Journal of Physiology (1993), **469**, *pp.* 549–570
With 11 *figures*
Printed in Great Britain

TESTING THE COMMON NEURAL INTEGRATOR HYPOTHESIS AT THE LEVEL OF THE INDIVIDUAL ABDUCENS MOTONEURONES IN THE ALERT CAT

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(*Received 26 October 1992*)

SUMMARY

1. As far as horizontal eye movements are concerned, the well-known hypothesis of a common neural integrator states that the eye-position signal is generated by a common network, regardless of the type of versional movement. The aim of this study was to evaluate the validity of this hypothesis by analysing the behaviour of the abducens motoneurones, the system into which the horizontal neural integrator(s) project(s). If there were a common neural integrator, the different motoneurones would receive the eye position signal through the same pathway and the sensitivity to eye position would be the same regardless of the type of versional movement. If there were multiple integrators, the sensitivity to eye position in one type of versional movement might be different from the sensitivity to eye position in another type of versional movement, at least for occasional motoneurones.

2. The discharge of thirty-one antidromically identified abducens motoneurones was recorded in the alert cat during spontaneous eye movements made in the light and in response to sinusoidal rotations of the head in complete darkness.

3. All of the abducens motoneurones exhibited a burst of action potentials for lateral saccades. During fixation between saccades, they maintained a steady firing rate that increased as the cat fixated increasingly lateral eye positions.

4. For each abducens motoneurone, the sensitivity to eye position (K_f) was determined from measurements carried out during intersaccadic fixations. K_f was calculated from the slope of the firing rate–eye position linear regression line.

5. The discharge rate of the identified motoneurones was observed during four sinusoidal vestibular stimulations ($\pm$ 10 deg, 0·10 Hz; $\pm$ 20 deg, 0·10 Hz; $\pm$ 30 deg, 0·10 Hz; $\pm$ 40 deg, 0·10 Hz). The motoneurones exhibited a burst of activity during fast phases in the lateral direction and paused during fast phases in the opposite direction. During slow phases, motoneurones modulated their activity as a function of the vestibularly induced eye movements except for slow phases that occurred in position ranges below their recruitment threshold. In these cases their activity was cut off.

6. A new method was developed to measure the sensitivity to eye position of neurones during vestibular slow phases. The difficulty came from the fact that, during slow phases, eye velocity and eye position changed simultaneously and that each of those two variables could influence neuronal activity.

7. For each motoneurone, the instantaneous firing rate was measured each time the eye passed through a given position during any slow phase generated during any vestibulo-ocular reflex. At a given position, the discharge rate of the motoneurone under study was plotted against the eye velocity. From the resulting linear regression line, two interesting values were obtained: its slope corresponding to the sensitivity of the motoneurone to eye velocity, R_v, (at that given eye position) and its y-intercept, $F(0)$, the interpolated firing rate when the eye velocity was zero. This procedure was repeated for different eye positions. The values of $F(0)$ were then plotted against the eye positions. The slope of this regression line gave the sensitivity of the motoneurone to eye position measured during vestibular stimulation. It was termed K_v.

8. We found that, for each of our thirty-one abducens motoneurones, the sensitivity to eye position measured during intersaccadic fixation in the light (K_f) was equal to the sensitivity to eye position measured during the vestibulo-ocular reflex elicited in complete darkness (K_v).

9. This result is compatible with the hypothesis of the common oculomotor neural integrator. It does not prove it but it is worth emphasizing that a converse result would have ruled out the hypothesis of the common oculomotor neural integrator.

INTRODUCTION

Eye movements are triggered by various neurones that encode only velocity signals (Robinson, 1968). Saccadic burst cells of the paramedian pontine reticular formation discharge at rates that reflect saccadic eye velocity (Van Gisbergen, Robinson & Gielen, 1981). Vestibular afferents carry information on head velocity (Fernandez & Goldberg, 1971). Cells within the visual cortex and brainstem nuclei encode retinal error velocity signals (Collewijn, 1975; Hoffmann & Schoppmann 1975; Komatsu & Wurtz 1988).

Alone, these signals would move the eye but would not allow the eye to hold the achieved position. For this reason, Robinson proposed that a mathematical integration was necessary to convert velocity signals into position signals (Robinson, 1968; Skavinski & Robinson, 1973). The involved neural network is usually referred to as the oculomotor neural integrator. Nowadays, the oculomotor neural integrator is not just an hypothesis: it has been located in the prepositus–vestibular nuclear complex for horizontal movements (Cheron,Godaux, Laune & Vanderkelen, 1986; Cheron & Godaux, 1987; Cannon & Robinson, 1987) and in the interstitial nucleus of Cajal for vertical movements (Crawford, Cadera & Vilis, 1991).

Theoretical and *indirect* experimental evidence suggest that the integration of all the eye movement commands is made by a *common* neural integrator (Robinson, 1975). But direct experimental evidence is still lacking. In fact, the uniqueness of the integrator would be directly proved if it was found that all the neurones of the neural integrator had the same sensitivity to the achieved eye position, whatever the velocity input leading to changes in eye position.

The present study is a first step in our *direct* experimental approach to explore the hypothesis that the neural integrator is common to all version eye movements.

In this paper, we focus our attention on one of the targets of the horizontal neural integrator, the abducens motoneurones. Hypothetical multiple integrators would lead to distinct output signals that could distribute themselves unequally among the pool of abducens motoneurones (Fig. 1*A*). As a result, the sensitivity to eye

