Journal of Physiology (1989), **419**, *pp.* 717–751
With 11 *text-figures*
Printed in Great Britain

NEURAL CORRELATES OF HORIZONTAL VESTIBULO-OCULAR REFLEX CANCELLATION DURING RAPID EYE MOVEMENTS IN THE CAT

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(*Received 20 June 1988*)

SUMMARY

1. The aim of the present study is to describe the behaviour of identified second-order vestibular neurones in the alert cat during eye saccades. A selection of neurones which are involved in horizontal eye movements has been made. The activity has been compared with a selected sample of abducens motoneurones recorded in the same animals.

2. Alert head-fixed cats were used for this study. Eye movements were recorded by the scleral search coil technique. Abducens motoneurones were identified by antidromic stimulation from the VIth nerve with chronically implanted electrodes. They were recorded extracellularly.

3. Second-order vestibular neurones were identified by orthodromic stimulation from the vestibular organs. They were recorded intra-axonally and injected with horseradish peroxidase after recording of their physiological characteristics. Their morphology was reconstructed from frozen sections.

4. All the recorded vestibular neurones showed various amounts of eye position sensitivity. The firing rate (F) – horizontal eye position (H) characteristics are compared for abducens and vestibular neurones. The population average values are $F = 33 + 4\,H$ for motoneurones and $F = 51 + 2{\cdot}4\,H$ for vestibular neurones.

5. All recorded vestibular neurones showed an increase of discharge rate during contralateral horizontal saccades and a strong decrease or pause during ipsilateral saccades. Firing rate – horizontal eye velocity sensitivity has been calculated.

6. Results suggest a strong inhibitory input on vestibular neurones from the saccadic generator. This mechanism underlies the suppression of the vestibulo-ocular reflex during saccades. Our results suggest that in the cat, for saccades of amplitude smaller than 20 deg, there is a variable degree of suppression which is provided by a projection of excitatory bursters (EBNs) on second-order vestibular neurones through inhibitory type II neurones.

7. We also conclude from this study that the eye position sensitivity of vestibular second-order neurones is in fact a motor signal indicating a motor error, i.e. the amount of head or eye movement which remains to be done in order to align gaze on target with the eyes centred in the orbit.

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INTRODUCTION

During natural eye and head movements some specialized reflexes, such as the vestibulo-ocular reflex (VOR), serve to keep gaze stable in space. However, these reflexes can be diminished and/or suppressed during orienting movements to a visual, acoustic or memorized target. There are obviously important species differences and within the same species, different modes of interaction depending upon the amplitude and direction of the gaze shift. However, most authors agree that *VOR suppression* during orienting movement is produced by an action of the saccadic generator on neurones subtending the VOR itself. Recent reviews on this problem have been published (Guitton, Douglas, & Volle, 1984; Laurutis, & Robinson, 1986; Pelisson & Prablanc, 1986; Guitton & Volle, 1987).

The detailed neuronal mechanisms of this suppression are, however, not clear. The first demonstrations that identified second-order vestibular neurones pause during quick phases of vestibular nystagmus and are modulated together with the slow phase was given by Baker & Berthoz (1971, 1974) for the oblique system, and by Maeda, Shimazu & Shinoda (1972) and Hikosaka, Maeda, Nakao, Shimazu & Shinoda (1977) and Hikosaka & Kawakami (1977) for the horizontal system, in *encéphale isolé* preparations. Since then, a large amount of data has been obtained on the activity of vestibular neurones in alert monkeys (Keller & Kamath, 1975; Keller & Daniels, 1975; Fuchs & Kimm, 1975; Waespe & Henn, 1979; Buettner, Buttner & Henn, 1978; Lisberger & Miles, 1980; Tomlinson & Robinson, 1984), and cats (Shinoda & Yoshida, 1973; Pola & Robinson, 1978; Keller & Precht, 1979; Anastopoulos & Mergner, 1982; Tomlinson & Robinson, 1984; Baker, Goldberg, Hermann & Peterson, 1984). From these studies has emerged the idea that there are several populations of vestibular neurones which are characterized by different types of behaviour in regard to the parameters of eye and head movement. This complexity leads to some confusion because of the lack of information about the afferent and efferent connections of the recorded neurones in all but one of these studies (Keller & Kamath, 1975), in spite of the existence of numerous interneurones in the vestibular nuclei (Shimazu & Precht, 1965, 1966). Recent examination of the activity of identified second-order vestibular neurones in the alert cats has confirmed by direct demonstration the presence of saccadic eye velocity and eye position signals in a large population of neurones projecting to the abducens nucleus and receiving a monosynaptic activation from the ipsilateral vestibular receptors (McCrea, Yoshida, Berthoz & Baker, 1980; Yoshida, Berthoz & McCrea, 1981; McCrea, Yoshida, Evinger & Berthoz, 1981; Berthoz & Vidal, 1981). Some premotor interneurones, projecting to the vestibular nucleus, which could be candidates to subserve this influence in the case of horizontal movements, have been identified. They are (a) inhibitory burst neurones (IBNs) located in the dorsomedial medullary reticular formation which also project contralaterally to abducens motoneurones (Hikosaka & Kawakami, 1977; Hikosaka, Igusa & Imai, 1980; Yoshida, McCrea, Berthoz & Vidal, 1982), (b) excitatory burst neurones (EBNs) located rostral to the abducens nucleus which also excite ipsilateral abducens motoneurones, and (c) prepositus hypoglossi neurones which entertain with the vestibular complex a strong reciprocal projection (McCrea & Baker, 1985) and carry both eye position and eye velocity signals (Baker, Gresty & Berthoz, 1976; Lopez-Barneo, Darlot, Berthoz &

Baker, 1982). But the only positive evidence for a clear inhibitory mechanism has been given by Sasaki & Shimazu (1981) and Ito, Matsuoka, Sasa & Takaori (1985), and Ito, Markham & Curthoys (1986), who have shown in the cat that EBNs project on type II vestibular nuclei neurones which in turn will inhibit type I second-order vestibular neurones. Recently E. May and R. McCrea (unpublished observations) have found three groups of cells which can contribute to the cancellation of the VOR in the vicinity of the abducens nucleus.

However, the exact changes of firing rate in identified second-order vestibular neurones (VNs) of the cat during saccades have not been well documented. The present results give a description of these properties for neurones which are mainly influenced by the horizontal eye movement generators. Two types of second-order vestibular neurones are known to mediate the horizontal VOR. They have been identified in the cat as either excitatory or inhibitory and projecting respectively either to the controlateral (cVN) or the ipsilateral (iVN) abducens motoneurones (Baker, Mano & Shimazu, 1969). In the present study, we have used the technique of intra-axonal recording in the alert cat in order to combine the description of the physiological properties of the neurones and the description of their morphology (see Yoshida *et al.* 1982). In addition, the present paper contains a survey of a sample of abducens motoneurones (AMNs) studied in the same cats in order to compare the eye movement signals associated to shifts of gaze in VNs and AMNs. This comparison is essential to answer the question of the possible role of VNs in mediating gaze signals to AMNs.

METHODS

Surgical procedures

The animals used in these experiments were selected because they were behaviourally and temperamentally suitable. Experiments were performed on fifteen alert cats prepared for chronic recording. Figure 1*A* shows the experimental protocol. Several days before the recording session, each animal underwent the following surgical procedures under pentobarbitone anaesthesia (40 mg kg^{-1} I.P.): (1) a coil of Teflon-coated stainless-steel wire was implanted on the eyeball to measure eye movements with the electromagnetic search coil method; (2) fine silver-wire electrodes were chronically implanted bilaterally near the oval and round windows for electrical stimulation of the vestibular nerves; bipolar electrodes were implanted bilaterally to stimulate the abducens nerves as they exit from the brain stem; (3) a metal head-piece with three bolts was cemented stereotaxically on the skull to immobilize the animal's head during recording sessions; (4) a small opening of about 3–5 mm in diameter was made on the lambdoidal suture to allow access of recording microelectrodes to the brain stem. Between recording sessions the hole was covered with a thin film of Silastic and bone wax.

Details of surgical procedures and methods for testing implantation of stimulating electrodes have been given elsewhere (Yoshida *et al.* 1982). The same cats were used for recording of either abducens motoneurones or vestibular neurones. The stimuli used, both peripherally (vestibular nerve) and centrally did not create any signs of behavioural stress in the experimental animals.

Vestibular stimulation

During the recording session, the animal's head was securely fixed, in a 25 deg nose-down position, to a stereotaxic frame mounted on a velocity-controlled turn-table which could rotate about the vertical axis. Sinusoidal rotations at peak-to-peak velocities of up to 20 deg s^{-1} in darkness or in the light were used. Frequency was 0·1–0·3 Hz. A large shutter mounted on the turn-table in front of the cat allowed the experimenter to test the neuronal activity either in the light or in darkness.

The duration of head fixation per session was less than 2 h per session. The frequency at which

cats underwent head fixation was once per day or once every 2 or 3 days. The mean length of the experiment in total for each cat was 1 to 2 weeks.

Eye movement recording

Eye movements were monitored by a recording system (Skalar) whose bandwidth was about 200 Hz. The precision was about 10 min of arc. Eye movements were calibrated by moving the

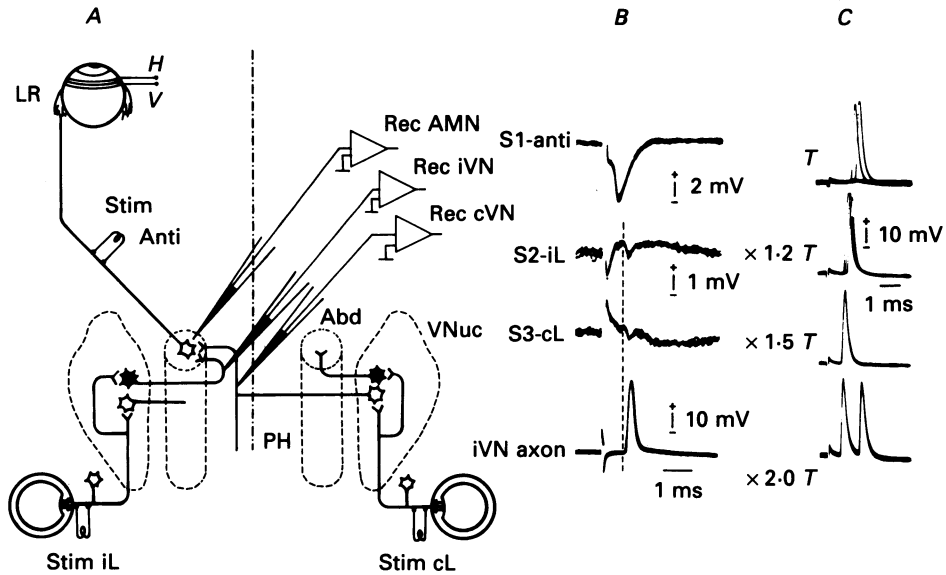

Fig. 1. Experimental protocol for the study of abducens motoneurones (AMNs) and second-order vestibular neurones (VNs) in the alert head-fixed cat. *A*, schematic description of the experimental arrangement. Horizontal (*H*) and vertical (*V*) components of eye movements are measured by the search coil technique. Stimulation electrodes are placed chronically on the abducens nerve (Stim, Anti) for antidromic activation of motoneurones, and on the vestibular nerves from the ipsilateral (iL) and contralateral (cL) labyrinth. Glass electrodes allow extracellular recording from abducens motoneurones (Rec AMN), and intra-axonal recording of second-order vestibular neurones from the ipsilateral (iVN) or contralateral (cVN) vestibular nuclei. LR, lateral rectus muscle; Abd, abducens nucleus; VNuc, vestibular nucleus; PH, prepositus nucleus. *B*, from top to bottom, extracellular field potentials recorded in the abducens nucleus following antidromic abducens nerve stimulation (S1-anti), and orthodromic ipsilateral (S2-iL) and contralateral (S3-cL) vestibular nerve stimulation. *C*, latency changes of monosynaptically evoked spike potentials for varying stimulus intensity. From top to bottom: threshold (*T*) intensity, and 1·2, 1·5 and 2 times threshold.

magnetic search coils around the head of the cat. This method does introduce a small error which is, however, not significant for our results (see discussion in Yoshida *et al.* 1982). To estimate the centre of gaze, the ranges of horizontal and vertical eye movements were determined from records of 20–40 min, and the median value of each range was taken as the zero position of the corresponding axis (Crommelinck, Guitton & Roucoux, 1977). The difference of the evaluation within different samples in the same animal was always within 2–3 deg.

Recording and identification of second-order vestibular neurones and abducens motoneurones.

