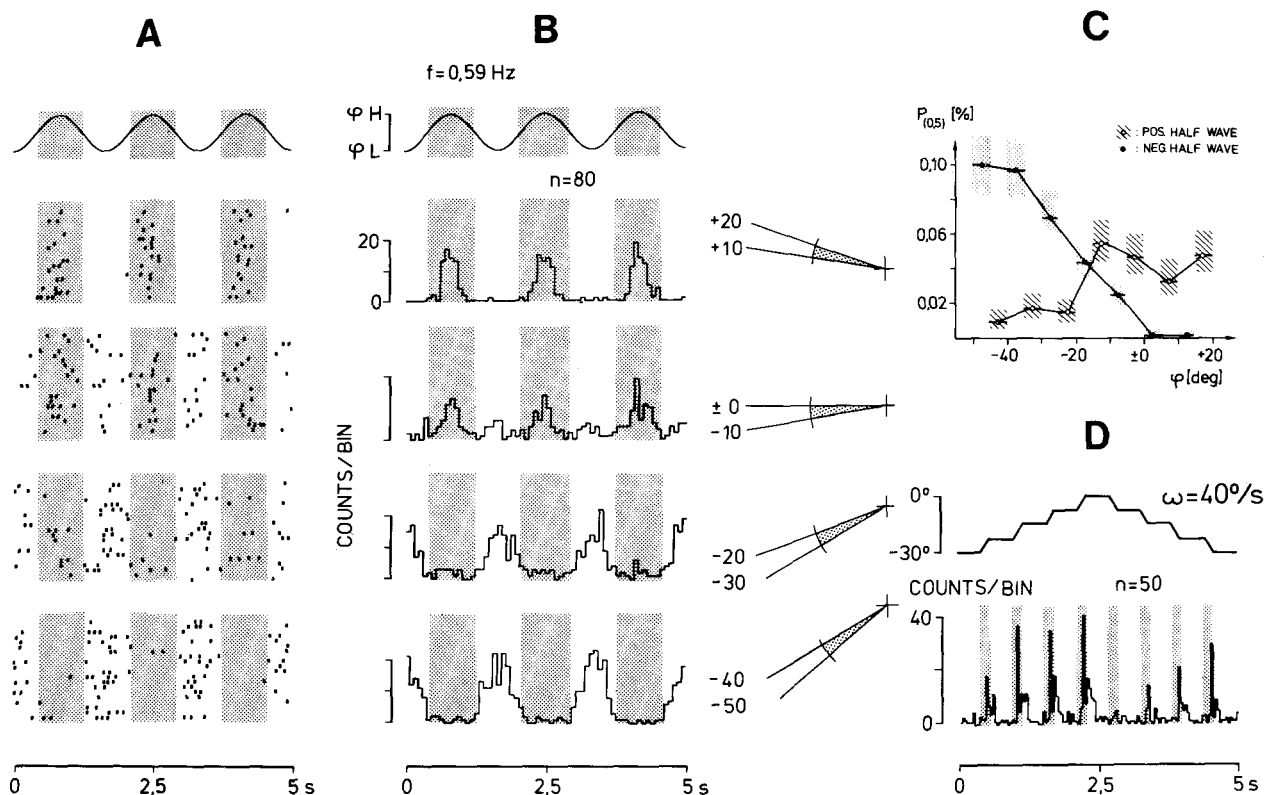
In a previous study (Rubia and Kolb 1978), we described that PCs discharged tonically with the CS while the paw was held in the upper position. Figs. 1B and 1C show two different PCs of this type. The tonic discharge can easily be seen in Fig. 1B and in the top specimen of Fig. 1C. The relation between the probability of CS discharges and the two static positions is shown in Fig. 1D. The mean frequency of tonic discharge increased about five times when the upper position was changed from  $+5^\circ$  to  $+20^\circ$ . The PC in Fig. 1B is a very good example of the CF system's capability to convey information to the cerebellum about peripheral events. The cell responded to (1) position, with an increased average discharge rate at the upper position; (2) momentary position during the upward movement, with an increase in the discharge rate proportional to ramp displacement at each instant during the movement; (3) positive velocity, which was constant during the movement, with an additive constant number of counts; and to (4) positive acceleration, at the



**Fig. 1A–D.** The stimulation arrangement is shown in A. The cat's left forepaw is moved by a DC-motor-driven device (M) from a lower ( $\varphi_L$ ) to a higher ( $\varphi_H$ ) position and back. Position "0°" coincides with the horizontal plane. All positions above the horizontal plane are considered positive and below negative. Responses of two different Purkinje cells (PCs) with complex spikes (CSs) to ramp movements are shown in Peri-Stimulus Time Histograms (PSTH) in B and C. For the PSTH here and in all subsequent figures: Ordinate: counts/bin; abscissa: time in seconds; times of dynamic sections are shaded (only for ramp movements); type of movements tested is shown above PSTH. The PSTH in B shows the averaged CS activity ( $n = 80$ ) to ramp movements with an amplitude of  $40^\circ$  and a velocity of  $40^\circ/s$ . C Another PC responding with CS to ramp movements within the operational range; the tested starting position and amplitude are shown to the right of each PSTH. D Mean probability of CS discharge with 95% confidence limits, calculated for the time when the paw is at different upper ( $\varphi_H$ ) or lower ( $\varphi_L$ ) positions