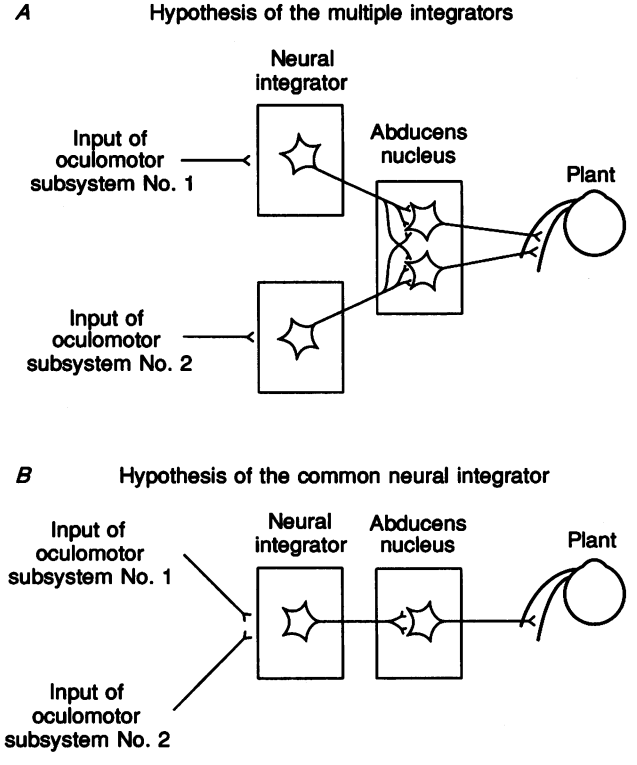

Fig. 1. Sketch showing the effects of the multiple integrators hypothesis (*A*) and of the final common neural integrator hypothesis (*B*) on the behaviour of the abducens motoneurones. A neural integrator is a network that converts an eye velocity command into an eye position signal. If each oculomotor subsystem had its own integrator (hypothesis *A*), two possibilities would exist. One possibility (not illustrated) would be that axons originating from distinct integrators would distribute evenly throughout the motoneurones pool. Another possibility (illustrated in *A*) would be that the distributions of the axonal terminals from distinct integrators would not match at the level of the individual motoneurones. In this latter case, the eye position signal carried by a motoneurone could be different, depending on the kind of input that triggers the eye movement. If the integrator was shared (*B*), the eye position signal would be supplied to the motoneurones by a sole pathway. As a result, each motoneurone would have the same sensitivity to eye position, whatever the command signal triggering the eye movement.

position of the abducens motoneurones could vary as a function of the involved oculomotor subsystem. Conversely, if the integrator was common, its output would be unique and each abducens motoneurone should have the same sensitivity to eye position, no matter what kind of command triggered the movement (Fig. 1*B*).

Hence, to find motoneurones, even if they were scarce, displaying a sensitivity to eye position that would vary according to the nature of the command signal of the movement, would implicate the existence of several pathways carrying the eye position signal from several integrators. The fact that we did not find motoneurones with such behaviours reinforces the hypothesis of a common neural integrator.

METHODS

Surgical procedure

Four adult cats between 2·5 and 3·5 kg were prepared for chronic recording of eye movements and discharges of antidromically identified abducens motoneurones. Under general anaesthesia (xylidino–dihydrothiazin, Rompun, Bayer, Germany, 3 mg kg^{-1} and pentobarbitone, Nembutal, Ceva, Belgium, 20 mg kg^{-1}) and aseptic conditions, cats were fitted with several chronic devices. Scleral search coils were implanted subconjunctivally on both eyes (Fuchs & Robinson, 1966; Judge, Richmond & Chu, 1980). A bipolar stimulating electrode was placed on each VIth nerve at its exit from the brainstem. The position of each electrode was adjusted to produce a lateral movement of both eyes with a single 0·1 ms pulse of less than 1 mA. Three bolts were cemented to the skull to immobilize the animal's head during the experimental sessions. A rectangular hole (4 mm wide and 8 mm long) was drilled in the occipital bone (stereotaxic co-ordinates L = 2 left, 2 right, P = 12–20; Berman, 1968). The dura mater was removed and a dental cement chamber constructed around the hole. Between recording sessions the surface of the cerebellum was protected with a silastic sheet and the chamber sealed with bone wax. Terminal wires from eye coils and stimulating electrodes were attached to a socket cemented to the holding system. Further details of this chronic preparation have been described by Delgado-Garcia, del Pozo & Baker (1986).

Experimental techniques

Eight days after surgery, each animal was trained to accept restraining conditions without stress. A week later, recording sessions began. Each experimental session began by attaching the animal's head to a holding bar by the implanted screws. In order to elicit the vestibulo-ocular reflex (VOR), the head was put in the centre of a turntable and placed so that the horizontal semicircular canals were about horizontal (nose 20 deg down). Eye movements were measured using the scleral search coil technique (Fuchs & Robinson, 1966). The measurement system had a bandwidth of 1000 Hz and a sensitivity of 0·25 deg. Calibration was obtained by rotating the two magnetic fields ± 5 deg around the horizontal and vertical axes with the cat's head kept still in space. The cranial opening was cleaned by sterile saline with antibiotics and local anaesthetics were poured onto the cranial opening in order to prevent any pain. The mean horizontal and vertical zero positions of the gaze were estimated during spontaneous ocular movements in the light during a period of 10 min (Crommelinck, Guitton & Roucoux, 1977).

A glass microelectrode (1–2 MΩ of impedance), attached to a micromanipulator tilted 30 deg posterior, was then lowered through the cranial opening in the direction of the abducens nucleus. The antidromic field potential, evoked by stimulation of the abducens nerve, was used to map out the location of the abducens nucleus. This nucleus was then explored in order to record discharges of individual neurones extracellularly. Our attention was focused only on identified motoneurones. An abducens neurone was identified as a motoneurone if its action potential was triggered by stimulation of the abducens nerve (antidromic identification). Furthermore, to confirm that an activated cell was indeed the cell under study and not a nearby one, the action potential of the cell under study was used to trigger the stimulus pulse after a short delay. This delay was gradually reduced to test for collision between the orthodromic and antidromic action potentials (collision block).

Once an abducens motoneurone was isolated and identified, its activity was recorded (1) during spontaneous eye movements in the light, then (2) during a set of vestibular stimulations in complete darkness and again (3) during spontaneous eye movements in the light. The VOR was elicited by submitting the animal's head to four horizontal sinusoidal rotations about the vertical axis : ± 10 deg, 0·10 Hz; ± 20 deg, 0·10 Hz; ± 30 deg, 0·10 Hz and ± 40 deg, 0·10 Hz.

Data processing

Neural activity, horizontal and vertical eye position signals and the angular velocity signal from the turntable were recorded on a magnetic tape and processed on a HP-486 computer. The eye position signals and the table velocity signal were sampled at 100 Hz and smoothed by the 3–5–3 algorithm. For neuronal activity, the time axis was divided in short intervals 250 μs wide. During each interval, the presence or the lack of an action potential was checked. For each occurrence of an action potential, the instantaneous firing rate was calculated as the inverse of the interspike interval (between the occurring spike and its predecessor). Finally, the instantaneous firing rates corresponding to the sampled eye signals were obtained by interpolation.

The slow phases of the horizontal VOR were detected by an algorithm we have described previously (Baland, Godaux & Cheron, 1987).