Axons of vestibular nucleus neurones were penetrated intracellularly in the vicinity of the abducens nucleus (see Fig. 1). The abducens nucleus was identified by the antidromic field potential evoked by stimulation of the abducens nerve (Fig. 1*A* and *B*). The axonal character of the recording was evidenced by (a) the positive deflection of the spike, (b) the absence of slow potential

preceding it, and (c) the absence of inflection on the rising phase of the spike. Spike amplitude varied between 10 and 30 mV. Axons were identified as secondary vestibular neurones projecting to the ipsilateral (iVNs) or controlateral (cVNs) side (Fig. 1*B* and *C*) by monosynaptic activation following single-shock stimulation of the vestibular nerves. Spike potentials were superimposed on small negative field potentials, attributable to second-order vestibular fibres in the abducens nucleus. The latency of evoked spike potentials which fluctuated at threshold intensity and shortened considerably with increasing stimulus intensity, indicated the trans-synaptic nature of activation. When tested with stimulus intensities of 1·5–2 times threshold, the latencies ranged from 0·6 to 0·9 ms, in good accordance with the results of Baker *et al.* (1969). This method of identification has some limitations because only vestibular neurones activated from the contralateral labyrinth (cVNs) can be identified with certainty. Axons that are activated from the ipsilateral vestibular nerve, can either be true vestibular neurones projecting to the ipsilateral side (iVNs) or cVNs that cross the mid-line after their passage in the nucleus.

For this reason we have complemented the identification of a small number of neurones by intracellular injection of horseradish peroxidase (HRP). The detail of the method has been described previously (Yoshida *et al.* 1981; McCrea *et al.* 1981; Yoshida *et al.* 1982; Grantyn & Berthoz, 1987). It allows the complete reconstruction of the description of both the functional and the morphological properties of these neurones. Abducens motoneurones were identified by antidromic activation from the VIth nerve. This was performed by chronically implanted electrodes which stimulated the VIth nerve intradurally before its exit from the brain stem.

Intra-axonal recording from vestibular neurones was made with glass microelectrodes (1–2 μm tips) filled with 3 M-KCl solution. For morphological studies, micropipettes were filled with 10% HRP in Tris buffer (ph 7·2) and 0·5 M-KCl. Electrode resistance varied from 15 to 40 MΩ.

Data processing

Neural activity, horizontal and vertical eye position signals and the angular position or velocity signal from the turn-table were recorded on a magnetic tape and processed on a HP 5451B and 1000 computers. Instantaneously firing rate was calculated as the inverse of the interspike interval measured with a time resolution of 10 μs. Eye position signals were sampled at 1250 Hz and instantaneous velocity was estimated as the slope of the line fitted to position samples contained in 15–40 ms.

Velocity signals were then used to detect rapid eye movements with the additional criteria given by the calculation of eye acceleration. Saccade onset was detected by a velocity criterion of 15 deg s^{-1}, an acceleration threshold and the time preceding by one-third of the sliding window (e.g. 13 ms in the case of a 40 ms window) was taken as saccade onset. The end of each saccade was flagged in a similar way by the computer. The numerical filtering used for the calculation of saccadic velocity has the advantage that it does not introduce any phase shift. However, because of the presence of a rather high level of noise in our recording due to the tape amplifier noise, we had to take a rather long window. Cut-off frequency was in the order of 50 Hz (3 dB). This does not modify too much the peak amplitude of saccadic velocities in our experiments because the head-fixed cat makes saccades whose amplitude is smaller than 20 deg. The cat, in this condition, tends also to make somewhat slower saccades than in the head-free condition (Guitton *et al.* 1984). Consideration must be given, however, when looking at the velocity traces of this paper, to the fact that some roundings of the onset of the velocity traces are indeed noticeable.

Coefficients of correlation between neurone firing rate and the components of eye position, and coefficient of variation were calculated by a standard statistical package. The calculation made to extract the saccadic velocity sensitivity will be described in the Results section.

RESULTS

The results will be presented in the following order. We shall first report the data concerning the main characteristics of the behaviour of abducens motoneurones during saccades and fixations. The method used to extract horizontal eye velocity sensitivity will be described in detail. Secondly we shall describe the physiological properties of second-order vestibular neurones during horizontal vestibular stimu-

lation, and during spontaneous or visually induced saccades. The purpose of this first part will also be to show how VNs were characterized as 'horizontal'. A quantitative comparison between firing rate and eye position will then be made between a selection of VNs and AMNs. Thirdly the horizontal saccadic eye velocity sensitivity of several neurones will be described and a quantitative evaluation of this sensitivity will be made for a population of horizontal VNs. Two examples of VNs, for which a combined physiological and morphological study could be made, will then indicate the neuronal targets of the signals carried by these neurones.

General firing characteristics of abducens motoneurones

A total of thirty-five abducens motoneurones were antidromically identified by stimulation of the abducens nerve. An example of antidromic response is shown in Fig. 2*A* and *B*. Antidromic spikes were characterized by their short and fixed latency at threshold straddling intensity (Fig. 2*A*) and by collision block with spontaneous action potentials (Fig. 2*B*). Latencies ranged from 0·30 to 0·80 ms with a mean of $0{\cdot}45 \pm 0{\cdot}15$ ms.

All identified abducens motoneurones exhibited a qualitatively similar firing pattern. The instantaneous firing rate of an abducens motoneurone during saccades and fixation is illustrated in Fig. 2*C*. During fixation between saccades, abducens motoneurones fired steadily at rates that increased monotonically with ipsilateral shift of eye position. During fixation in the contralateral directions, they decreased their firing rate or ceased to fire. Firing rate of abducens motoneurones was also correlated with horizontal saccadic eye movements. They exhibited high-frequency bursts of discharges in association with ipsilateral directed saccades, and paused during contralateral saccades. This firing behaviour was quantified based on the detailed analysis of twelve abducens units. The inspection of other units indicated that the range of firing characteristics obtained from these twelve AMNs units roughly covers the overall range for the entire population observed.

Regularity of firing during fixations

For each of the twelve abducens motoneurones, the firing rate and the regularity of firing during fixation were determined by calculating the mean and standard deviation of interspike intervals (see Table 1). Interspike intervals were measured for the whole period of each fixation except for the initial and last 100 ms portions to exclude abrupt activity change associated with adjacent saccades. As a measure of regularity of firing, the coefficient of variation was then obtained by dividing the standard deviation by the mean. The mean firing rate was calculated as a reciprocal of the mean interspike interval. When a number of such firing rates and coefficients for different fixations were plotted against horizontal eye positions, relationships similar to those illustrated in Fig. 2*D* (lower panel) resulted.

The coefficient of variation depended on the mean firing rate, which in turn was closely related to horizontal eye position. For mean rates of about 50–100 spikes s^{-1}, the coefficient was smallest and the mean value for individual motoneurones ranged from 0·06 to 0·09 (Table 1). The minimum value of the coefficient varied from 0·03 to 0·07 among different units. For firing rates lower than 50 spikes s^{-1}, interspike

intervals became less regular. The coefficient of variation also tended to increase as the mean rate approached toward the higher end, i.e. during extreme lateral fixations. It was suggested, however, that this increase does not necessarily imply the dependence of the regularity on the mean rate *per se*. For fixation following large

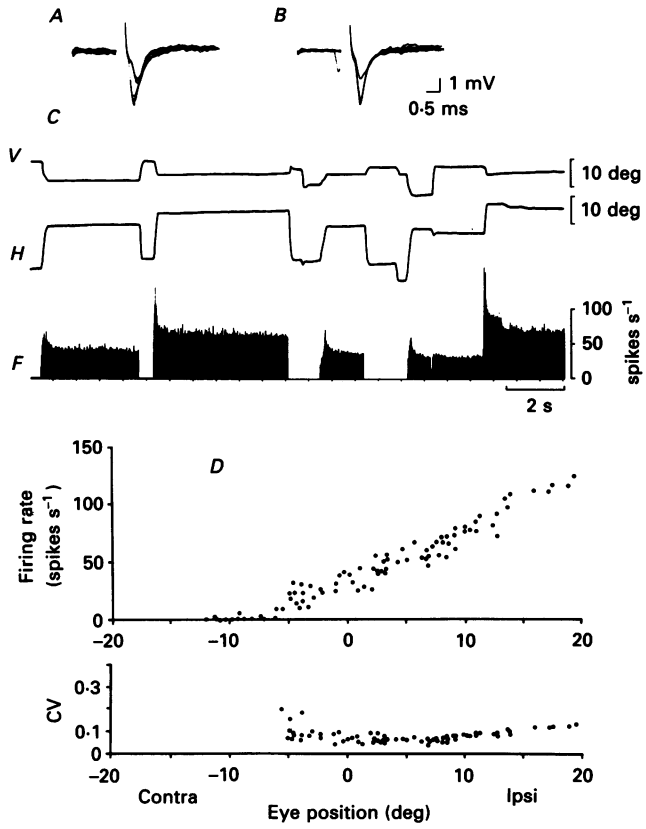

Fig. 2. Identification and behaviour of an abducens motoneurone. *A*, unitary spikes evoked by antidromic stimulation of the abducens nerve at threshold intensity. *B*, collision of antidromic spike with a spontaneous spike. Stimulus intensity was slightly above threshold. *C*, change of instantaneous firing rate (*F*) during spontaneous eye movements. Upward displacement of horizontal (*H*) and vertical (*V*) eye position records indicate respectively ipsilateral and upward movements. *D*, relationship between firing rate and horizontal eye position. Mean firing rate during fixation (upper diagram) and coefficient of variation of interspike interval (CV; lower diagram) is plotted against horizontal eye position for fixations containing more than ten interspike intervals.

ipsilateral saccades, it was often noted that the instantaneous firing rate declined gradually over 100–500 ms periods after the end of the preceding saccade. Thus, this continuous change in firing rate must, at least partly, contribute to the increase of the coefficient of variation. It should be noted that this change was not attributable to the firing rate–velocity relationship (see below), but instead it might reflect some slow process in peripheral orbital mechanics, since the eye position was steady during these periods.

Relationship between firing rate and eye position

As shown in Fig. 2*D*, the relationship between the firing rate and horizontal eye position was approximately linear over the range where motoneurones were active. Single line regression analysis indicated that the correlations were highly significant

TABLE 1. Firing characteristics of twelve abducens motoneurones

Unit	CV	$F(0)$ (spikes s^{-1})	T_H (deg)	k (spikes $s^{-1}deg^{-1}$)	k'	k''	r_{on} (spikes s^{-1} deg^{-1} s^{-1})	r_{off}	r_{on}/k (s)
1	0·07	30	−7·0	4·3	4·6	3·8	0·74	> 0·33	0·17
2	0·08	33	−5·2	6·4	7·3	6·9	1·40	0·79	0·22
3	0·06	36	−8·9	4·1	4·5	4·0	0·70	0·62	0·16
4	0·07	27	−5·8	4·7	5·1	5·0	1·0	> 0·51	0·22
5	0·07	12	−2·0	5·4	6·4	6·1	0·80	> 0·40	0·15
6	0·07	37	−8·8	4·2	4·1	4·2	0·70	0·72	0·17
7	0·09	29	−7·0	6·4	4·1	4·6	0·70	0·75	0·17
8	0·08	34	−8·9	3·8	4·5	4·9	0·70	0·91	0·17
9	0·07	46	−11·8	3·9	4·9	4·6	0·90	0·61	0·24
10	0·08	41	−9·4	4·3	5·1	5·4	0·70	0·72	0·16
11	0·08	45	−10·9	4·1	5·2	4·5	0·90	0·55	0·22
12	0·09	22	−6·6	3·3	3·7	3·4	0·50	0·51	0·15
Mean	0·08	33	−7·7	4·38	4·94		0·81	0·68	0·18

From left to right: unit number; CV, coefficient of variation (the ordinate at $H = 0$); $F(0)$, intercept of the rate–position regression line with rate axis (firing rate for central fixation at the primary horizontal eye position); T_H: threshold; k, slope of regression line; r_{on} and r_{off}, eye velocity sensitivity for saccades to the contralateral and ipsilateral side, respectively.

for all twelve units, with the coefficient of correlation ranging from 0·91 to 0·98 (Table 1). Thus the firing rate, F, of abducens motoneurones during fixation can be approximated by the equation (Robinson, 1970):

$$F(H) = F(0) + kH, \tag{1}$$

in which H represents horizontal eye position (positive value being taken as ipsilateral) and $F(0)$ and k are the vertical intercept and the slope of the fitted line respectively. The value of $F(0)$, corresponding to the firing rate for central fixation, ranged from 12 to 46 spikes s^{-1} with the mean of 33 ± 9 spikes s^{-1}. The slope k, representing the position sensitivity, ranged from 3·3 to 6·4 spikes s^{-1} deg^{-1} with the mean of $4{\cdot}4 \pm 0{\cdot}8$ spikes s^{-1} deg^{-1}. Zero intercepts of the regression lines for twelve motoneurones, representing the thresholds, T_H, ranged from 2 to 12 deg in the contralateral direction. All identified motoneurones in our sample had a threshold within the ocular motility range and became silent during the most eccentric contralateral fixations. The relationships for individual units are shown in Fig. 6*B* and in Table 1.