**Fig. 2A–D.** CS discharge of a PC during a displacement ( $\alpha$ ) of  $5^\circ$  at different paw positions. A Dot rasters: each dot represents the occurrence of one CS. Each of these rasters and those of all subsequent figures read from the bottom to the top. B PSTH: Ordinate division represents 10 counts/bin. C Stack plot of the PSTH shown in B. D Mean probability of unit's discharge during upward ( $m_u$ ) and downward movements ( $m_d$ ). The marked zones indicate 95% confidence limits (vertical direction) and amplitude of movement (horizontal direction)



**Fig. 3A–D.** PC responding with CS to sinusoidal movements with a stimulation frequency of 0.59 Hz. The periods of the positive halfwaves are shaded in the applied movement as well as in the dot rasters (A) and the PSTH (B). Movement amplitudes within the operational range are at the right of each histogram. C Mean probability of unit discharge calculated during periods of positive and negative halfwaves plotted against the position within the operational range. D Another PC responding with CS to a multiple ramp movement from  $-30^\circ$  to  $0^\circ$  in four equal steps with constant velocity of  $40^\circ/\text{s}$

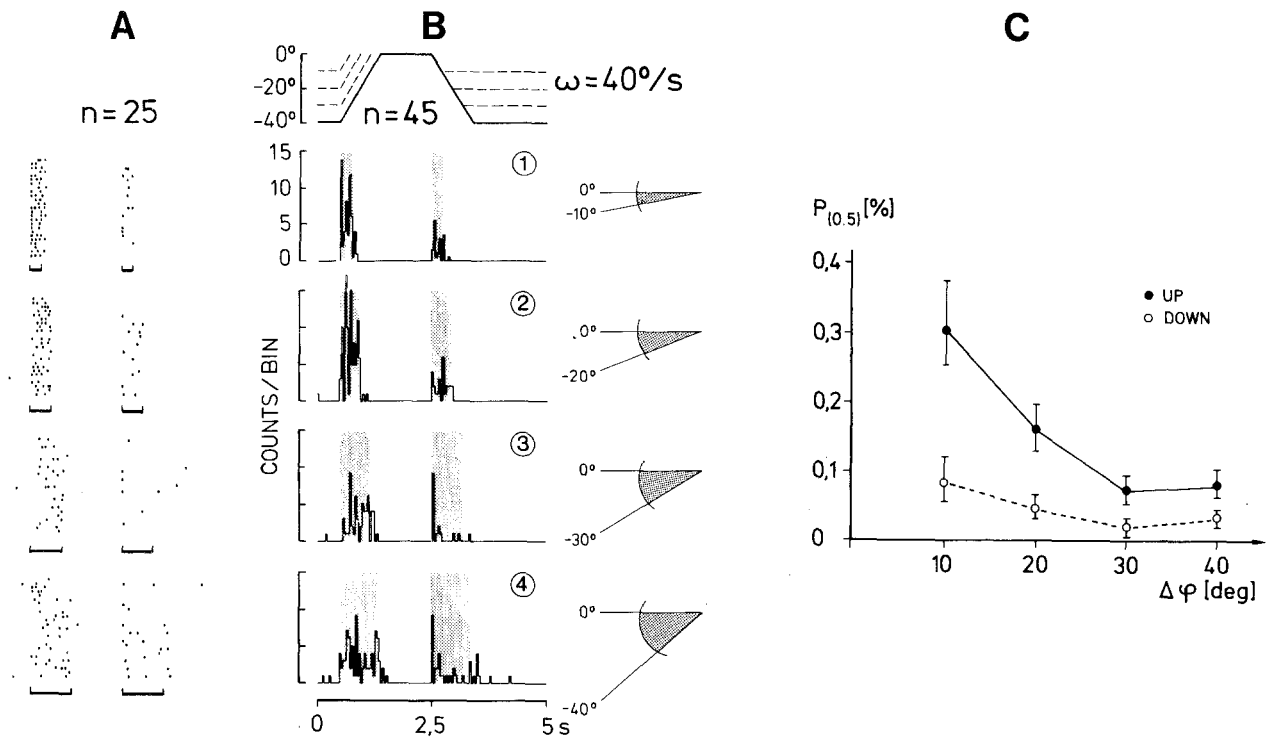
beginning of the upward and at the end of the downward movement.