RESULTS

Identification of the neurones of the abducens nucleus

Antidromic stimulation of the abducens nerve was used to locate the abducens nucleus and to identify the abducens motoneurones. An electric shock delivered to the abducens nerve created an antidromic volley that reached the nucleus highly synchronized so that the antidromic field potential was large. The maximum negative peak reached up to 5 mV at 2 × threshold stimulation. In addition, the antidromically evoked response was a closed field. This characteristic, coupled with the large field potential, made the antidromic field potential very sensitive in locating the abducens nucleus (Fig. 2*B*). However, the large antidromic field handicapped identification of single motoneurones by antidromic stimulation. This difficulty was overcome in two ways. One way was to take advantage of the fact that the fields were smaller in the peripheral part of the nucleus, so we could identify motoneurones in the classical way. The antidromic activation of a peripherically located motoneurone is shown in Fig. 2*Ca*. Confirmation that the antidromically evoked spike belonged to the targeted motoneurone was achieved by the collision technique (Fig. 2*Cb*).

When the antidromic spike was obscured by a large massed antidromic field potential, another identification procedure was applied. The field potential elicited randomly (Fig. 2*Da*) was compared with that triggered 0·5 ms after the occurrence of a spontaneous action potential of the neurone under study (Fig. 2*Db*). If the collision test reduced the amplitude of the antidromic field potential (Fig. 2*Dc*), we concluded that the triggering neurone was a motoneurone (traces *a* and *b* of Fig. 2*D* are superimposed in Fig. 2*Dc*). In this study, thirty-one motoneurones were identified antidromically, twelve by the first procedure, nineteen by the second one.

Method for determining position sensitivity during intersaccadic fixation

Spontaneous eye movements consisted of rapid saccades followed by fixation intervals. All of the abducens motoneurones in our sample had burst–tonic discharge patterns. They exhibited a burst of action potentials for lateral saccades. During fixation between saccades, they maintained a steady firing rate that increased as the cat fixated increasingly lateral eye positions. A reverse behaviour was observed for movements in the medial direction. In this case, the abducens

motoneurones paused during saccades and decreased their firing rate or ceased to fire during intersaccadic fixation. This typical behaviour is illustrated in Fig. 3*A* for one unit.

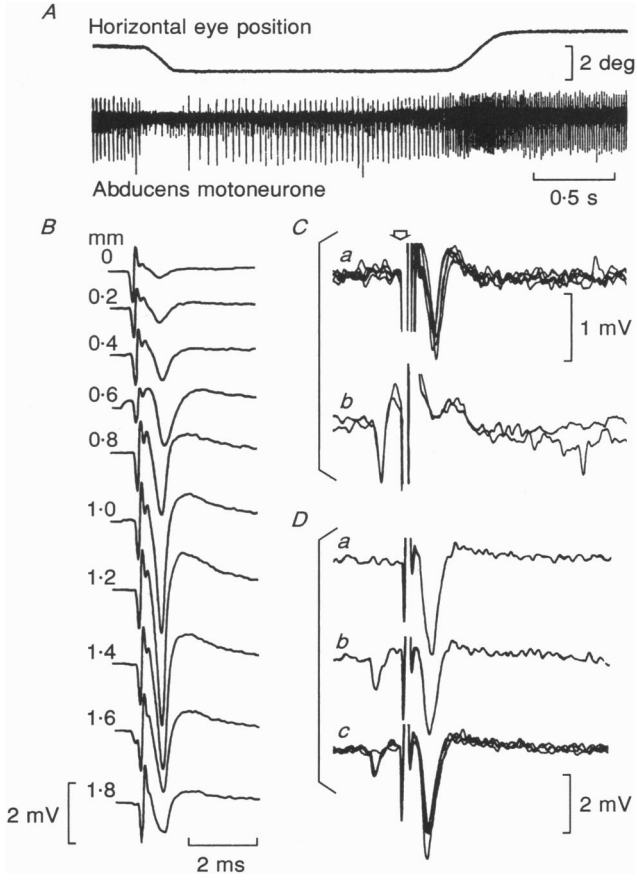

Fig. 2. Locating the abducens nucleus and procedures used to identify abducens motoneurones. *A*, discharge pattern of a representative abducens motoneurone during shifts of fixation made in the light. *B*, field potentials recorded in the abducens nucleus following electrical stimulation (2 × threshold) of the ipsilateral abducens nerve. Records were obtained as the microelectrode was lowered from the floor of the fourth ventricle (top trace, 0 mm) by steps of 0·2 mm. In this case, the negativity of the field potential was maximal when the tip of the microelectrode was 1·2 mm below the floor of the fourth ventricle. *C*, antidromic identification of an abducens motoneurone located in the peripheral area of the abducens nucleus (where the antidromic field potential was small). Stimulation of the abducens nerve at 5 Hz evoked an antidromic spike (*a*). When the same stimulus was applied to the abducens nerve 0·5 ms after a spontaneously occurring action potential, the antidromic spike was occluded (*b*) (collision block). *D*, antidromic identification of an abducens motoneurone in a site where the antidromic field potential was large. Stimulation of the abducens nerve evoked a large antidromic field potential (*a*). When the same stimulus was applied to the abducens nerve 0·5 ms after a spontaneously occurring action potential, the antidromic field potential was reduced (as a result of a collision block) (*b*). In *c*, the responses to one experimenter-triggered stimulation and to two spike-triggered stimulations are superimposed.

During lateral saccades, the firing rate of the abducens units began to change before saccades, increasing rapidly to reach a maximum coincident with or before the peak of velocity of the saccade and decreasing then with an approximately