In the present experiments we also encountered neurones which had firing patterns quite similar to those of abducens motoneurones, but which were not antidromically activated even by the stimulus evoking maximum antidromic field potential. They

were located within or close to the abducens nucleus, suggesting that they included internuclear neurones of the abducens nucleus (Delgado-Garcia, Del Pozo & Baker, 1986*a*, *b*). Some of these neurones had firing rates distinctly higher than those of abducens motoneurones and did not stop firing even for extreme contralateral fixations.

Relationship between firing rate and saccadic eye velocity

All abducens motoneurones observed participated in saccades by exhibiting bursts of discharge during ipsilateral saccades, and pauses during contralateral ones. The time between the onset of burst and that of eye movement (determined on the velocity trace of the horizontal component of the eye position) varied considerably from saccade to saccade. In most cases, burst onset preceded eye movements by up to 15 ms. For small saccades following contralateral fixations at which given units were silent, the lead times tended to be small and, in some cases, the first spike occurred after the onset of eye movement. The average lead time, measured from saccades following the fixations above threshold, ranged from 4 to 10 ms for the twelve units.

The lead time of pause was estimated from the time between the last pre-saccadic spike and the beginning of saccades, $t1$, and the mean interspike interval prior to saccade, $t2$. The values of $t2$ and $t1-t2$ were assumed to give a possible range of true lead time. Both of the minimum value of $t1$ and maximum value of $t1-t2$ obtained from five to twenty saccades in individual units ranged from 5 to 15 ms. The typical changes in firing rate at the beginning of ipsilateral and contralateral saccade are shown in Fig. 3.

In order to determine the relationship between firing rate and saccadic horizontal eye velocity, the activity changes during saccades in twelve motoneurones were analysed in detail as follows. Based on the assumption that the rate–position relationship described above holds true during saccades and adds linearly to the saccadic eye velocity sensitivity, the firing component proportional to eye position (kH) was calculated and then subtracted from the instantaneous firing rate (F) over an 800 ms period beginning 300 ms prior to the onset of each saccade. The curve thus obtained represents saccade-related activity superimposed on approximate resting rate ($F(0)$). Figure 3*A* and *B* exemplifies for one motoneurone such curves (F–kH) together with horizontal eye velocity ($\dot{H}$), eye position (H), and original firing rate (F) for three ipsilateral saccades with different sizes. Comparisons between burst firing rate and eye velocity for many saccades indicated that maximum firing rate depended upon, and is roughly proportional to, peak eye velocity. Moreover, there was a gross similarity between the time course of burst firing rate and eye velocity, which became more conspicuous when comparisons were made for saccades having slow and long time course. These observations indicate that the instantaneous firing rate in the burst is closely related to the instantaneous horizontal eye velocity.

To clarify and quantify this relationship, both types of curves were separately averaged for five to fifteen saccades. Only those saccades which were preceded and followed by fixations showing firing activity were selected. As a general rule, when a simple average was made for a limited number of saccades, the baseline of the burst

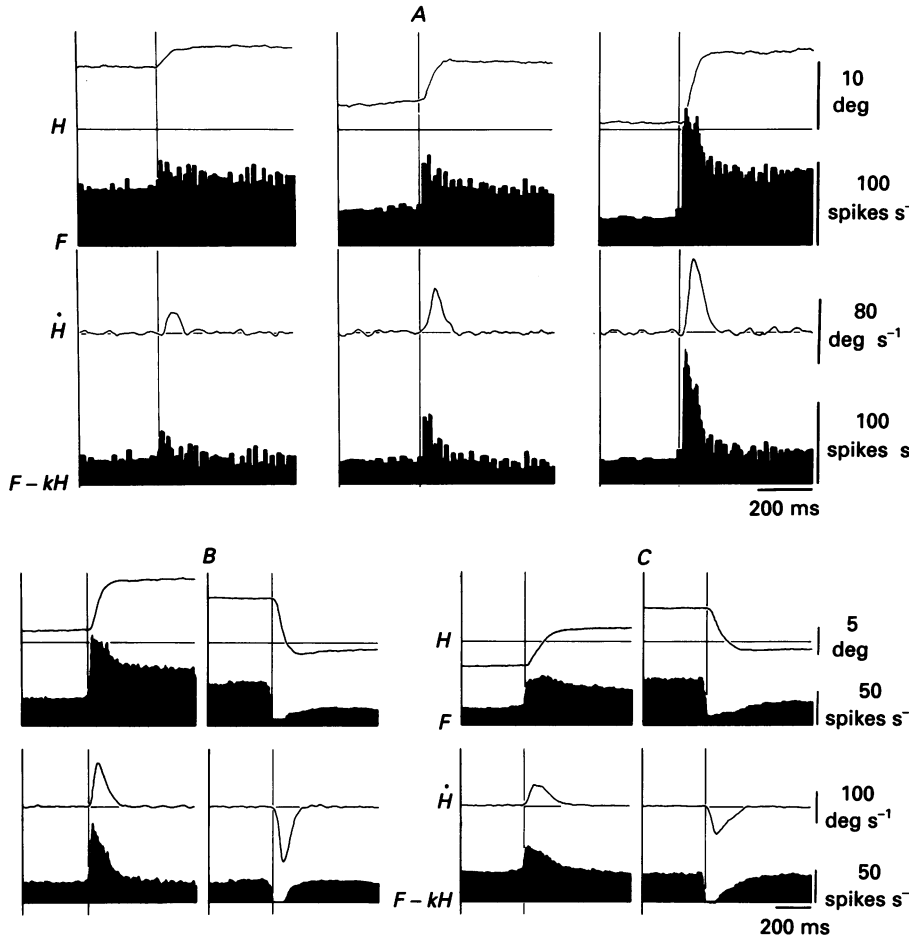

Fig. 3. Relationship between abducens motoneurone firing rate and horizontal saccadic velocity. *A*, three ipsilateral saccades having different peak velocities are shown. From top to bottom: horizontal component of eye position (H); instantaneous firing rate (F); horizontal component of eye velocity ($\dot{H}$). Firing rate in which the contribution of the eye position sensitivity has been deduced ($F - kH$). The tonic component of the firing rate corresponds to central fixation. k is the slope of the firing rate–eye position curve (4·3 spikes s^{-1} deg^{-1}). Upward eye movement traces displacement indicate ipsilateral movement respectively. *B* and *C*, average firing rate–horizontal eye velocity relationship during spontaneous saccades for two abducens motoneurones during fast (*B*) and slow (*C*) saccades. Same notations as in *A*. Six to eight ipsilateral (left panels) and contralateral (right panels) saccades were selected for each neurone and averaged. See text for detail.

firing rate curve was not exactly the same for pre- and post-saccadic periods. This was due to the scatter in rate–position relationship (Fig. 2*D*) and also to the gradual change of firing rate mentioned above. To account for this difference, a position sensitivity k' was recalculated from the averaged instantaneous firing rate curve and averaged eye position curve similar to those shown in Fig. 3*B* and *C* (bottom and

third trace respectively). The averaged pre- and post-saccadic firing rates were determined as mean rates for the initial and last 300 ms periods, where eye velocity was virtually negligible, and then compared with corresponding averaged eye positions. In most units (10/12), the value of position sensitivity k' thus obtained was slightly higher than that obtained from the rate–position (Fig. 6*B*) plots with a mean difference of about 0·5 spikes s^{-1} deg^{-1} (Table 1). It was suggested that this rather consistent difference was due to the firing component which followed burst activity and decayed very slowly over 100–500 ms after the end of the saccade. This slow decay can be also seen in the example shown in Fig. 3. When the position component was recalculated as described above, the overestimation of burst component due to this slow component became much smaller. The same calculation was made to determine the time course of inhibition during contralateral saccades, and the values of position sensitivity used in the following analysis are listed in Table 1 for individual units.

Figure 3*A* and *B* illustrates typical time courses of individual or averaged burst firing rate and that of horizontal eye velocity obtained from ipsilateral saccades. Burst firing rate rapidly increased and attained its peak 5–20 ms after its onset. A comparison between the burst and velocity profiles indicated that the burst duration was approximately equal to the duration of horizontal eye movement. Moreover, instantaneous firing rate was closely related to instantaneous eye velocity except for the early acceleration phase of saccades where firing rate rises more steeply than velocity. It should be noted that the apparent difference in rising phases seen in Fig. 3*B* is overemphasized, since the velocity profile was smoothed out by its calculating process (see Methods). The velocity sensitivity r correlating the burst firing rate with horizontal eye velocity was estimated as the ratio of area under the burst firing rate curve with that under the velocity curve.

The area was calculated over 200 ms from the onset, and pre- and post-saccadic level of burst curve was taken as a baseline. For twelve motoneurones analysed, velocity sensitivity r_{on} was $0{\cdot}81 \pm 0{\cdot}22$ spikes s^{-1} deg^{-1} s^{-1} (mean $\pm$ S.D.; range, 0·51–1·40). Since the discrepancy seen in rising phases has not been corrected, these values might slightly overestimate the true sensitivity.

Figure 3*B* (right) illustrates averaged change in firing rate during contralateral saccades for the same motoneurone. Both the firing rate profiles before and after the subtraction of position component (bottom and second trace, respectively) are representative for all the twelve units. For most contralateral saccades, motoneurones remained silent until near the end of eye movement. However, in these instances, the instantaneous firing rate during saccades would reflect merely the duration of actual inhibition and would underestimate its magnitude. For the purpose of quantification, therefore, averaged data were obtained by selecting only those saccades during which more than two spikes were observed. They had generally low peak velocity and four to ten such saccades were available for nine units. An example of averaged data is shown in Fig. 3*C* (right). For comparison, averaged burst activity of the same unit during ipsilateral saccades having similar low velocity is shown in Fig. 3*C* (left). It is apparent that the decrease in firing rate during slow contralateral saccades was also closely related to eye velocity. Moreover the value of velocity sensitivity obtained from contralateral saccades, r_{off}, was similar to the one

obtained from ipsilateral saccades, r_{on}. For example the motoneurone shown in Fig. 3*C* had velocity sensitivities of 0·72 and 0·70 spikes s^{-1} deg^{-1} s^{-1} for contralateral (right) and 0·70 spikes s^{-1} deg^{-1} s^{-1} and ipsilateral (left) saccades respectively, the latter being essentially the same as that obtained from faster saccades. The values of r_{off} for individual motoneurones are listed in Table 1. They ranged from 0·51 to 0·91 with a mean of 0·69 spikes s^{-1} deg^{-1} s^{-1}. The mean value of r_{on} for the same nine units was 0·80 spikes s^{-1} deg^{-1} s^{-1}. Taking into account the fact that the measurement of r_{off} tends to underestimate the real velocity sensitivity, it might be concluded that the relationship between the firing activity and horizontal eye velocity is approximately linear over a wide range of saccadic velocity.

Relationship between the position sensitivity and velocity sensitivity

Since firing rate of motoneurones depended linearly on both eye position and velocity, the combined relationship can be approximated by a single first-order differential equation (Robinson, 1970):

$$F = F(0) + kH + r\dot{H}, \tag{2}$$

or alternatively be defining threshold, $T_H = -F(0)/k$,

$$F = k(H - T_H) + r\dot{H}. \tag{3}$$

By replacing each of the parameters by the mean values obtained above, the firing rate of an 'average' motoneurone could be described by

$$F = 33 + 4{\cdot}4H + 0{\cdot}8\dot{H}. \tag{4}$$

The corresponding values determined for individual units are listed in Table 1. The variations in each of parameters among different units suggested no evident segregation of units types. Nevertheless comparisons of these variations indicated that some parameters tended to co-vary. A notable relationship was found between the position sensitivity, k, and the velocity sensitivity, r. When the values of r determined from ipsilateral saccades were plotted against the k, highly significant positive correlation was obtained (coefficient of correlation = 0·83). Consequently, the ratio of the two parameters, r/k, which represents the time constant of motoneurones (Robinson, 1970; see Discussion), varied only little among different units (mean, $0{\cdot}18 \pm 0{\cdot}2$ s; range, 0·15–0·22 s).