In 14% of the units, an analysis of the operational range of the CS discharges of the PC was performed. Fig. 2 shows the responses of a unit which discharged only with CSs. SSs, as in many other cells, were not present. Ramp movements with a displacement of  $5^\circ$  and constant velocity of  $40^\circ/\text{s}$  at different limb positions were used in a range between  $-30^\circ$  and  $+15^\circ$ . The PSTHs shown in Fig. 2B indicate that the unit discharged preferentially in the more positive range and mainly for upward movements (see also the PSTH stack plot in Fig. 2C). The dot raster in Fig. 2A demonstrates that the lower the starting position the greater the dots' dispersion. Fig. 2D shows the relationship between the probability of discharge within a time interval of 0.5 ms and the operational range. An increase of probability could only be observed during upward movements, with starting positions more positive than  $-10^\circ$ . The probability of discharge at the highest position was 4.4 times that at the lowest.

During sinusoidal movements of the paw (16% of movements tested) it was observed that for some

units the phase relation between the response and the stimulus was dependent upon where in the operational range the response was elicited. In Figs. 3A and 3B a sinusoidal movement with a frequency of 0.59 Hz and a constant amplitude of  $10^\circ$  was applied within a range of  $-50^\circ$  to  $+20^\circ$ . If the discharge during the positive half-wave of the sinusoidal function is defined as "inphase" (shaded in Figs. 3A and 3B) and during the negative as "outphase", then an inphase modulation of CS activity could be observed in the higher positions, and an outphase modulation in the lower parts of the range tested. In the middle position, the CSs were modulated inphase as well as outphase. The change from inphase to outphase discharge was not a continuous shift in phase but seemed to be a reciprocal increase or decrease of two different discharges (Figs. 3A and 3B). Fig. 3C shows the probability of discharge calculated during the second of the three sinusoidal cycles. Within a wide range, the outphase probability shows a strong linear dependency on the operational range.

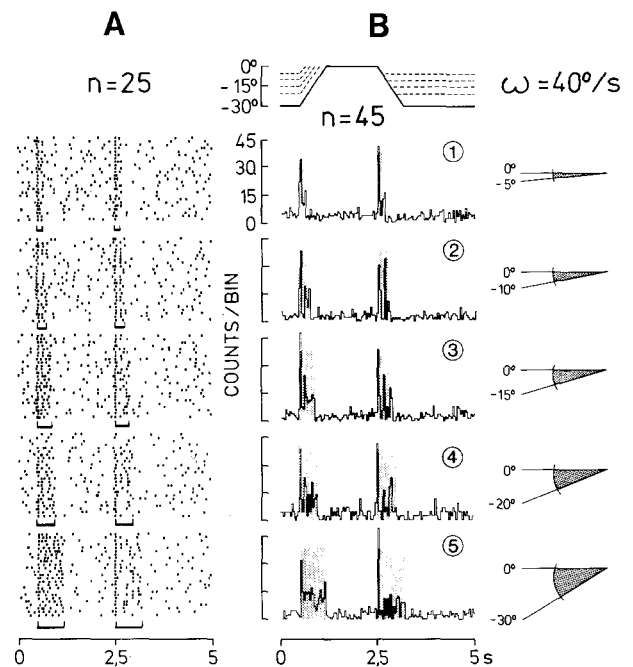
A similar behavior can be observed for the PC shown in Fig. 3D during a movement following a multiple ramp function with constant velocity ( $40^\circ/\text{s}$ ).