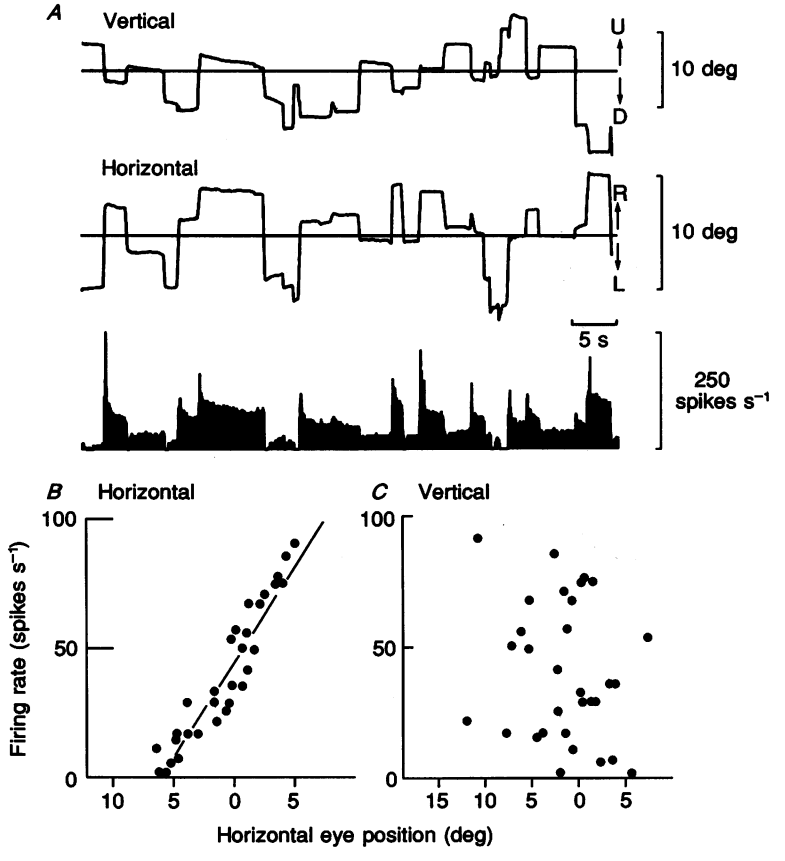

Fig. 3. Behaviour of a representative abducens motoneurone during shifts of fixation made in the light. *A*, change of instantaneous firing rate during spontaneous eye movements. U, upward; D, downward; R, rightward; L, leftward. *B*, relationship between firing rate and horizontal eye position. The data points are fitted well by a linear regression line ($r = 0{\cdot}93$). The slope of the regression line, termed K_f, corresponds to the sensitivity of the motoneurone under study to horizontal eye position. It is expressed in spikes s^{-1} deg^{-1}. *C*, relationship between firing rate and vertical eye position. Note the lack of correlation between the two variables ($r = 0{\cdot}08$).

exponential decay. Figure 4*A* and *B* illustrates two typical time courses of individual burst firing rate obtained during lateral saccades. A symmetrical behaviour was observed for saccades in the medial direction. The leading time of the firing rate on the saccade was reported by Delgado-Garcia *et al.* (1986) to range between 5 and 25 ms. The same authors measured the time constant of the decay of the burst activity of the abducens units: it ranged from 10 to 150 ms. As our purpose was to analyse the firing rate related to eye position only during fixation,

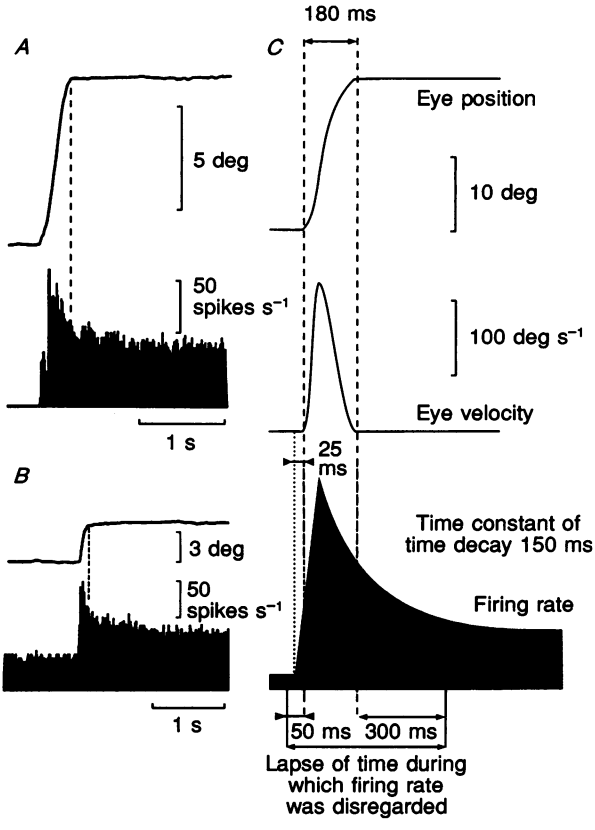

Fig. 4. Evaluation of the lapse of time during which a saccade occurrence modified the firing rate of an abducens unit. *A* and *B*, typical time courses of the change in firing rate during a horizontal saccade. Upper traces, horizontal eye position; lower traces, related firing rate of an abducens motoneurone. *C*, simulated eye position, eye velocity and firing rate of an abducens motoneurone during a 20 deg horizontal saccade made by a cat. The time courses of the eye position and of the eye velocity are drawn according to the data of Evinger & Fuchs (1978). These authors found that the duration of a 20 deg saccade was about 180 ms and that the deceleratory phase of any saccade constituted usually 70 % of its duration. The firing rate related to a large saccade (20 deg) was simulated in the lower part of *C* according to the data of Delgado-Garcia *et al.* (1986). These authors found that the firing rate of the abducens units began 5–25 ms before the saccade. The maximum of the discharge occurred at or before the peak of the saccade velocity. The firing rate decreased then with an exponential decay whose time constant ranged from 10 to 150 ms. The illustrated simulated activity begins 25 ms before the saccade; its peak is coincident with the peak of eye velocity and the time constant of its decay is 150 ms. To analyse abducens activity during intersaccadic fixation, firing rate was disregarded each time a saccade occurred over an interval equal to the sum of a 50 ms lapse of time before the saccade *plus* the saccade duration *plus* a 300 ms lapse of time after the saccade. It can be seen on the lower graph of *C* that when such a large rejection interval was used, analysis of the firing rate during intersaccadic fixation was not influenced significantly by a residual activity related to the saccade.

previous considerations led us to disregard unit activity occurring not only during the saccade but also during the 50 ms interval preceding it and during the 300 ms interval following it. In Fig. 4*C* the boundaries of the rejection interval used are marked on a simulated burst activity, assuming that the saccade amplitude was

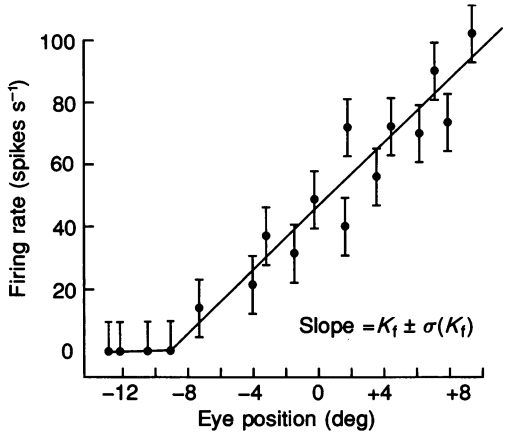

Fig. 5. Relationship between firing rate and horizontal eye position. Lateral position is considered as positive, medial position as negative. The standard deviation associated with each point is the mean of the standard deviations of the firing frequency measured for the different analysed intersaccadic fixation periods. Data illustrated in this figure are those of abducens motoneurone No. 7. The slope of the regression line of firing frequency on eye position, K_f, measures the sensitivity of the neurone to eye position during intersaccadic fixation in the light. In this particular case $K_f = 5{\cdot}03$ spikes s^{-1} deg^{-1}. The x-intercept of the regression line gives the position at which the motoneurone begins to fire, that is its recruitment threshold (−9 deg, in this case).

large (20 deg), that the leading time was large (25 ms) and that the decay of the firing rate was slow ($\tau = 150$ ms).