There was also a slight indication that the threshold eye position T_H tended to be lower (more contralateral) for the units having smaller position sensitivity k (coefficient of correlation = 0·58). No other significant correlations among parameters including the coefficient of variation were found.

Characteristics of vestibular neurones

A total of more than sixty identified second-order neurones were recorded. Only twenty-three were studied in detail which responded to horizontal rotation and were mainly modulated together with horizontal eye position. Because the turn-table did not allow us to test the vestibular sensitivity in other planes than horizontal, we cannot infer the exact optimal plane of head motion detection for these neurones. We

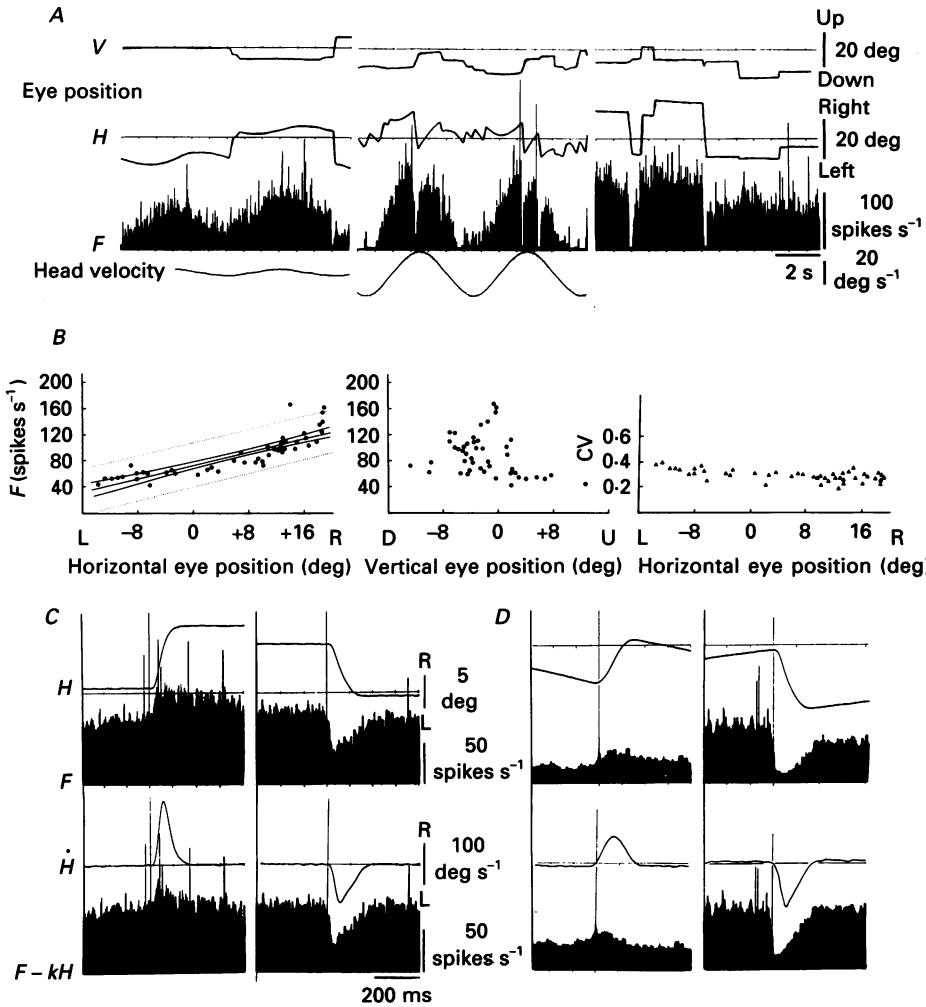

Fig. 4. Firing characteristics of an excitatory (cVN) second-order vestibular neurone monosynaptically activated from the left vestibular nerve. *A*, left and middle, response of the neurone to sinusoidal horizontal rotation in darkness. From top to bottom, vertical (*V*) and horizontal (*H*) components of eye position; firing rate (*F*) of the neurone (averaged in bins of 6·5 ms); head velocity. Records for two values of peak-to-peak sinusoidal head velocity. Right, firing of the neurone during saccades in the light. Same notations as in *A*. Head velocity is zero. *B*, rate–position relationship for the horizontal (left) and vertical components of eye position and coefficient of variation (CV) of interspike intervals during fixations (right). The regression line and the confidence interval are shown for the horizontal saccades (see text). *C* and *D*, extraction of the saccadic eye velocity sensitivity of the neurone during saccades (*C*), and quick phases of nystagmus. Same notations as Fig. 3. From top to bottom, horizontal component of eye position (*H*); instantaneous firing rate (*F*); eye velocity ($\dot{H}$); firing rate minus eye position sensitivity ($F - kH$). Averages of five to seven saccades are shown. In this and following figures, upward displacements in the horizontal eye position records indicate contralateral eye movements with respect to the soma.

TABLE 2. Firing characteristics of twenty-three vestibular neurones

Unit	Fig.	C	CV	$F(0)$ (spikes s^{-1})	k (spikes s^{-1} deg^{-1})	r_{on} (spikes s^{-1} deg^{-1} s^{-1})	r_{off}	r_{on}/k (s)	r_{off}/k (s)
1	—	0·83	0·40	—	1·7	0·43	0·32	0·250	0·190
2	7	0·92	0·?4	75	6·0	0·76	0·54	0·130	0·009
3	4	0·86	0·30	73	2·6	0·32	0·67	0·120	0·260
4	9	0·72	0·34	26	1·1	0·45	0·60	0·400	0·540
5	—	0·84	0·45	27	1·5	—	—	—	—
6	—	0·83	0·50	33	1·3	0·39	0·52	0·300	0·400
7	—	0·81	0·52	27	3·1	0·78	0·29	0·250	0·100
8	—	0·86	0·31	44	1·8	0·46	0·10	0·250	0·050
9	—	0·74	0·49	25	1·4	0·15	0·68	0·110	0·480
10	—	0·86	0·41	83	1·6	0·26	0·18	0·160	0·400
11	—	0·71	0·47	62	1·2	0·32	0·24	0·260	0·200
12	—	0·95	0·48	64	3·2	0·65	0·21	0·200	0·060
13	—	0·80	0·34	20	2·2	0·03	0·06	0·010	0·020
14	—	0·91	0·46	29	1·8	−0·07	0·32	0·040	0·017
15	11	0·95	0·35	105	5·8	0·89	—	—	0·150
16	5	0·75	0·52	21	0·9	0·06	0·19	0·060	0·210
17	—	0·68	0·52	43	2·6	—	—	—	—
18	7	0·85	0·17	80	1·4	0·20	0·54	0·140	0·380
19	—	0·79	0·29	56	3·5	0·01	0·70	0·002	0·200
20	—	0·77	0·49	51	2·6	0·31	0·37	0·120	0·140
21	—	0·91	0·47	55	3·2	0·57	0·25	0·180	0·080
22	—	0·84	0·27	75	2·3	0·25	0·68	0·110	0·290
23	—	0·93	0·29	39	2·5	0·14	0·82	0·060	0·320
Mean	—	—	—	51	2·4	0·34	0·40	0·14	0·200
S.D.	—	—	—	23	1·3	0·24	0·24	0·18	—

The columns in this table indicate successively from left to right: unit number; figure on which the characteristics of some neurones are described; C, coefficient of correlation between horizontal component of eye position and instantaneous firing rate; CV, coefficient of variation; $F(0)$, mean instantaneous firing rate at the primary horizontal position ($H = 0$); k, slope of the regression line between instantaneous firing rate and horizontal component of eye position; r_{on}, eye velocity sensitivity in the on direction (see Methods and text); r_{off}, eye velocity sensitivity in the 'off' direction.

have only characterized them on the basis of the main direction of their eye position sensitivity.

Description of the firing pattern of vestibular neurones

Figure 4 shows an example of recording from a cVN activated monosynaptically from the left vestibular nerve (whose soma was therefore probably located in the left vestibular nucleus). The behaviour of the neurone during horizontal sinusoidal head rotation in darkness at two angular velocities is shown on Fig. 4*A*. The influence of eye position on VN firing rate which has been previously reported (McCrea *et al.* 1981; Yoshida *et al.* 1981; Berthoz *et al.* 1981) is clearly seen both at low and high velocity. This neurone followed the general rule which has been previously established: the firing rate increased with contralateral eye displacement. In addition, an almost complete suppression of firing could be observed during large ipsilateral quick phases or saccades.

The characteristics of the firing pattern during spontaneous saccades is shown on the right of Fig. 4*A*. Eye position sensitivity of this neurone has been calculated with respect to the horizontal and vertical components of eye position. The rate position relationship is shown on Fig. 4*B* together with the coefficient of variation.

An extensive statistical analysis was performed on each of the neurones in order to obtain a precise description of the relation between eye position and firing rate (eye position sensitivity). This rigorous approach is necessary if one subsequently subtracts the eye position sensitivity from the firing rate to calculate eye velocity sensitivity. We shall give an example of the complete set of calculated parameters on this particular neurone. In the following sections of this paper, we shall only refer to some of them depending upon the question under discussion, but they have been calculated for all the twenty-three neurones described in this study. Table 2 only contains a sample of these parameters. The neurone shown on Fig. 4 is neurone 3 on Table 2.

Another important remark should be made before giving any numbers: because it was a general rule that VNs increased their firing rate with *contralateral* eye movements (either fixations, saccades or quick phases) all numbers below are *positive* although on the figures the horizontal eye position varies from 0 deg to either plus or minus values. All numbers refer therefore to contralateral or ipsilateral eye position. Only thresholds will therefore sometimes be negative.

For the neurone shown on Fig. 4 the calculated parameters for the horizontal eye position sensitivity were the following: number of fixations (data points), $n = 47$; mean coefficient of variation, CV = 0·3; firing rate at the primary position ($H = 0$), $F(0) = 73$ spikes s^{-1} (confidence interval, 67·5, 78·6); coefficient of correlation between firing rate and horizontal eye position, $C = 0{\cdot}86$; slope of the firing rate–horizontal eye position relationship, $k = 2{\cdot}6$ spikes s^{-1} deg^{-1} (confidence interval, 2·1, 3·1); mean deviation of data points with respect to the regression line, 16 spikes s^{-1}; threshold of firing with respect to horizontal eye position, $T_H = -28{\cdot}3$ deg.

For this neurone visual inspection shows that the rate–position relation is not linear. An attempt was therefore made to fit the data with second-order and exponential curves. The three following equations show the differences in the results:

$$\text{Linear: } F = 73{\cdot}0 + 2{\cdot}6H \text{ (deviation, 16 spikes s}^{-1}\text{)}; \quad (5)$$

$$\text{Second-order: } F = 60{\cdot}9 + 1{\cdot}8H + 0{\cdot}12H^2 \text{ (deviation, 12 spikes s}^{-1}\text{)}; \quad (6)$$

$$\text{Exponential: } F = 48{\cdot}5 + 15{\cdot}5\exp(0{\cdot}94H) \text{ (deviation, 12 spikes s}^{-1}\text{)}. \quad (7)$$

As a first approximation the linear regression was retained for all the other neurones. As there was obviously no relation between vertical eye position and firing rate (Fig. 4*B*), the neurone was classified as having horizontal eye position sensitivity.

The calculation of horizontal saccadic eye velocity sensitivity is illustrated on Fig. 4*C* and *D* for averaged spontaneous saccades and quick phases of vestibular nystagmus respectively. In the upper part of each diagram the horizontal component of eye position (H) is shown together with the firing rate. In the lower part, the horizontal component of eye velocity is shown together with the firing rate calculated from the relation F-kH in which F is the firing rate, k the eye position sensitivity and H the horizontal eye position. For this neurone the dynamic index (r) representing saccadic eye velocity sensitivity was computed to be $r = 0{\cdot}32$ spikes s^{-1} deg^{-1} s^{-1} for the 'on' direction and $r = 0{\cdot}67$ spikes s^{-1} deg^{-1} s^{-1} for the 'off' direction. The same method as the one described above was used for the calculation of r of motoneurones. As in many cases of other neurones, the relation was clearer for 'off' saccades than for 'on' direction.