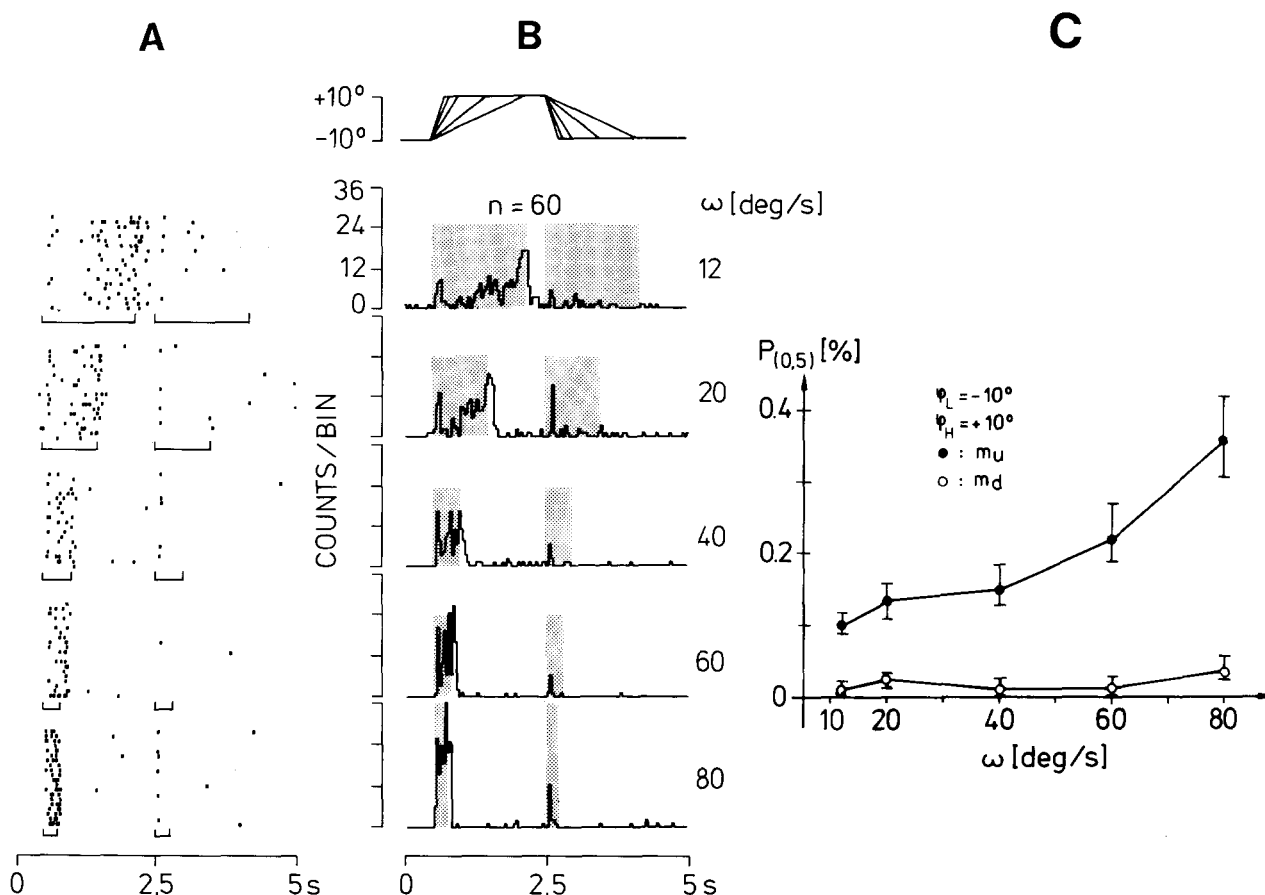
**Fig. 4A-C.** Responses of a PC with a CS to displacement changes shown in dot rasters (A) and inPSTH (B). The starting position was varied as indicated by the dashed lines in the diagram above PSTH (B); the end position was constant at 0°. The velocity was constant (40°/s). C Mean probability of the unit discharge calculated during the dynamic sections of the stimulus function plotted against the range covered by the movement

The unit responded to the different displacements with different average discharge rates, conveying information about each particular limb position. This information, however, was transmitted primarily during positional changes. Interestingly, there was no qualitative difference in the discharge pattern with respect to the direction of the movement. Changing the position resulted in an increase of the average discharge rate which was quantitatively higher during upward movements in higher positions and during downward movements in lower positions. In addition, it must be pointed out that within the range tested the positive direction of a movement was signalled by a higher frequency than the negative direction.

The CS discharge of the PC in Fig. 4 was analyzed by changing the starting position of the paw from -40° to -10° (Figs. 4A and 4B) and maintaining the upper position constant at 0° so that the displacement amplitude was varied. The dot rasters and PSTHs (Figs. 4A and 4B) of this unit clearly show that the greater the displacement the lower the probability of discharge and the greater the dispersion of responses. It is remarkable that this occurred in spite of the fact that in all cases the displacement of the paw covered the movement in B1 (-10° to 0°). Similar but less



**Fig. 5.** A Dot raster; B PSTH of a PC which was discharging spontaneously only with CSs. This unit responded to ramp movements at different starting positions and with different amplitudes. The end position was kept constant at 0° (shown by the dashed lines in the diagram above the PSTH (B) and also at the right of each histogram). The velocity was constant (40°/s)



**Fig. 6A–C.** CS discharge of a PC at different movement velocities. **A** Dot rasters. **B** PSTH; the value of movement velocity is indicated at the right of each histogram. **C** Mean probability of unit discharge during the dynamic phases of the movement plotted against movement velocities

pronounced responses were obtained during downward movements. The number of counts during the whole movement remained fairly constant in every specimen, independent of changes in the starting position. Notice also that this PC discharged only during dynamic phases of the ramp function and responded only with CSs, while SSs were absent.