To determine the relation between tonic rate and horizontal eye position, a computer program first searched for the fixation intervals where both horizontal and vertical eye positions remained stable (eye velocity less than 2 deg s^{-1}). This analysis was performed with data collected over four periods of 2 min. The firing rate during each of these fixation intervals was then determined as the mean of the instantaneous firing rates measured over the whole interval except over its initial 300 ms and its last 50 ms portions. When discharge rate was plotted against vertical eye position during fixation, no trend appeared, as seen for a typical unit in Fig. 3*C*. When firing rate was plotted against horizontal eye position kept during fixation, the correlation coefficients were high, as seen in Fig. 3*B*: they ranged from 0·60 to 0·98. Hence, the data points could be fitted by straight lines with slopes of K_f.

For statistical comparison, however, it was necessary to assess not only the slopes of the linear regressions, K_f, but also the associated errors in the slopes. So K_f and

its variation were obtained by the following procedure. For any intersaccadic fixation period (excluding the first 300 ms and the last 50 ms), the firing frequency was measured every 10 ms and the mean and standard deviation of these measurements were calculated. Then, the mean of the standard deviations

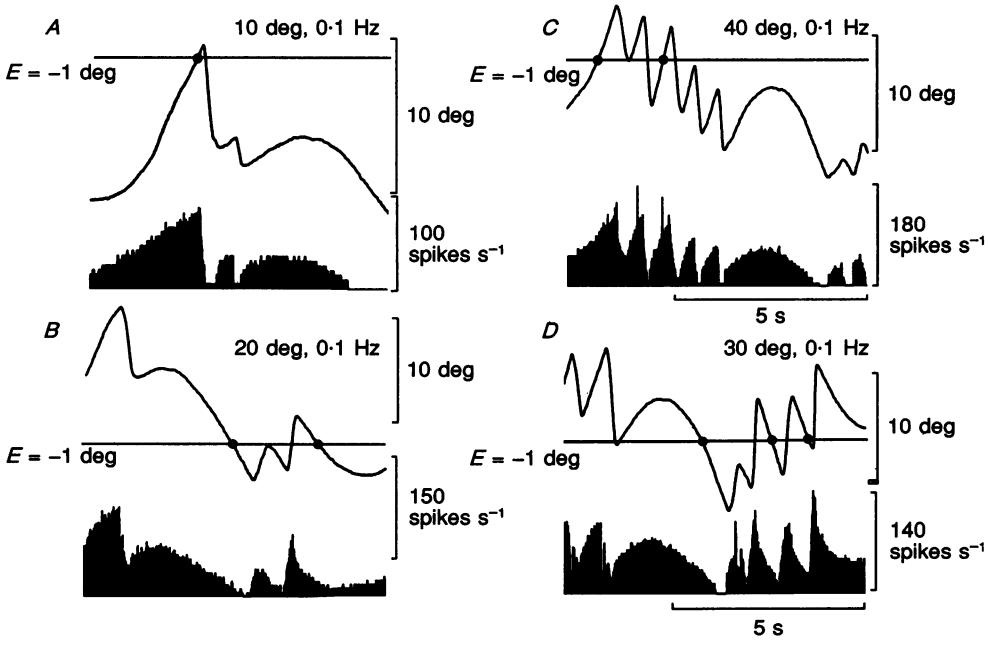

Fig. 6. Firing rate (spike s^{-1}) of an antidromically identified abducens motoneurone during four sinusoidal rotations of the head. The frequency of the rotation was 0·10 Hz throughout. Its amplitude (peak-to-peak) was ± 10 deg in *A*, ± 20 deg in *B*, ± 30 deg in *D* and ± 40 deg in *C*. In each block are shown the horizontal eye position (top) and the instantaneous firing rate (bottom). The position 1 deg medial ($E = -1$ deg) is indicated in each block by a horizontal line.

associated with the different intersaccadic fixation periods was calculated. The result of this computation was estimated to be the mean error associated with each mean firing rate. K_f and its variation, $\sigma(K_f)$, were then calculated using a linear regression analysis adapted to the case where both following conditions are fulfilled (see Meyer 1975, pp. 365–367). (1) For each value of the independent variable (eye position in this case), there are several measurements of the dependent variable (firing rate in this case), whose mean and standard deviation are calculated by classical formulae. (2) For all values of the independent variable, the corresponding standard deviations of the dependent variable are equal. This procedure is displayed in Fig. 5 for abducens motoneurone No. 7. So, for any motoneurone, we determined $K_f \pm \sigma(K_f)$ (Table 1).