All the neurones analysed in the following sections have been studied with the same method. For five of them, 'the head velocity sensitivity' (V) was calculated from the responses to sinusoidal head rotations (0·1–0·3 Hz), assuming that the rate–position relationship holds true during vestibular stimulation. Only the data obtained during slow phase modulation were used for the calculation. Although it was not possible to clearly distinguish head velocity sensitivity from eye velocity sensitivity, the amplitudes of slow phase modulation in firing rate showed little change regardless of rotation being made in the dark or light, in contrast to the slow phase eye velocity which could vary considerably. These observations suggest that the firing modulation during slow phase represents mainly the sensitivity to head velocity rather than eye velocity. The average value was $V = 2{\cdot}1 \pm 0{\cdot}4$ spikes s^{-1} deg^{-1} s^{-1}. The general equation for this average behaviour of the five neurones was:

$$F = 51 + 2{\cdot}4H + 0{\cdot}34(0{\cdot}46)\dot{H} - 2{\cdot}1V. \quad (8)$$

To exemplify the range of unit behaviour observed in our sample, the firing characteristics of another neurone (no. 16 on Table 2) are shown on Fig. 5. This neurone was more irregular than the neurone shown on Fig. 4. It was activated from the ipsilateral right labyrinth and could therefore be either a true iVN or a cVN (see discussion in the Methods section). Its firing rate increased when the head was rotated to the right and the firing rate increased when the eye position was displaced to the left. The rate–position coefficient of correlation was $C = 0{\cdot}75$ ($n = 31$) and the equation of the regression line was

$$F = 21{\cdot}0 + 0{\cdot}9H. \quad (9)$$

The mean coefficient of variation was CV = 0·52.

The eye position sensitivity of this neurone was extremely small (0·9 spikes deg^{-1}).

However, there is no doubt from the complete statistical analysis that it was significant and clearly specific to the horizontal plane.

Quantitative analysis of the relation between firing rate and eye position

The rate position curves for the horizontal direction are plotted on Fig. 6 for the twenty-three vestibular neurones (six iVNs and seventeen cVNs). The distribution of

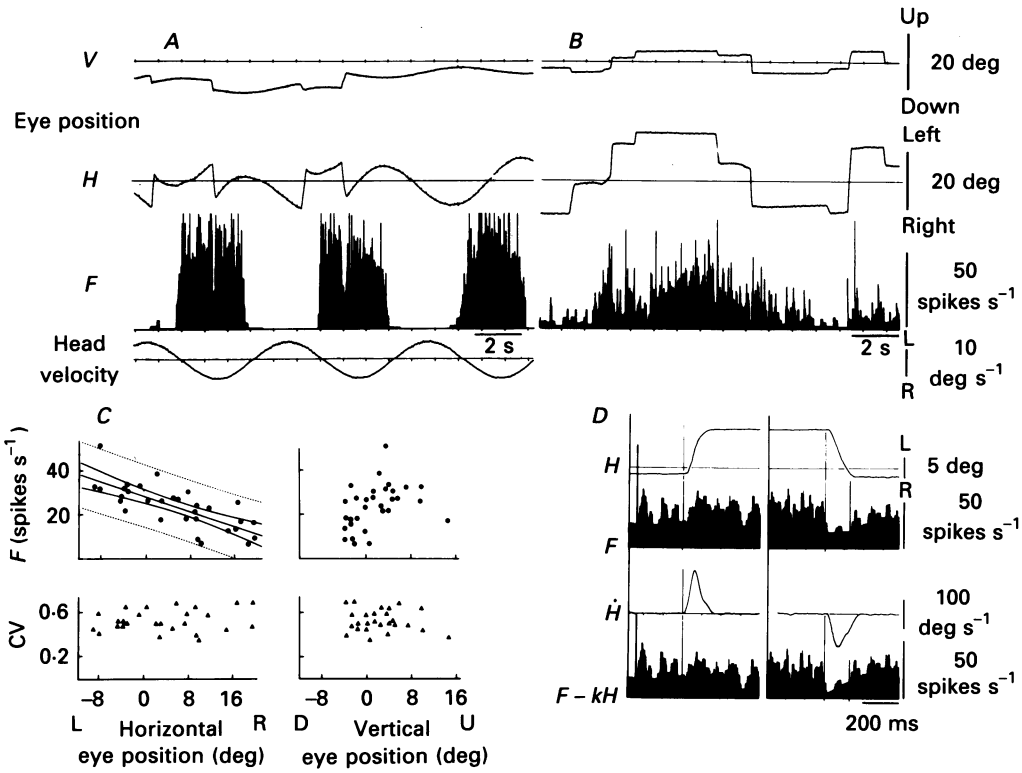

Fig. 5. Firing characteristics of a (iVN) second-order vestibular neurone during vestibular stimulation and saccades. Same notations as in Fig. 4. *A*, response of the neurone to horizontal sinusoidal rotation in darkness. *B*, firing of the neurone during saccades in the light. *C*, rate position relationship between the horizontal (left) and the vertical (right) components of eye position and distribution of the coefficient of variations (CV) during fixations. *D*, extraction of the saccadic eye velocity sensitivity (see text).

the coefficients of variation is shown in the inset. These data are compared in the same figure with the rate–position curves for the twelve abducens motoneurones. Note that the scale for the coefficients of variation is divided by ten in this latter case indicating that abducens motoneurones have a firing variability which is one order of magnitude smaller than second-order vestibular neurones.

The rate–position slopes are detailed in Table 2. They ranged from 0·9 to 6·0 spikes s^{-1} deg^{-1} (mean = 2·4; S.D. = 1·3; n = 23). Resting discharges at the primary eye position ranged from 21 to 83 spikes s^{-1} (mean $\pm$ S.D., 51 $\pm$ 23).

Although it may be a crude simplification to consider an average behaviour, it is interesting to compare the firing characteristics of these two populations of neurones

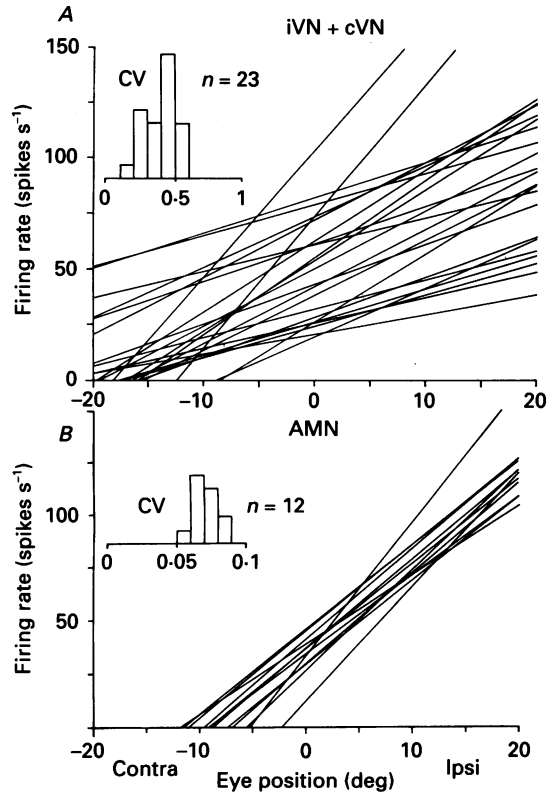

Fig. 6. Comparison of the relationship between firing rate and horizontal eye position for second-order vestibular neurones and abducens motoneurones. *A*, relationship between firing rate and horizontal eye position for twenty-three second-order ipsilateral (iVN) or contralateral (cVN) vestibular neurones (see Fig. 1), classified as horizontal (see text). Single lines were calculated from the least-squares error. The coefficient of variation (CV) of interspike intervals (shown in the inset) was calculated for fixations containing more than ten intervals. *B*, relationship between firing rate and horizontal eye position for twelve abducens motoneurones (AMN). Same notations as in *A*.

by calculating their average parameters. For the twenty-three VNs and the twelve AMNs described on Fig. 6 and Tables 1 and 2, the equation $F = F(0) + kH$, relating instantaneous firing rate, F, firing rate at the primary position, $F(0)$, and eye position sensitivity, k, had the following parameters:

$$F = 51(\pm 23) + 2{\cdot}4(\pm 1{\cdot}3)H \text{ for VNs}, \tag{10}$$

and

$$F = 33(\pm 9) + 4(\pm 0{\cdot}8)H \text{ for AMNs}. \tag{11}$$

Therefore, on the average, the slopes of the rate–position curves were twice as great for abducens motoneurones as they were for second-order vestibular neurones. Average threshold was also clearly different. It was lower (more eccentric in 'off' direction) for VNs (see Fig. 6).

Saccadic eye velocity sensitivity

We have seen above how saccadic or quick-phase eye velocity sensitivity could be assessed. The values of r_{on} and r_{off} varied considerably from neurone to neurone. In addition, 'on' and 'off' direction sensitivities were clearly different from each other in most units. For instance the neurone shown on Fig. 4 and r_{on} and r_{off} values of respectively 0·32 and 0·67 spikes s^{-1} deg^{-1} s^{-1}. Another example of comparison of saccadic eye velocity sensitivities is shown for two neurones on Fig. 7. Figure 7*A* and *B* shows the behaviour of a rather regular neurone (CV = 0·17; no. 18 on Table 2) whose firing rate increases with leftward (contralateral) eye deviation ($C = 0{\cdot}85$, $n = 58$). The rate position equation for this neurone was:

$$F = 79(76, 82) + 1{\cdot}44(1{\cdot}28, 1{\cdot}68)H \tag{12}$$

Values in parentheses indicate the range for $F(0)$ and k. The intercept with the eye position axis is 55 deg. Figure 7*B* shows that a 15 deg saccade to the left (contralateral) was associated with an increase of firing rate of less than 20 spikes s^{-1} when the eye position sensitivity was subtracted. By contrast, and although the eye position sensitivity was rather low, the suppression of activity which was associated with a rightward (ipsilateral) saccade of about the same amplitude was nearly complete and represented about 80% of the firing rate. The average time course of the suppression followed very closely the time course of average saccadic velocity. (Note, as mentioned in the Methods section, that the velocity trace has been low-pass filtered.) On average a sample of saccades yielded values for saccadic eye velocity sensitivity of $r_{on} = 0{\cdot}2$ and $r_{off} = 0{\cdot}54$ spikes s^{-1} deg^{-1} s^{-1}.

The second neurone shown in Fig. 7*C–E* (neurone no. 2 on Table 2) had a higher eye position sensitivity. This secondary vestibular axon was penetrated in the right side. It was activated by stimulation from the left vestibular nerve and was therefore a cVN (excitatory neurone). The firing pattern during a rotation of the head in the horizontal plane (Fig. 7*C*) was compared with the behaviour of the neurone during spontaneous saccades (Fig. 7*D*). The activity of the neurone was completely suppressed during quick phases to the left. The correlation between firing rate and horizontal eye position was highly significant ($C = 0{\cdot}92$). The rate position relation was:

$$F = 75(65, 84) + 6{\cdot}0(5{\cdot}0, 7{\cdot}0)H. \tag{13}$$

The horizontal threshold was $T_H = 12{\cdot}5$ deg (ipsilateral).

The suppression of activity during 'off' saccades for this neurone was almost complete: $r_{off} = 0{\cdot}54$ spikes s^{-1} deg^{-1} s^{-1}. Its time course followed closely the saccadic eye velocity profile. The 'on' effect was very striking. By contrast with the rather small effect of a saccade in the 'on' direction for the neurone of Fig. 7*A* and *B*, this neurone exhibited a clear burst of discharge during rightward saccades. The eye velocity sensitivity obtained from averaged saccades (Fig. 7*E*) is strong: $r_{on} = 0{\cdot}76$ spikes s^{-1} deg^{-1} s^{-1} and represented nearly 100% of the resting discharge at saccade onset.