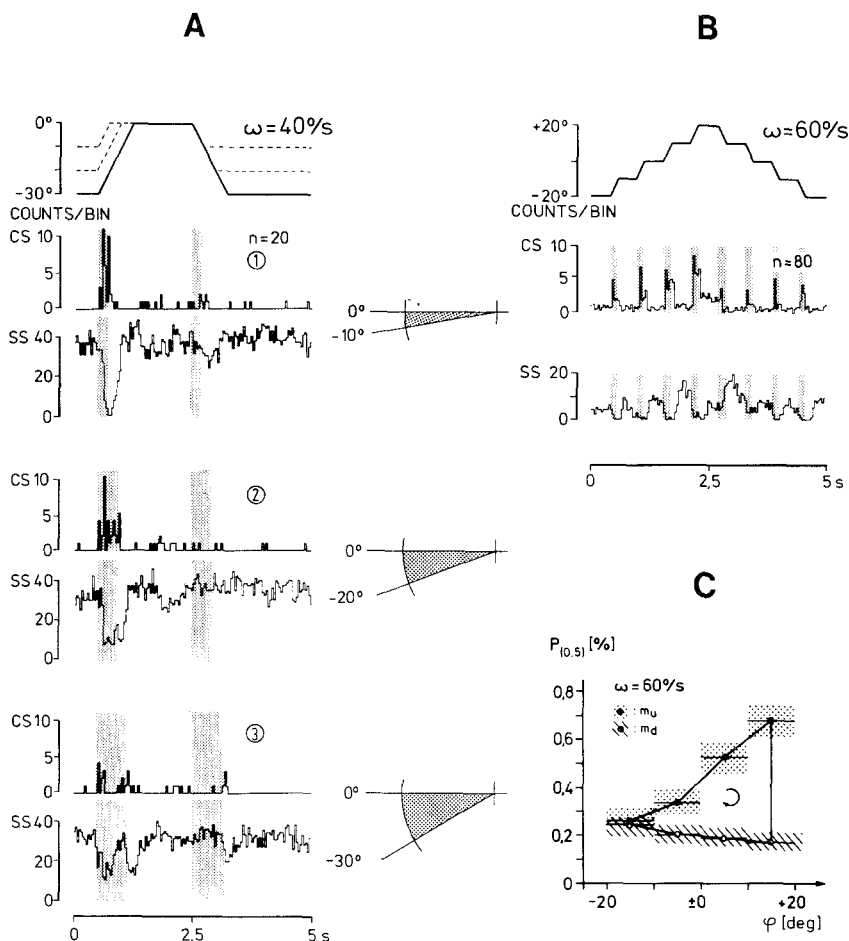
#### Responses Independent of Position

Figs. 5A and 5B show another unit which only responded with CSs, but was spontaneously active. The starting position of the paw was changed from  $-30^\circ$  to  $-5^\circ$  and the upper position was maintained constant at  $0^\circ$ . The velocity was also kept constant at  $40^\circ/\text{s}$ .

In contrast to the previous cases (Figs. 1–4), the responses of this unit were independent of the starting position since the qualitative discharge pattern did not change appreciably. The unit showed increased frequency of discharge during the dynamic

phase, and this discharge pattern was similar during the different displacements, suggesting that it was correlated to the velocity. The first peak in the PSTH, presumably transmitting information about the acceleration of the movement, also remained relatively constant.

In 10% of the units, the relation of cell discharge to changes in movement velocity was tested. The unit in Fig. 6 demonstrates such a relation. During analysis, the amplitude of forepaw movement was kept constant between  $-10^\circ$  and  $+10^\circ$  while the velocity of the movement was changed from  $12^\circ/\text{s}$  to  $80^\circ/\text{s}$ . Fig. 6B shows the corresponding PSTHs; this PC discharges with CSs alone. It can be seen that during the dynamic phase of the movement the frequency increase of the unit discharge was approximately proportional to the velocity. As in the units in Fig. 1 and Fig. 2, the upward movement was preferentially signalled. It is interesting to note that during the upward movement the momentary paw position was also indicated by an increase of the average discharge rate. The peaks shown on the PSTH at the beginning



**Fig. 7A–C.** PC discharging with both types of spike (CSs and SSs). PC in **A** responds to different starting positions and amplitudes of movement (shown to the right of the PSTH). **B** PSTH of both types of spikes of another PC responding to a multiple ramp function. **C** Mean probability of the CS activity during dynamic phases is plotted against the tested range