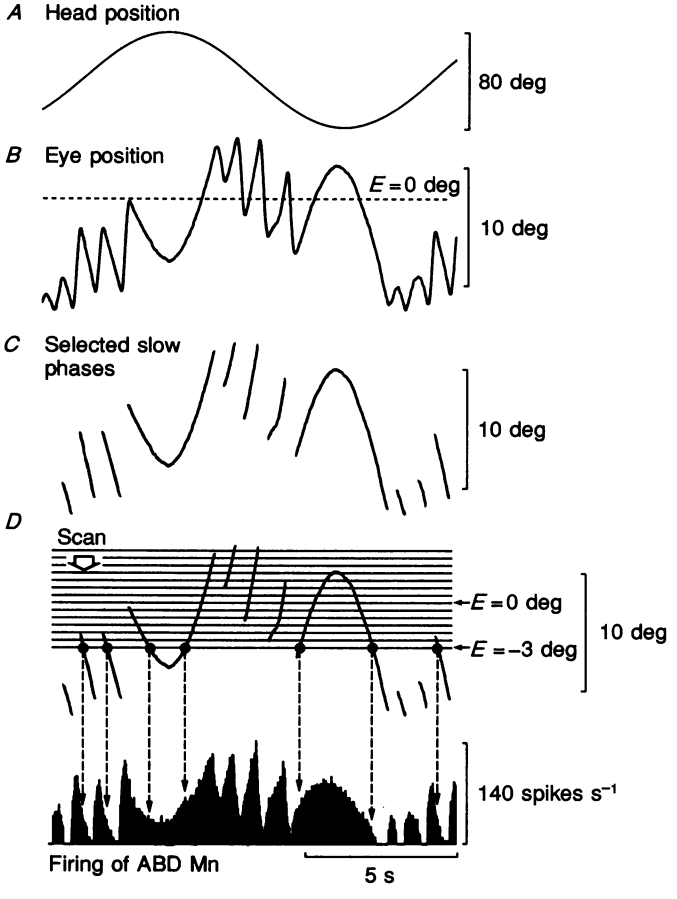

Fig. 7. Algorithm used to establish the relationship between firing rate, on the one hand, and eye position and eye velocity, on the other hand, during the slow phases of the vestibulo-ocular reflex. All the records displayed on the figure (*A–D*) are synchronous. *A*, horizontal head position during a sinusoidal rotation of the head (0·10 Hz, ± 40 deg). *B*, horizontal eye position during the head rotation. Slow phases alternate with quick phases. *C*, from the preceding raw record, the computer algorithm selected the slow phases. *D*, in the next step, the algorithm scanned all the crossings of the slow phases through a given position (see points on the line $E = -3$ deg). This procedure was done repeatedly over the whole range of positions achieved by the eye, at 0·5 deg intervals. For each crossing point, the instantaneous eye velocity and the related firing rate (lower trace) were determined. ABD Mn, abducens motoneurone.

Method for determining velocity sensitivity and position sensitivity during vestibular stimulation

When the head was rotated sinusoidally, the compensatory eye movement was primarily sinusoidal, but was interrupted repeatedly by fast movements in the direction of head rotation. The whole curve of eye movement as a function of time had thus a saw-tooth appearance consisting of slow phases in the compensatory direction and quick phases in the anticompensatory direction. In this study, we

were only interested in the slow-phase behaviour of the abducens motoneurones. Therefore, we disregarded the discharges of the neurones during each quick phase and during the first 300 ms (lapse of time following a quick phase) and the last 50 ms (lapse of time preceding a quick phase) of each slow phase.

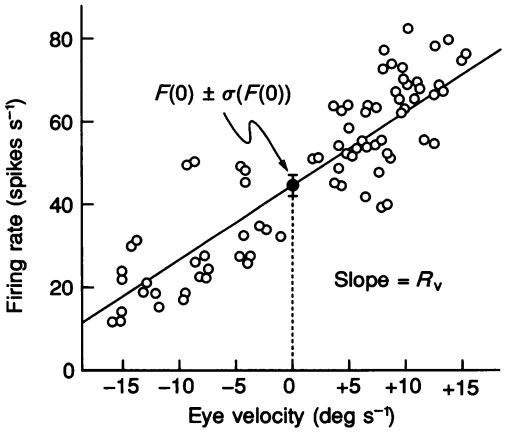

Fig. 8. Relationship between firing rate and eye velocity when slow phases of vestibulo-ocular reflex passed through a given position (in this case $E = -1$ deg). The data were obtained according to the procedure presented in Figs 6 and 7. Data points (○) are fitted well by a linear regression line that can be described by a slope, R_v, and a y-axis intercept, $F(0)$. R_v corresponds to the sensitivity of the studied motoneurone to eye velocity (spikes s^{-1} (deg s^{-1})$^{-1}$) for a considered eye position ($E = -1$ deg in this particular case). $F(0)$ (●) corresponds to the firing rate of the motoneurone for a considered eye position (−1 deg in this case) when the eye velocity is null. The error bar around the point corresponding to $F(0)$ is the calculated standard deviation of $F(0)$. Data illustrated in this figure concern motoneurone No. 7 (whose behaviour during intersaccadic fixation is illustrated in Fig. 5)

Because of the occurrence of quick phases, the curve of the eye movement induced by a sinusoidal head rotation consisted of pieces of a sinusoidal curve shifted randomly along the eye position axis. As a result, during the slow phases of the sinusoidal vestibulo-ocular reflex, gaze passed through a given position at different velocities. Furthermore, to promote the occurrence of a variety of velocities at the same position, sinusoidal vestibular stimuli with four different maximal velocities were used (see Methods and Fig. 6).

In practice, a computer program searched for the points of intersection between the horizontal line corresponding to a given position and the slow phases belonging to the four vestibular stimuli (Fig. 6). For each intercept of a chosen position with a slow phase, the eye velocity and the corresponding instantaneous firing rate were calculated (Fig. 7).

The velocity of the eye was calculated by dividing the difference in eye position reached 100 ms before and 100 ms after the selected position by 200 ms. The related