A quantitative analysis of eye velocity sensitivity during saccades for twenty-one neurones is listed in Table 2. In Fig. 8, the r values have been plotted *versus* eye

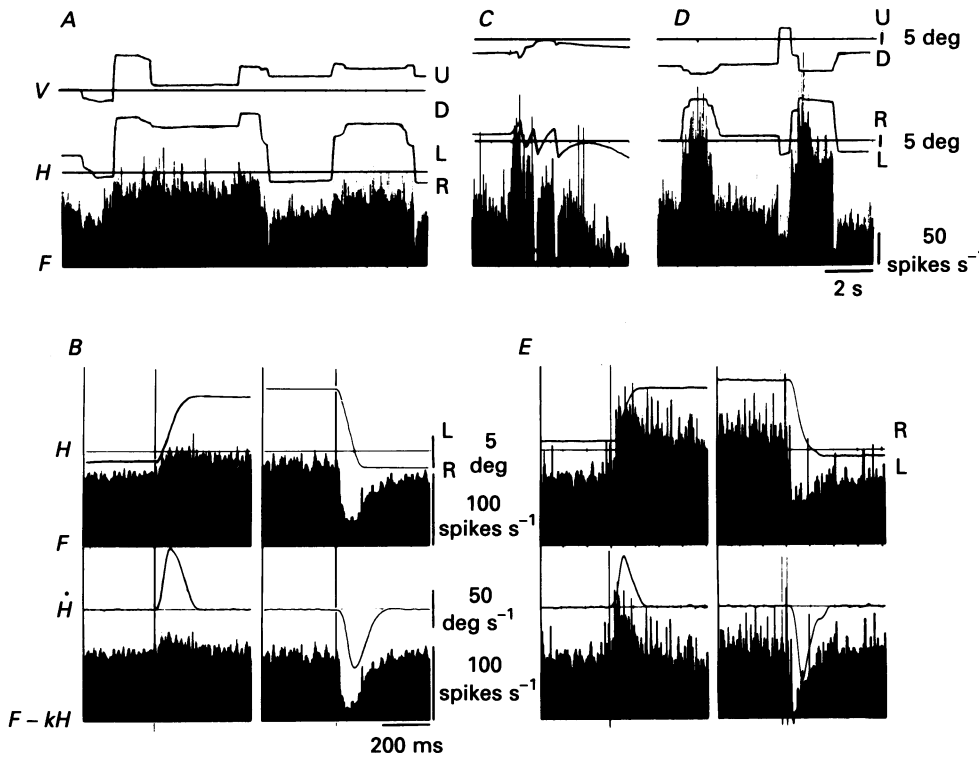

Fig. 7. Two examples of saccadic eye velocity sensitivity in two second-order vestibular neurones. One is regular (*A* and *B*, iVN) and the other irregular (*C–E*, cVN). Average of five ipsilateral and seven contralateral saccades for each neurone. Same notations as in Fig. 4.

position sensitivity for the 'on' and 'off' directions. No obvious correlation exists between eye position sensitivity and saccadic eye velocity sensitivity although a trend in the data points would suggest an increase of r value with k values. The mean and standard deviations for these twenty-one neurones are:

$$r_{on} = 0{\cdot}34 \pm 0{\cdot}24,$$

and

$$r_{off} = 0{\cdot}42 \pm 0{\cdot}24.$$

These values are lower than those obtained in our sample of motoneurones (Table 1) for which the r values are:

$$r_{on} = 0{\cdot}81,$$

and

$$r_{off} = 0{\cdot}68.$$

The saccadic horizontal eye velocity sensitivity of vestibular neurones is therefore only about half that of abducens motoneurones. The mean ratio between r_{on} values

and k is 0·14 s for VNs and 0·18 s for AMNs. It is therefore very close for both types of neurones.

Morphological properties of saccadic eye movement—sensitive vestibular neurones

Although our electrophysiological identification of second-order VNs gave a great certainty concerning their nature, we completed this identification with HRP

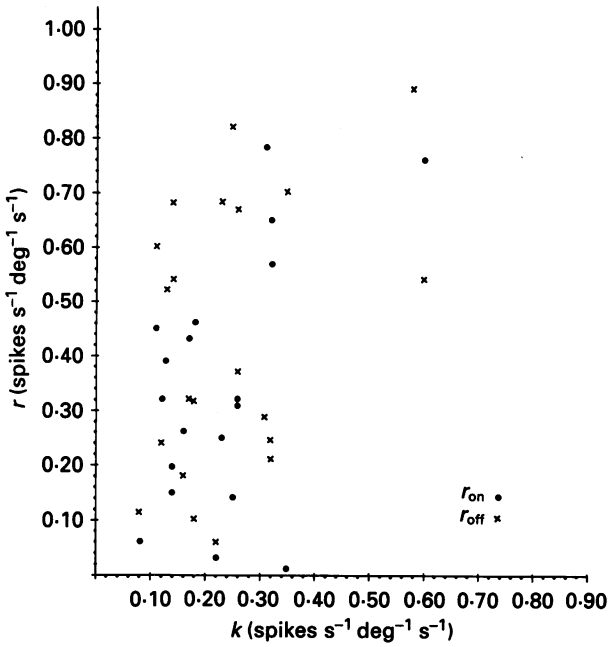

Fig. 8. Relationship between saccadic horizontal eye velocity sensitivity and horizontal eye position sensitivity for second-order vestibular neurones. Data for 'on' and 'off' directions.

injection in the alert animal after the recording of the physiological properties of the neurones. This approach was performed successfully on nine neurones (five iVNs and four cVNs). It has allowed us to relate structure and function and is particularly interesting in the study of the targets structures of a given neurone.

The first interesting question, which arises from the fact that second-order vestibular neurones can have their activity modulated by saccadic eye position and velocity, concerns the effect on the vestibulo-ocular reflex (VOR). Are these neurones the second-order vestibular neurones which mediate the VOR in the horizontal plane? Two types of VNs are known to mediate the horizontal canal input to abducens motoneurones: they are contralateral projecting excitatory (cVN) and ipsilateral projecting inhibitory (iVN) (Baker *et al.* 1969). We shall now give one example of each of these neurones in which combined morphological and physiological study could be made.

Excitatory (cVN) neurone. Figure 9*A* shows a cVN (neurone no. 4 in Table 2) which is certainly excitatory (Baker *et al.* 1969). The soma is in the left medial vestibular nucleus. The axon branches in the contralateral medial longitudinal fasciculus. The

ascending branch could not be followed to its targets. The descending branch gives axon collaterals. The first one projects to the contralateral abducens nucleus where it branches rather profusely. This termination is certainly the anatomical substrate for the excitatory action of this vestibular neurone which will induce the discharge of abducens motoneurones on the right side.

One of the branches of this collateral continues to the contralateral medial vestibular nucleus and can therefore be considered as being involved in commissural connections; one branch even reaches the Deiters nucleus. The second collateral terminates in the reticular formation caudally to the abducens nucleus in a region which may be the region of inhibitory burst neurones (Hikosaka & Kawakami, 1977; Yoshida *et al.* 1981). The third collateral terminates in the rostrocaudal half of the prepositus nucleus and it is noteworthy that this termination is distributed at several levels of this nucleus. The fourth collateral could terminate in the area of nucleus of Roller.

The axon descends below the level of the obex and we speculate that it reaches the cervical spinal cord. This neurone is therefore influencing not only the contralateral abducens but also the main structures which have been known to play an important role in the brain stem control of gaze.

The characteristics of the relation between firing rate and eye movements have been recorded in this neurone before its injection with HRP. They are illustrated in Fig. 9*B–D*. The coefficient of correlation for the horizontal component of eye position is $C = 0{\cdot}72$ ($n = 52$) and the rate–horizontal eye position relationship is:

$$F = 26(23, 28) + 1{\cdot}1(0, 1{\cdot}4)H. \tag{14}$$

The linear and exponential fitting gave very similar parameter values for the above relationship. The threshold is $T_H = -24$ deg. The coefficient of variation was rather dispersed with an average value of CV = 0·34. The r values are respectively $r_{on} = 0{\cdot}45$ and $r_{off} = 0{\cdot}60$.

In conclusion this neurone is probably mediating the vestibulo-ocular and the vestibulo-collic reflex in the horizontal plane. The activity of both of these reflexes will be suppressed when the animal shifts his eye position to the left.

Inhibitory (iVN) neurone. If the above results clearly document the influence of eye movement signals on excitatory crossed (cVN) neurones, we have mentioned earlier (see Methods section) that the identification of inhibitory vestibular second-order neurones by their sole response to electrical stimulation of the ipsilateral vestibular nerve leaves an ambiguity as to their real nature. We have therefore injected a small sample of these neurones with HRP in order to obtain a clear identification.

An example of an uncrossed second-order vestibular neurone (iVN) which has been injected with HRP is shown on Figs 10 and 11. This neurone was activated monosynaptically from the right vestibular nerve. The soma of this neurone lies in the dorsomedial part of medial vestibular nucleus lateral to the abducens nucleus (Fig. 10*A* and *B*). This axon runs medially beneath the genou of the facial nerve. Before it enters the ipsilateral medial longitudinal fasciculus, two collaterals are observed. One collateral terminates in the ventral and lateral border of the abducens nucleus and in the reticular formation below the abducens nucleus. The other long collateral courses caudally in the medullary reticular formation below the prepositus

and gives off many branches. It terminates in an area extending about 1 mm below the ventral border of the PH (Fig. 10*A* and *C*). The main axon runs down in the medial longitudinal fasciculus and sends collaterals to both the caudal part of prepositus nucleus and the reticular formation (Fig. 10*A* and *D*) continuing to the

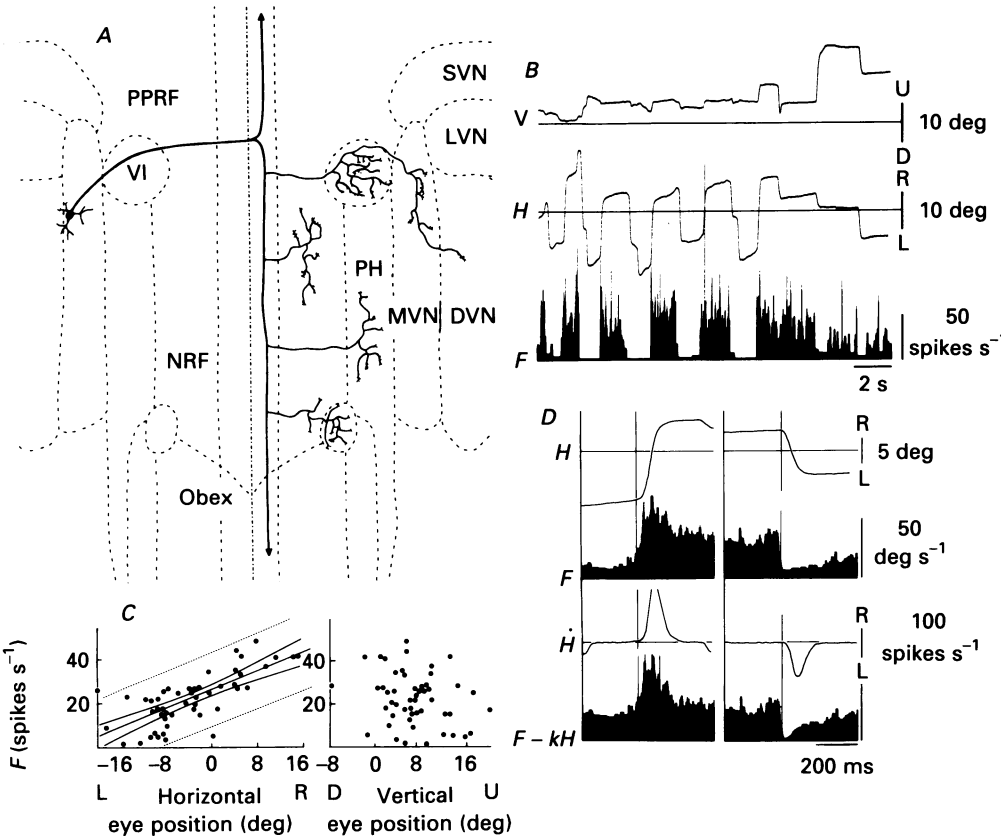

Fig. 9. Morphological and physiological properties of a second-order excitatory vestibular neurone. *A*, reconstruction of the cell body and axonal terminations of the neurone. Abbreviations: VI, Abducens nucleus; PH, prepositus nucleus; PPRF, paramedian pontine reticular formation; MRF, medial reticular formation; MVN, SVN, LVN, DVN, respectively medial, superior, lateral, and descending vestibular nuclei. *B*, firing of the neurone during spontaneous saccades in the light. Same notations as in Fig. 4. *C*, rate position relationship for the horizontal (left) and vertical (right) components of eye position. Same notation as in Fig. 4. *D*, extraction of saccadic eye velocity sensitivity. Same notation as in Fig. 4.

area on which the first collateral also terminates. This axon could be traced as far as 6 mm caudal from the abducens nucleus and could be thought to descend in the spinal cord. This neurone is certainly inhibitory because the effect of disynaptic pathways from the vestibular nerve to abducens motoneurones on the ipsilateral side via second-order VNs have been shown to be always inhibitory (Baker *et al.* 1969).

The physiological properties of this neurone are shown on Fig. 11 (cell no. 15 on Table 2). During a single cycle of rotation in the light (Fig. 11*A*) the firing rate (*F*)

of this rather irregular neurone (CV = 0·35) follows very closely the horizontal eye position component (H). The very significant eye position sensitivity of this neurone can be seen on Fig. 11A during spontaneous saccades in the light. A quantitative assessment of the horizontal and vertical eye position sensitivity is shown on Fig.