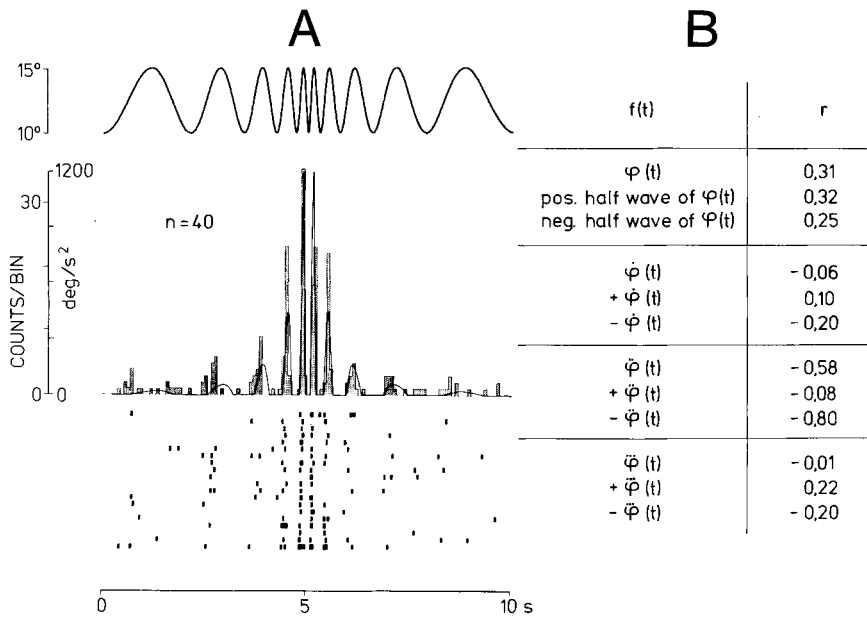
and near the end of the movement can be interpreted as responses to acceleration signals. Fig. 6C shows the probability of discharge plotted against the velocity of the movement; the former was 3.6 times higher during a velocity of 80°/s compared to 12°/s.

*Responses to the Acceleration Components of the Movement*

As illustrated in Fig. 4, the shorter the displacement, or the higher the movement velocity (Fig. 6), the closer the acceleration signals within the dynamic phases of a ramp movement. This can be especially well seen in Fig. 7A, 3, where the PC responded with CSs to the acceleration signals at the beginning and the end of the upward movement. With smaller displacements (Fig. 7A, 1 and 2) responses to both signals summated in time, increasing the number of counts per unit time in the PSTH. The activity of both types of spike were inversely related, an increase in CS activity being accompanied by a decrease in SS activity. Hence, by using larger

movement amplitudes the responses to positive and negative accelerations were clearly separated during the upward movement. These responses were visible for both types of spike. In Fig. 7B, another PC is shown responding to a multiple ramp function with CSs and SSs; both types of spike showed phasic and tonic components in inverse relationship. Information about the position of the paw was signalled by both systems in different ways. At the position of +20°, CS activity was increased 2.5 times in comparison to all other static positions. With respect to the positional changes within the tested range, the mean average discharge rate showed an approximately linear dependency. This response was observed – although less clearly – in the negative direction (Fig. 7C). The peaks in the histogram (Fig. 7B) could be attributed to acceleration signals, as in Fig. 1B.

The movement applied to the paw in Fig. 8 consisted of a constant amplitude of 5° (from +10° to 15°) and a logarithmic increase and decrease of the frequency. The maximal velocity achieved near the middle of the movement was 60°/s. The unit recorded (Fig. 8A) discharged only with CSs. The relative



**Fig. 8.** A PC discharging with CSs only, in response to a sinusoidal movement with a constant amplitude of  $5^\circ$  and a logarithmically increasing or decreasing frequency. The solid line of the PSTH represents the absolute value of negative acceleration. **B** Table of Pearson correlation coefficients evaluated between the PSTH in **A** and different functions  $f(t)$ . The correlated functions are:  $\varphi(t)$ , sinusoidal movement function; positive halfwave of  $\varphi(t)$ ; negative halfwave of  $\varphi(t)$ ; the positive (+  $\dot{\varphi}(t)$ ) and negative (-  $\dot{\varphi}(t)$ ) velocity; the acceleration  $\ddot{\varphi}(t)$ , second derivative of  $\varphi(t)$ ; the positive (+  $\ddot{\varphi}(t)$ ) and negative (-  $\ddot{\varphi}(t)$ ) acceleration; the third derivative of  $\varphi(t)$ , its positive values (+  $\dddot{\varphi}(t)$ ) and its negative values (-  $\dddot{\varphi}(t)$ )

maxima of the averaged discharge rate of the unit lie approximately on a power function, which suggests that the discharge was related preferentially to the dynamic parameters of the movement. The Pearson correlation coefficient was calculated between the PSTH (Fig. 8A) and (1) the movement function, (2) its first, second and third derivatives and (3) certain sections of them (Fig. 8B). The best correlation was found between the averaged discharge rate and negative acceleration. It must be noted that the responses of this unit were supposedly a superposition of responses to different parameters of the movements.

## Discussion

The results presented in this study strongly support the view that the CF system is able to transmit precise information about parameters of ongoing movements to the cerebellar cortex. We have shown that the position of the extremity, the velocity and the acceleration are well signalled via the CF system. Moreover, a single olivary neuron and its corresponding PC can receive information from different groups of receptors in different parts of the periphery. Consequently, it can be concluded that in the absence of central influences, sensory feedback information from the periphery is accurately transmitted to the cerebellum via the CF system.