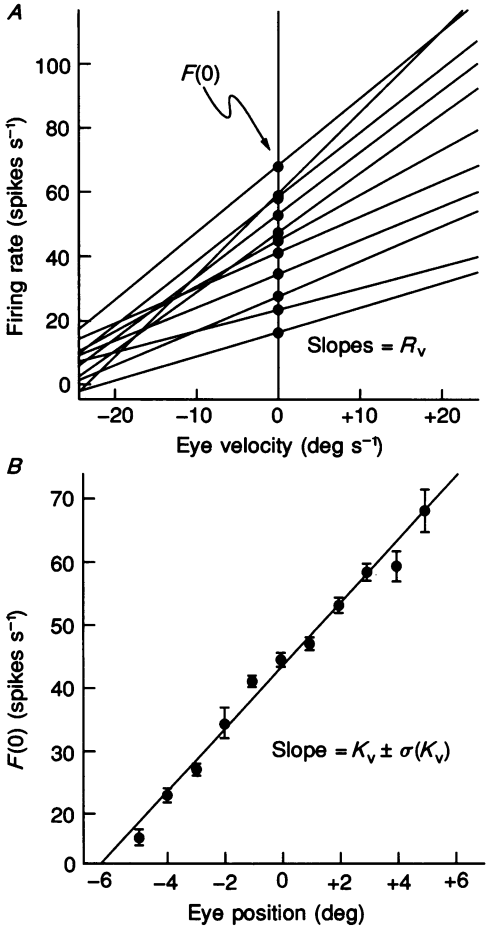

Fig. 9. Method used to determine the sensitivity of an abducens motoneurone (motoneurone No. 7) to eye position during vestibulo-ocular reflex. *A*, the linear regression of firing rate on eye velocity was established for a set of eye positions according to the procedure displayed in Fig. 8. For each of those lines, the firing rate at zero eye velocity, $F(0)$, was calculated by interpolation, as shown in Fig. 8. *B*, relationship between $F(0)$ and horizontal eye position. The data points are fitted well by a linear regression line. The slope of this line, termed K_v, corresponds to the sensitivity of the targeted motoneurone to horizontal eye position. It is expressed in spikes s^{-1} deg^{-1}. To determine K_v, the variations associated with the measurements were taken into account. The firing rate measured when the eye reached a given position at a given velocity (Fig. 5*D*) was not given by a single value. In fact, several measurements were made during the 200 ms interval surrounding the selected point. A mean and a standard deviation (S.D.) of these measurements were calculated. These values (mean $\pm$ S.D.) were then used to calculate not only the firing rate at zero eye velocity, $F(0)$, but also the associated variation, $\sigma(F(0))$. The above figure shows the relationship between the values of $F(0)$ (mean $\pm$ S.D.) and the eye positions. It is shown that the standard deviations associated with the different points are not equal. This point has to be taken into consideration to select the formulae appropriate to calculate the regression parameters (see text and Meyer, 1975, pp. 365–367).

firing frequency was measured every 10 ms in that 200 ms period, so that the mean and the standard deviation of the firing frequency could be determined. As for the computation of K_f (see above), a mean standard deviation was calculated and

TABLE 1. Identified abducens motoneurones

Unit	K_f	K_v	T
MN1	3·31 ± 0·54	3·85 ± 0·42	0·94
MN2	3·86 ± 0·38	3·43 ± 0·32	1·01
MN3	4·36 ± 0·30	3·94 ± 0·05	1·36
MN4	4·66 ± 2·13	5·45 ± 1·56	0·24
MN5	4·66 ± 0·58	5·61 ± 0·76	1·14
MN6	5·02 ± 0·90	6·33 ± 0·55	1·37
MN7	5·03 ± 0·25	4·93 ± 0·31	0·37
MN8	5·16 ± 0·21	5·31 ± 0·38	0·60
MN9	5·29 ± 0·83	4·68 ± 0·44	0·71
MN10	5·45 ± 0·96	4·70 ± 0·78	0·64
MN11	5·46 ± 0·90	4·52 ± 0·45	1·01
MN12	5·65 ± 0·67	5·20 ± 0·51	0·60
MN13	5·81 ± 1·70	5·12 ± 0·83	0·37
MN14	6·22 ± 0·54	5·81 ± 0·44	0·70
MN15	6·36 ± 0·54	5·72 ± 0·20	1·05
MN16	6·43 ± 1·34	6·53 ± 0·83	0·05
MN17	6·66 ± 0·68	6·75 ± 0·65	0·11
MN18	6·74 ± 1·89	4·49 ± 0·95	1·07
MN19	6·95 ± 0·52	8·77 ± 1·50	0·77
MN20	7·06 ± 1·73	7·45 ± 1·65	0·11
MN21	7·32 ± 1·93	8·20 ± 0·66	0·44
MN22	7·82 ± 0·61	7·23 ± 1·21	0·37
MN23	8·55 ± 1·32	7·44 ± 1·04	0·64
MN24	9·28 ± 1·27	9·40 ± 0·97	0·07
MN25	11·03 ± 1·20	9·80 ± 0·67	0·93
MN26	11·37 ± 0·63	11·14 ± 0·63	0·23
MN27	12·35 ± 1·41	10·30 ± 0·50	1·36
MN28	12·50 ± 1·70	11·40 ± 0·26	0·48
MN29	12·73 ± 3·23	11·02 ± 0·64	0·51
MN30	14·04 ± 3·50	13·49 ± 1·10	0·20
MN31	15·43 ± 2·27	14·82 ± 1·01	0·24

K_f is the sensitivity to eye position measured during intersaccadic fixation (in the light). K_v is the sensitivity to eye position measured during the VOR (in complete darkness). Values for K_f and K_v (spikes s^{-1} deg^{-1}) are means ± S.D. T is a statistical variable used to establish if K_f and K_v are statistically different with a confidence level of 0·01. T is defined by the ratio $|K_f - K_v|$ divided by $\sqrt{(\sigma^2(K_f) + \sigma^2(K_v))}$. K_f is different from K_v if $T > 2{\cdot}6$. This is the case in none of the 31 units. The abducens motoneurones are arranged in increasing values of K_f.

assessed to be the mean error associated with each mean firing rate. Figure 8 displays the firing rate of abducens motoneurone No. 7 as a function of the eye velocity when the gaze passed through the −1 deg position.