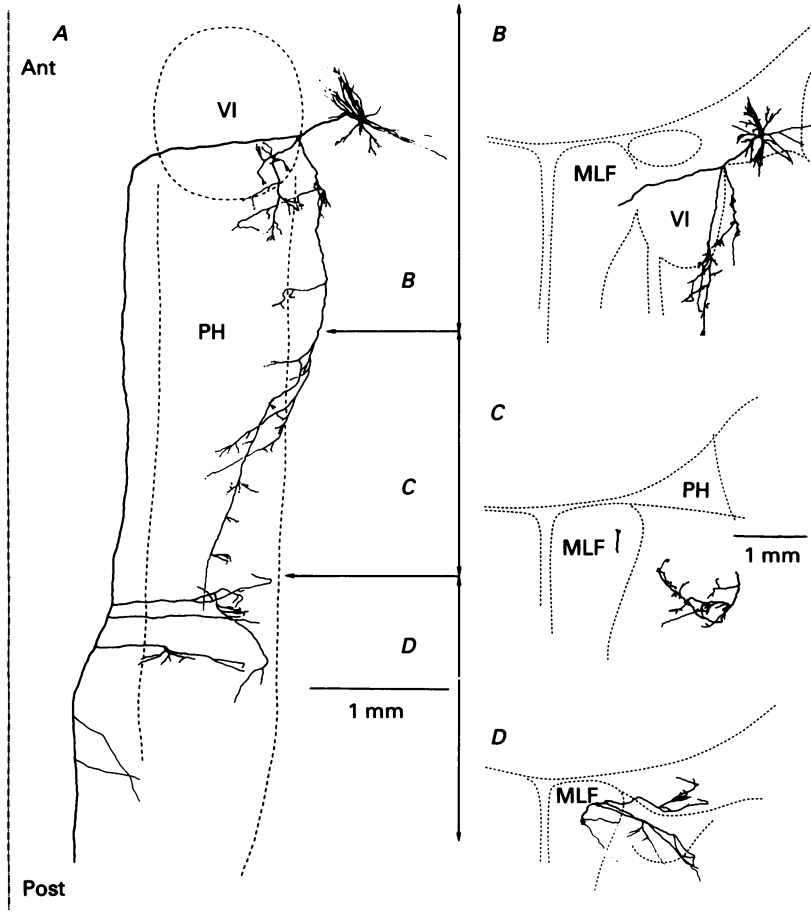

Fig. 10. Reconstruction of an inhibitory ipsilateral (iVN) second-order vestibular neurone (the physiological properties of this neurone are shown on Fig. 11). A, reconstruction of the cell body and axonal terminations of the neurone in the horizontal plane. Same notations as in Fig. 9. B, C and D indicate the levels at which the frontal projections shown on the right side have been made. B–D, projection of the reconstructed neurone on frontal planes at rostro-caudal locations indicated in A by the same letters. MLF, medial longitudinal fasciculus; PH, prepositus nucleus; VI, abducens nucleus.

11B. The coefficient of correlation for the horizontal component, $C = 0{\cdot}95$ ($n = 14$). This neurone has no relation to vertical eye position. The horizontal rate position relationship is:

$$F = 105(99, 111) + 5{\cdot}8(6{\cdot}8, 4{\cdot}7)H. \quad (15)$$

The behaviour of this neurone during saccades is shown on Fig. 11D. The relation

between firing rate and eye velocity was clear only for saccades in the 'off' direction. Eye velocity sensitivity was $r_{off} = 0{\cdot}89$.

It can be concluded from these data that inhibitory second-order vestibular neurones belonging to the horizontal vestibulo-ocular reflex carry not only an

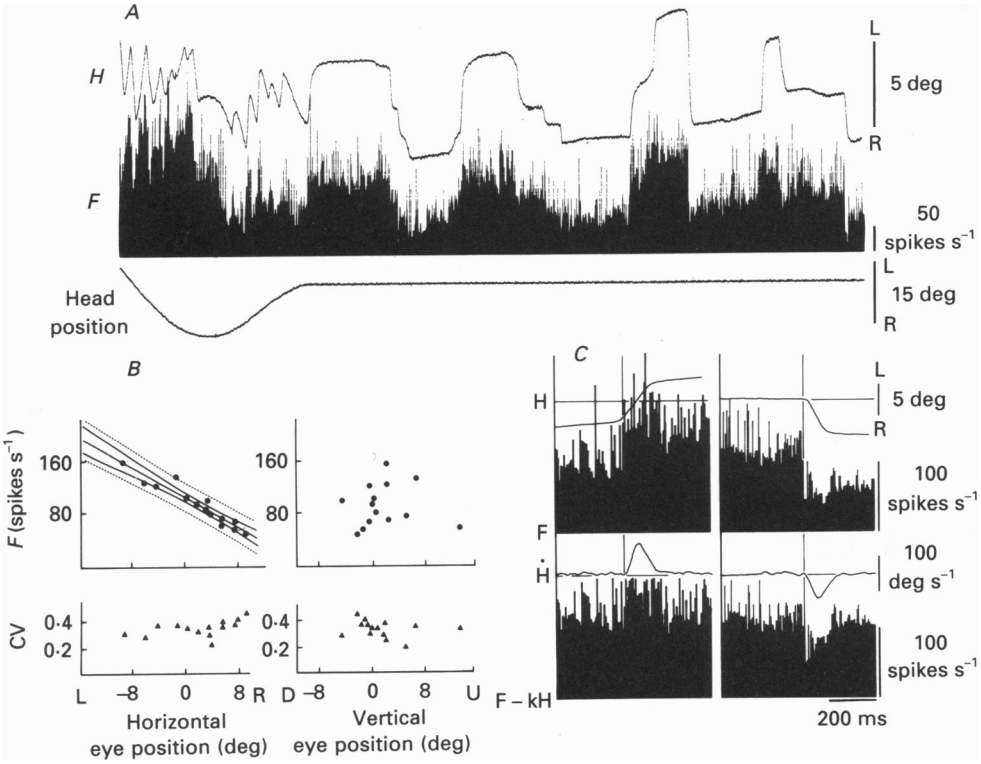

Fig. 11. Physiological properties of the second-order vestibular neurone shown in Fig. 10 during head rotation and spontaneous saccades. *A* and *B*, firing characteristics of the neurones during head rotation in darkness (*A*) and during spontaneous saccades in the light (*B*). Same notations as in Fig. 4. *C*, rate–position relationship between horizontal eye position and firing rate. Same notation as in Fig. 4.

horizontal eye position signal but also an eye velocity signal whose characteristics seem qualitatively very similar to excitatory neurones (cVNs). In addition, the fact that the axon projects to the spinal cord suggests that, as in the case of cVN, the same signal is sent to the eye and neck muscles.

DISCUSSION

Abducens motoneurones

The abducens motoneurones recorded in the present experiment show a remarkably consistent behaviour. During ipsilateral saccades, instantaneous burst firing rate of each abducens motoneurone has a quasi-linear relationship with instantaneous horizontal eye velocity. Moreover, the observation during slow

contralateral saccades indicates that the firing rate–velocity relationship linearly extends to the contralateral velocity range as far as the motoneurone is active. Combined with eye position dependence, firing behaviour of feline abducens motoneurones during saccades can be approximated fairly well by eqns (2) and (4). The mean value of $F(0)$ and k, as well as the range of minimum coefficient of variation, obtained in the present study are in agreement with those described previously in the cat ($F(0)$, 57 spikes s^{-1}; k, 5·3 spikes s^{-1} deg^{-1}; minimum coefficient of variation, 0·02–0·07, $n = 12$; Goldberg, 1980). In the latter study, r was also measured as a ratio of maximum net burst firing rate with peak eye velocity, and was found to range from 0·65 to 1·23 spikes s^{-1} deg^{-1} s^{-1} ($n = 6$), which agrees well with that obtained in this study. Delgado-Garcia *et al.* (1986*a*, *b*) found, in the cat, k values ranging from 2 to 7·7 spikes s^{-1} deg^{-1} ($n = 40$; mean, 8·7) and r values during saccades ranging from 0·64 to 2·2 spikes s^{-1} deg^{-1} s^{-1} ($n = 14$; mean 1·13) (see also Gomez, Canals, Torres & Delgado-Garcia, 1986*a*; Gomez, Torres, Jimerez-Ridruejo & Delgado-Garcia, 1986*b*).

In the monkey, behaviour of extraocular motoneurones has been extensively investigated (Fuchs & Luschei, 1970; Robinson, 1970; Schiller, 1970; Keller & Robinson, 1972; Skavenski & Robinson, 1972). It has been demonstrated by Robinson (1973) that eqn (2) which describes motoneurone behaviour reflects the relationship between muscle force and eye position, and that the ratio r/k corresponds to a dominant time constant of mechanical characteristics in the orbit, although the peripheral mechanics is more correctly described by higher-order equation with non-linearities (Robinson, 1964; Thomas, 1967; Cook & Stark, 1968). In the monkey, firing rate of motoneurones during saccades tends to saturate and the relationship with instantaneous eye velocity is less linear than that in the cat. The value of r measured from saccades is generally lower than that obtained from smooth pursuit movement. The mean time constant estimated from smooth pursuit is 0·198 s (Robinson, 1970). In the present study the mean time constant estimated from saccades was found to be 0·18 s.

It is of particular interest to compare the firing characteristics of abducens motoneurones with those of premotor neurones whose efferent connections and physiological properties are known. Two types of burst neurone have recently been identified as terminating directly on abducens motoneurones. Inhibitory burst neurones (IBNs) are located in the dorsomedial reticular formation caudal to the abducens nucleus and monosynaptically inhibit contralateral abducens motoneurones (Hikosaka & Kawakami, 1977; Hikosaka *et al.* 1980; Yoshida *et al.* 1982). They exhibit a burst of discharge during saccades coincident with a pause in motoneurone activity. The striking similarity between the lead time of burst onset in IBNs (4–14 ms) and that of pause in abducens motoneurones (5–15 ms) suggests that the onset of pause is largely determined by IBNs. Moreover, the burst firing rate–velocity relationship in IBNs is essentially the same as in abducens motoneurones (Yoshida *et al.* 1982).

It is thus suggested that the eye velocity information carried by IBNs is transmitted to abducens motoneurones in an almost unchanged form. The clear velocity dependence of decrease in motoneurone activity seen during contralateral saccade is consistent with this suggestion. The similarity in burst profiles of

motoneurone and of IBNs further suggests that they receive common afferent inputs. In fact, it has recently been demonstrated that a separate group of burst neurones (EBNs) located rostral to the abducens nuclei monosynaptically excites both motoneurone and IBNs (Igusa & Shimazu, 1980; Sasaki & Shimazu, 1981). The firing activity of EBNs seems, however, to be less precisely related to eye velocity than that of IBNs (Kaneko & Fuchs, 1981). One possible explanation is that a convergence from many EBNs onto a single motoneurone and an IBN provides more accurate information. Intracellular recording from abducens motoneurones has shown, however, that motoneurones are not only excited but also disinhibited during ipsilateral quick phases of nystagmus (Maeda *et al.* 1972; Baker & Berthoz, 1974). The present study has shown that secondary vestibular neurones terminating in the abducens nucleus exhibit activity change during saccades as well as quick phases, which is consistent with the above observation.

Vestibular neurones

We have been able to study the firing characteristics of a sample of identified horizontal second-order vestibular neurones in the alert cat, together with their morphology. The originality of the study lies in the fact that we have been able to combine the identification and the functional and morphological characteristics of a type of neurone believed to be the middle leg of the three neurone arc of the horizontal VOR. We will discuss successively the eye velocity sensitivity of these neurones, their eye position sensitivity and finally their morphology.

Discharge during rapid eye movements

Pause or decrease of neuronal activity. A review of the literature indicates that pause of activity during rapid eye movements is a common attribute of many vestibular neurones. This has been demonstrated in the cat (Keller & Precht, 1979; Anastopoulos & Mergner, 1982) and monkey (Keller & Daniels, 1975; Fuchs & Kim, 1975; Pola & Robinson, 1978; Buettner *et al.* 1978; Lisberger & Miles 1980). However, the monkey exhibits a property not found in the cat: at least some VNs pause during rapid eye movement in all directions, although these neurones were not identified as second order, whereas in the cat the pause is only associated with ipsilateral ('off') direction. Amongst the neurones which pause during rapid eye movements in the cat are the secondary vestibular neurones of the horizontal and oblique system (Baker & Berthoz, 1974; Hikosaka *et al.* 1977). The pause of activity of these vestibular neurones is state dependent (Buettner *et al.* 1978; Nakao, Sasaki, Schor & Shimazu, 1982). It should be added that the pause during rapid eye movements is far from being ubiquous in all the vestibular neurones recorded by various authors.