Nevertheless, these results raise questions which cannot be answered at the present stage of research. For example, what is the meaning of this information

in a physiological context? We have seen that the CF system is able to convey specific information about static parameters in two different ways. First, directly (Fig. 1) by an increased discharge frequency during the static upper position, and secondly indirectly (Fig. 2) in connection with a dynamic parameter of the movement. The majority of units, however, did not respond to a static parameter.

A second remarkable finding is the relation which seems to exist between the PC discharge via CF and the acceleration. Considering the results shown in Fig. 4, it is apparently unexplainable that during a displacement of the forepaw from  $-40^\circ$  to  $0^\circ$  the PC does not discharge with at least the same number of CSs per unit time as during the displacement from  $-10^\circ$  to  $0^\circ$ . There are at least two possible interpretations for these results. One is that the olivary cell responds predominantly to the acceleration parameter. Thus, during a short movement the acceleration signals are so close together in time that they summate and produce a more powerful response. The other possibility is that the receptors responding to acceleration are located in the upper part of the operational range and that they are excited only if an acceleration occurs there. In case 4 of Fig. 4B ( $-40^\circ/0^\circ$ ) the movement covers the same range, but at position  $-10^\circ$  no acceleration signal is present.

The importance of the arrangement of the receptors responsible for the discharge seems to be clear from Fig. 2A and 2B. With the same displacement and velocity of movement, the responses are different depending on the starting position of the paw within the operational range, suggesting a varying



sensitivity of the receptors stimulated. The responses of the cell shown in Figs. 5A and 5B are quite different from those in Figs. 4A and 4B. Although the peaks at the beginning of the upward and downward movements are probably responses to acceleration signals, there seem to be no responses to the acceleration at the end. Therefore, no summation occurs with shorter amplitudes. The response of the PC in Fig. 3D to multiple ramp movements can be interpreted as a result of the convergence of two different receptors with varying directional sensitivity. Here again the cerebellum is well informed about the position within the range in which the paw was moved. The same phenomenon holds true for the cell in Fig. 3A and 3B which responded either inphase or outphase to sinusoidal movement, depending on the location of the paw. In the intermediate position of  $-10^\circ$  to  $0^\circ$ , the presumed receptors were activated alternately depending on the movement phase.

The movement applied to the paw in Fig. 8A was used to test the responses of the PC to these movement's dynamic parameters by using a sinusoidal curve with logarithmically increasing and decreasing frequencies. By comparing the discharge of the cell in Fig. 8A with the first, second and third derivatives of the movement function, it turns out that the discharge pattern is more closely correlated to the acceleration component than to the velocity (Fig. 8B). Our results agree with those reported by Rushmer et al. (1976) in that they show small passive displacements of the forepaw eliciting strong PC responses via the CF system in the  $c_1$ -zone of the cerebellar anterior lobe (Voogd 1969). In addition, the pathway conveying these responses was extremely sensitive to changes in the environmental situation. There are, however, several differences between our results and those reported in the paper mentioned above. These authors reported that in most of the PC studied, the CS responses to the initial dynamic phase of the movement were independent of the starting paw position and the direction of movement. In our experiments, paw position and movement direction elicited different CS responses. We have also found strong differences among cells within the  $c_1$ -zone, not only with respect to their direction sensitivity, but also in relation to their signalling of the different parameters of the movement. The "CS-doublet" found by these authors, was a common observation in our results. As can be seen in our dot rasters, even "triplet" and "quadruplet" responses occurred. Comparing the results obtained by these authors with our own, we can say that at present it is difficult to ascribe to this system a different function from that of the MF system. It can of course be claimed that the specific information transmitted may

serve as an "event detector", but we do not find a rational reason why the same assertion would not be valid for the MF system. The spatial distribution of the CF within the cerebellar cortex in parasagittal zones and especially the way in which the PC axons converge on the target cells (supposedly also parasagittal) might help to explain the differences found between the PC responses via the two different inputs. After sufficient averaging of CS at the level of the PC, it is possible to obtain similar responses in the two input systems. It seems obvious to us that the CF system may play a role in locomotion. More important is to show how this system participates in conjunction with the MF system.