Our results confirm these previous data in several ways. They demonstrate unambiguously that most secondary horizontal vestibular neurones in the alert preparation pause or decrease their discharge rate during all rapid eye movements in the ipsilateral direction. This pause or decrease of activity is clearly state dependent and vanishes with drowsiness together with the rapid eye movements. In contrast with what has been demonstrated in the monkey (Keller & Kamath, 1975; Buettner *et al.* 1978; Lisberger & Miles, 1980; see however, Fuchs & Kim, 1975), the pause

always occurs in a stereotyped pattern. Since the 'off' direction during fixation corresponds to the side of activation for type I neurone (activated during ipsilateral horizontal head rotation), this pause has an obvious functional meaning during the VOR. If one takes a type I cVN second-order vestibular neurone whose soma is in the right medial vestibular nucleus, it will discharge during rotation of the table to the right and will pause during the saccade to the right. As a consequence, the left abducens motoneurones it contacts will be disfacilitated during rightward saccades. By the same mechanisms, a pause of a right iVN will induce disinhibition of right abducens motoneurones. This mechanism is therefore adequate to suppress in a graded manner the VOR during orienting eye–head movements.

Sasaki & Shimazu (1981) and Nakao *et al.* (1982) have proposed a neuronal mechanism for the saccade-related decrease of discharge of VNs: excitatory burst neurones (EBNs) contact monosynaptically the type II vestibular neurones which in turn inhibit type I iVNs and cVNs of the same side. Our results entirely support that scheme since the profile of the decrease of discharge of secondary vestibular neurones strictly mimics in its time course the profile of discharge of the EBN and IBN neurones (Yoshida *et al.* 1982). Along that line of thought it is therefore not surprising that the duration of the pause equals the duration of the saccade and that the amplitude of the decrease of discharge rate is related to the velocity of the horizontal component of the rapid eye movement. In fact our results would support the idea that EBNs excitatory input is transmitted in an inhibitory format through type II neurones to the type I without further processing. This last point has a very important functional implication, i.e. that there is not such a clear distinction between large and small saccades in the range we observed (20 deg) as far as VOR suppression is concerned. Based on our data and on the work of Nakao *et al.* (1982) we would like to propose that the more rapid the saccade the more pronounced the inhibition of the VOR. However, when and if saccades are greater than 20 deg, a saturation of VOR suppression is probably observed and a non-linear behaviour could be expected.

These statements may of course only be true for the cat. The mechanisms could differ in the monkey.

Phasic 'on' discharge during saccades. As a rule, burst activity recorded in the vestibular nucleus of the monkey is far less prevalent than the pause (Keller & Kamath, 1975; Fuchs & Kim, 1975; Lisberger & Miles, 1980; Buettner *et al.* 1978). In the cat such bursts have been also observed (Keller & Precht, 1979; Anastopoulos & Mergner, 1982) including in the discharge of the secondary vestibular neurones (Baker & Berthoz, 1974; Hikosaka *et al.* 1977). However, in the cat they always occurred during rapid eye movements oriented towards the side contralateral to the soma, i.e. opposite to the side of occurrence of the pause. Our results in the alert cat confirm this. However, the structure of the burst varies from neurone to neurone. Firstly the occurrence of a pause does not imply the existence of burst. Secondly the profile and the duration of the burst is extremely variable. Finally the amplitude of the burst is less reliably related to the amplitude of the saccade or the quick phase than for the pause. Because of the loose coupling between the burst of discharge and the parameters of rapid eye movements, we would like to suggest the following: the

weak bursting activity suggests that the burst is not due to a true eye velocity sensitivity but results from a disinhibition of iVNs and cVNs by type II interneurones at the onset of each rapid eye movements. As demonstrated anatomically (McCrea *et al.* 1980; Ishizuka, Mannen, Sasaki & Shimazu, 1980) and electrophysiologically (Shimazu & Precht, 1966), type I cVNs give off a collateral to the contralateral vestibular nucleus. It may synapse on type II neurones (Shimazu & Precht, 1966) and be at the origin of commissural inhibition. Therefore when the pause occurs in the activity of these excitatory vestibular commissural neurones, type II neurones could be disfacilitated. As a consequence, type I iVNs and cVNs that they inhibit would be briskly disinhibited. Incidentally, as suggested by Hikosaka *et al.* (1977), these bursts of activity can contribute firstly to the depolarization of the agonist motoneurone together with the EBN, secondly to the hyperpolarization of the antagonist motoneurone together with the IBN firing, and thirdly to the depolarization of the contralateral type II neurone together with the EBN (although with a longer latency). The contribution of the 'burst driving neurones' recently discovered by Okhi, Shimazu & Suzuki (1988) to the burst in VNs is still to be established. These neurones have not yet been studied during saccades.

Eye position sensitivity. The eye position signal which biases the discharge of second-order vestibular neurones was unambiguously demonstrated in the *encéphale isolé* cat by Baker & Berthoz (1974) in the oblique system, and by Hikosaka *et al.* (1977) in the horizontal system. A first important result is that most cat VNs with an horizontal head velocity sensibility have some eye position sensitivity. A number of authors have denied this probably for two reasons: the first one is that a very good state of alertness of the animal is required to measure it in the low sensitivity group; the second is that in this group a careful statistical analysis is necessary to demonstrate such low values as 0·5 spikes s^{-1} deg^{-1}. Drowsiness was very effective in abolishing the eye position signal. In the five neurones analysed during vestibular nystagmus (see Table 2) the eye position sensitivity was roughly proportional to the head velocity sensitivity. Concerning the absolute value of k, the only data available in the literature are the slopes of the rate position curves that we calculated manually from Fig. 7 of Fuchs & Kim (1975) and from Fig. 4 of Keller & Daniels (1975). They range respectively from 0·6 to 3·3 spikes s^{-1} deg^{-1} ($m = 1{\cdot}35 \pm 0{\cdot}76$, $n = 21$) and from 1·7 to 5·1 spikes s^{-1} deg^{-1} ($m = 3{\cdot}1$, $n = 3$). These values fit well with our data.

We now have to discuss the rationale of an eye position signal in the discharge of the second-order vestibular neurones. The first and most parsimonious explanation is that the second-order vestibular neurones constitute one of the outputs of the integrator. Following that line of thought Baker, Evinger & McCrea (1981) have suggested that 'nearly all the necessary phase shift, including that of the more than 90 degrees required at low frequencies, could in fact be produced by the straightforward logical progression of signals from the semicircular canal end organ to the motor unit'. Following that reasoning the integrator would be disseminated amongst different structures. This would have several advantages. Firstly the eye position signal would be distributed over the available inputs to the membrane of the motoneurones (these inputs being in limited numbers), secondly it would make the oculomotor system less vulnerable in case of lesion.

The existence of an eye position signal in the second-order VN discharge may suggest that these neurones participate directly in the integration which is required to generate the adequate motor command. The ratio eye velocity sensitivity/eye position sensitivity exhibited by VN behaviour (0·14 s) is close to, or even smaller than, the one exhibited by abducens motoneurones (0·18 s). However, during head oscillations, VNs carry a compensatory eye velocity signal (nearly equal and opposite to the vestibular signal), which has also to be integrated. If VNs participate directly in the integration of this compensatory eye velocity signal, one would expect a very important phase lag of VN firing rate with respect to head velocity, but this was not observed. Therefore, it is more likely that VNs do not participate directly in the eye velocity integration process, and their eye position sensitivity merely results from the input of an eye position signal (probably generated by the PH) to the vestibular neurones.

Secondly, one could think that it is useful that the vestibular input (related to head velocity) is recalibrated by a signal proportional to the eccentricity of the attempted direction of gaze. The role of the eye position signal could be to introduce a bias on the VOR modulation which would adjust the working range of the VOR to the location in space where gaze has to be stabilized. In other words, the addition of gaze signals to compensatory vestibular signals is not made only at the level of motoneurones. There is a blending of the two functions at the level of the vestibular nuclei.

More generally we now know that so-called vestibular neurones have extremely complex functions which are far from simple relay functions of vestibular signals. The processing of gaze-related signals provides more evidence that we probably have to revise our models of these structures.

It is also striking that the reticular neurones (Vidal, Corvisier & Berthoz, 1983; Grantyn & Berthoz, 1987; Grantyn, Berthoz & Ong-Meang, 1987), which appear to constitute one of the premotor pathways of the orienting system for the oculo-motor, the facial and the neck system, project also to the vestibular nucleus.

The eye position signal may be a 'head motor error' signal. Taking into account that the second-order vestibular neurones are not only involved in the vestibulo-ocular reflex, but also receive projections from the eye–head orienting system and project to neck premotor structures, the eye position signals observed in VN firing rate during orienting movements could be reformulated in terms of *head position* with respect to gaze direction, i.e. the direction in spatiotopic co-ordinates in which the animals have seen some point of interest. Head position with respect to gaze is equal and opposite to the eye position with respect to the head. Reformulating the eye position sensitivity in terms of head position (with respect to gaze), and therefore in terms of a head motor error signal, sounds more logical since the VN firing rate would code a combined head velocity signal (mainly originating from vestibular inputs) plus head position signal.

Finally, the saccadic eye velocity sensitivity of VNs, observed during head-fixed orienting movements, could be explained by the fact that a common gaze-orienting command is sent to both oculomotor and neck motor systems, and simultaneously serves to prevent the on-going active head-orienting movements being compensated by vestibulo-ocular and vestibulo-colic reflexes.

Axonal projections of horizontal secondary vestibular neurones

The results of this study and those from previous anatomical studies (Ishizuka, Mannen, Sasaki & Shimazu, 1980; McCrea *et al.* 1981; Uchino, Hirai & Suzuki, 1982) indicate that secondary vestibular neurones which project to the abducens nucleus in the cat commonly have collaterals projecting to several other areas in the brain stem as well as to the spinal cord. The major target areas in the brain stem are similar to those of secondary neurones in the squirrel monkey described by McCrea, Strassman, May & Highstein (1987*a*) and McCrea, Strassman & Highstein (1987*b*) though the caudally projecting collaterals of most primate secondary neurones appear to terminate at the level rostral to the obex and not to reach the spinal cord. As already mentioned in the results sections, the perihypoglossal nuclei and dorsomedial part of the reticular formation have been known to contain various neurones whose activity is related with saccadic eye movements and vestibular nystagmus in the horizontal plane. Moreover many of these eye movement-related neurones, including position or position–velocity neurones (Baker & Berthoz, 1974; Lopez-Barneo *et al.* 1982), inhibitory burst neurones (Hikosaka & Kawakami, 1977; Yoshida *et al.* 1982) and burster-driving neurones (Okhi, Shimazu & Suzuki, 1988), have been suggested to receive disynaptic inputs from the horizontal semicircular canal. It is therefore likely that the collaterals of secondary neurones to the caudal medulla may terminate directly on these neurones.

On the other hand, available data indicate a wide variety of different patterns of axonal branching. For example, collaterals to the perihypoglossal nuclei and the dorsal reticular formation are usually given off from the stem axon descending in the MLF, but, in some instances, collaterals also arise from the branch running in the reticular formation as in the neurone shown in Fig. 10. It is of interest, in this regard, that collaterals showing quite different trajectories could terminate in close proximity to each other (Fig. 10*A* and *D*). Apparently, a larger sample of neurones is needed to understand the functional significance of different projection patterns and to correlate them with various physiological properties. It should also be emphasized that the secondary neurones injected in this study included only those whose activity was related with eye movements and that morphological properties of other physiological types of secondary neurones have not been studied.

The destinations of descending collaterals projecting toward the spinal cord were not examined in this study. However, bilateral connections between labyrinths and neck motoneurones are well documented in the cat (Wilson & Yoshida, 1969; Wilson & Maeda, 1974). Furthermore previous results obtained by antidromic stimulation of the spinal cord in decerebrate or anaesthetized cats suggest that these collaterals terminate in the upper cervical segments. Shimazu & Smith (1971) reported that 21% of type I secondary neurones were antidromically activated from the spinal cord at C2–C3 level. A more detailed study by Isu & Yokota (1983) further indicated that almost all secondary type I neurones projecting to the contralateral abducens nucleus have a contralateral axon which reaches the level of the obex, but the percentage of antidromic activation gradually decreases as the stimulation site shifts from C1 to C3 (43% from C1, 23% from C2, 19% from C3, 0% from C5–6). Intraxonal injection of HRP showed that these collaterals terminated in the neck

motoneurone pools (Isu & Yokota, 1983). Thus it seems reasonable to suggest that eye movement-related activity of secondary neurones is transmitted to neck motoneurones as well as abducens motoneurones. This suggestion is consistent with the results of Vidal, Roucoux & Berthoz (1982) showing that electromyographic activities of some neck muscles are closely correlated with horizontal eye movements. Although it is unlikely that secondary neurones would be sufficient by themselves to determine overall activity in motoneurones (Ezure & Sasaki, 1978), the eye movement signals in vestibulo-oculo-collic pathways may contribute to eye–head co-ordination.

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