The following question arises: how is this accurate information transmitted to the cerebellum? The  $c_1$ -zone of the lobule Vc is the terminal site of two spino-olivocerebellar paths which convey information from the forelimb: the dorsal funiculus spino-olivocerebellar path (DF-SOCP; Oscarsson 1969) and the dorsolateral funiculus spino-olivocerebellar path (DLF-SOCP; Larson et al. 1969a). According to these authors, the DF-SOCP is activated by electrical stimulation of flexor reflex afferents from wide receptive fields, but natural excitation of group I muscle afferents, cutaneous receptors, and moderate bending of joints or vibration fail to elicit any effect on the neurons in this pathway. On the other hand, Ebbeson (1968) reported that the path linking the dorsal column to the dorsal accessory olive (the relay nucleus for the DF-SOCP and presumably for the DLF-SOCP also) relays specific information from joint receptors and cutaneous mechano-receptors to the cerebellum. The second pathway (DLF-SOCP) should forward modality and space specific information, especially from cutaneous afferents to the cerebellum. Rushmer et al. (1976) reported that the recorded characteristics of the CS discharges during small displacements of the forepaw are consistent with those expected from the DLF-SOCP, but concluded that several pathways may be involved in the responses. In our experiments we did not closely examine this question. Nevertheless, the specific information forwarded to the cerebellum during natural stimulation of the forepaw led us to suppose that since it was possible to find a similar discharge pattern in both the MF and CF systems (see Rubia and Kolb 1978), it is highly probable that information in both pathways relay at the same stations, i.e. the dorsal column nuclei. A common observation in our experiments was the high sensitivity of some units to manipulation of hairs and application of a small pressure to the forepaw pads. This observation has already been reported by other authors (Eccles et al, 1972a, b, c, d) who observed strong CF mediated PC

responses by stimulating presumed Pacinian corpuscles and hair follicle receptors. The fibers in the dorsal funiculus originate from different receptors, such as vibration, hair, claw, pad and subcutaneous pressure receptors (Uddenberg 1968a, b) which have response characteristics similar to those of our PCs.

The present results do not support Oscarsson's (1967) ideas about the functional role of the spino-olivocerebellar paths, according to which the information forwarded through these paths might be primarily concerned with activity within the central nervous system. It is, of course, possible that this could be a function of the CF system, but our results strongly suggest that this system also directly informs the cerebellum about peripheral events. For this reason, we do not need to assume that in order to elicit PC responses via the CF system during natural stimulation, a convergence from ascending and descending pathways would be necessary. This is not only because we have used decerebrate animals, but also because, as previously reported (Bauswein et al. 1978), the interaction during active movements of command signals and peripheral feedback information does not seem to result in an increase but rather a suppression of the peripheral information reaching the cerebellar cortex. Andersson and Sjölund (1978) as well as Sjölund (1978) reported that in the  $c_1$ -zone and  $c_3$ -zone, flexor reflex afferent information related to peripheral events is forwarded via the ventral funiculus spino-olivocerebellar path. These experiments were performed on decerebrate cats using electrical stimulation.

The present stage of research does not allow a clear definition of the function of the two inputs to the cerebellar cortex. However, some conclusions can be drawn from our results which may contribute to the discussion about this interesting question. Many cells in this study discharged only with CSs. Thach (1970) showed in the awake monkey that PCs can discharge in relation to active movements either which CSs or SSs alone. These findings suggest that PCs might operate properly with the information transmitted via one single input. The ability of the CF system to convey information about peripheral events supports this opinion. In this connection, the idea that the CF system should serve as a kind of "event detector" (Rushmer et al. 1976) appears too restrictive. An event detector should inform unspecifically the cerebellar cortex about changes in environmental conditions, but not necessarily about all the different parameters of the movement.

If the PC discharges with both types of spike, in the majority of cases these show an inverse relationship. By assuming that the lower frequency of the CSs compared to SSs is counterbalanced by the

greater efficacy of the former on target cells, an opposite behavior of both types of spike may have the function of maintaining the target cells under continuous inhibition. A strong modulation of the target cell should be achieved when both types of spike of the PC behave similarly or when the PC discharges with only one type of spike as compared to those cases where both types of spike behave inversely to each other. In our experiments, these two last possibilities were found in approximately one third of the recorded PCs. Assuming that the most significant signals for the inhibitory function of the cerebellar cortex are sent by these types of PC, it remains to be explained why the greater majority of the cell discharge with both types of spike in an inverse relation to each other. One possible explanation is that the cerebellar cortex is specifically used if corrections are needed and that the constant task is to maintain the target cells under inhibitory control.

It is assumed that there is a ratio of convergence of 200:1 between PCs and nuclear cells. In our experiments, the PCs did not respond with CSs to each movement so that unit activity during a certain number of movements had to be averaged to obtain the described phenomena. Thus, we presume that a target cell receives an amount of information about the parameters of one single movement which is comparable to the information contained in the averaged discharge of one PC during several movements.

In our investigations the similarity of the responses of the two input systems to passive movements might suggest that they act either independently or together in a complementary manner. If they act together, they can potentiate or reduce the inhibition, depending on the relative timing of the two types of spike. In this context, the existence of two different inputs with similar characteristics greatly enhances the possibility of fine modulation of movements by the cerebellum.

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