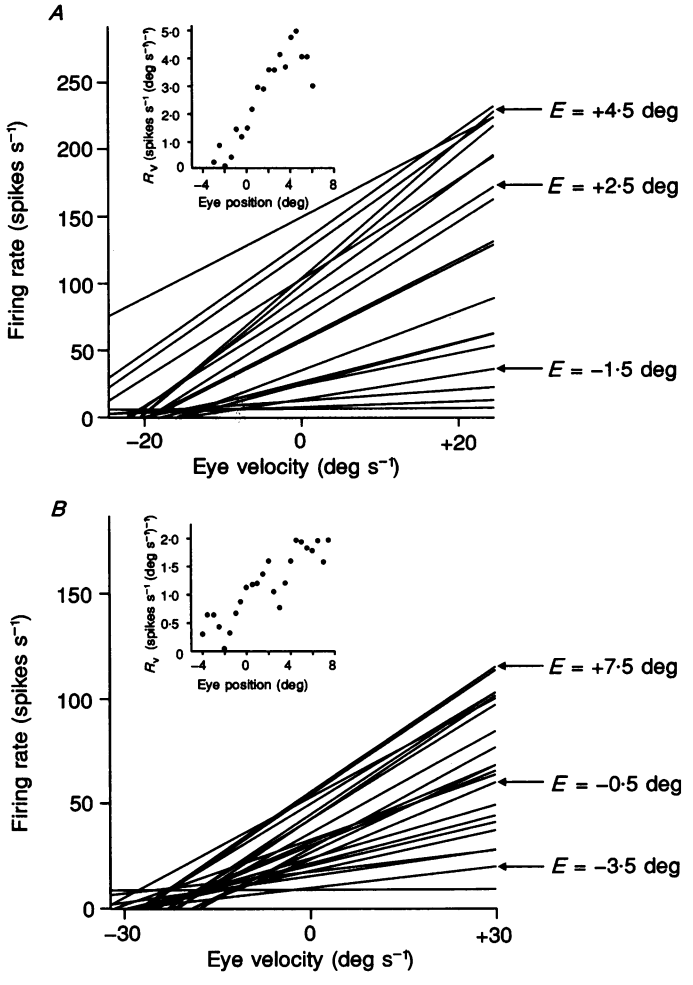

Fig. 10. Variation in eye–velocity sensitivity of two abducens motoneurones with eye position during vestibulo-ocular reflex. Each straight line in *A* and *B* is the regression line of the firing rate on the eye velocity for a particular eye position. The slope R_v of each of these lines corresponds to the sensitivity of the targeted motoneurone to horizontal eye velocity for a particular eye position. It is expressed in spikes s^{-1} (deg $s^{-1})^{-1}$. It is clear that, in neither of the two illustrated motoneurones, are the slopes of the straight lines equal. The graphs in each upper left inset plot the velocity sensitivity R_v *versus* eye position to illustrate the change occurring with more eccentric fixations.

These data were represented by a regression line of slope R_v (spikes s^{-1} (deg $s^{-1})^{-1}$). R_v gave the sensitivity of the motoneurone to eye velocity at a given eye position. R_v, the firing rate at zero velocity, $F(0)$, and the associated error in $F(0)$, $\sigma(F(0))$, were obtained by using the same linear regression analysis as that used to calculate

K_f and its variation. Similar rate–velocity regressions were computed for different eye positions (Fig. 9 *A*).

Only those regression lines based on at least ten points were considered. Finally, the firing rate at zero velocity, $F(0)$, of each rate–velocity relationship was plotted

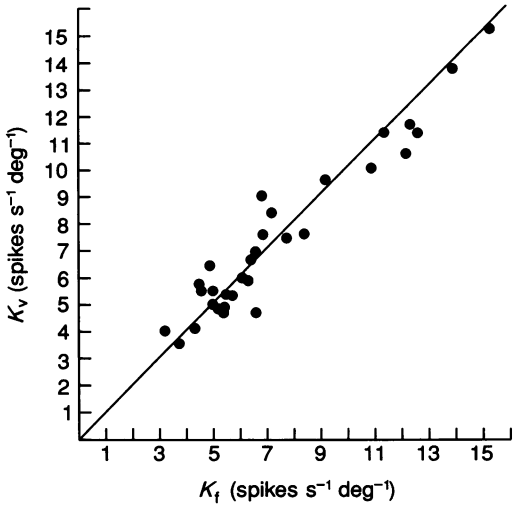

Fig. 11. Relation between the sensitivity to eye position measured during the vestibulo-ocular reflex elicited in complete darkness (K_v) and the sensitivity to eye position measured during intersaccadic fixation in the light (K_f) for thiry-one abducens motoneurones.

versus its eye position (Fig. 9 *B*). The regression line was calculated and its slope K_v (spikes s^{-1} deg^{-1}) gave the sensitivity of the motoneurone to eye position for movements induced by vestibular stimuli. K_v was not calculated in the same way as K_f. K_v and its variation, $\sigma(K_v)$, were calculated using a linear regression analysis adapted to the case where the standard deviations of the dependent variable corresponding to the different values of the independent variable are *not* equal (see Meyer 1975, pp. 365–367). This procedure is displayed in Fig. 9 *B* for abducens motoneurone No. 7. So, for any motoneurone, we determined $K_v \pm \sigma(K_v)$ (Table 1).

Analysis of abducens motoneurone parameters

Sufficient data were available to determine K_f and K_v on thirty-one units. Values of K_f and K_v are listed in Table 1.

The eye position sensitivities (K_f) during intersaccadic fixation ranged from 3·31 to 15·43 spikes s^{-1} deg^{-1}. Their mean was 7·50 ± 3·23 spikes s^{-1} deg^{-1}.

In nine of our thirty-one units, the eye velocity sensitivity, R_v, varied with the eye position at which it was measured. R_v increased with more eccentric eye positions. This phenomenon is illustrated by two examples in Fig. 10.

In Fig. 10 *A*, R_v changed from 0·00 to 4·97 spikes s^{-1} (deg s^{-1})$^{-1}$ as position varied over 9 deg. In Fig. 10 *B*, R_v changed from 0·00 to 1·96 spikes s^{-1} (deg s^{-1})$^{-1}$ as position varied over 11·5 deg.

The eye position sensitivities (K_v) during vestibulo-ocular reflex ranged from 3·43 to 14·82 spikes s^{-1} deg^{-1}. Their mean was 7·18 ± 2·95 spikes s^{-1} deg^{-1}.

In Fig. 11, K_v is plotted against K_f for the thirty-one abducens units studied. If K_f and K_v were equal, the related points would be on the diagonal of the graph ($y = x$). This was roughly the case. Indeed the calculated regression line was $y = 0{\cdot}88\ x + 0{\cdot}61$ ($r = 0{\cdot}95$). This finding suggested that the corresponding K_f and K_v values were equal.

In order to scrutinize even more precisely the question of a possible difference between K_f and K_v, the values of each pair of coefficients characterizing the behaviour of every unit were compared by a test of comparison of two Gaussian populations. As the worst risk in the statistical decision here was to decide wrongly that a K_f value was different from the related K_v value, the chosen confidence level was 0·01. The individual values of K_f and K_v were not found to be statistically different for any of the thirty-one studied motoneurones ($P > 0{\cdot}01$).

DISCUSSION

The oculomotor neural integrator

The general question posed in this study asks if the oculomotor neural integrator is shared by the different inputs eliciting eye movements. Based on the fact that ocular motoneurones carry information about eye position and eye velocity while their command signals encode only velocity (see Introduction), Skavenski & Robinson (1973) hypothesized that a mathematical integration was necessary to convert velocity commands into position signals. This hypothesis was demonstrated to be correct when it was found that electrolytical or chemical lesions in the prepositus–vestibular nuclear complex caused pathological eye movements similar to those that would occur in case of complete failure of the neural integrator (Cheron *et al.* 1986; Cheron & Godaux 1987; Cannon & Robinson 1987). Robinson hypothesized further that a *common* neural network would integrate all of the eye movement commands (Robinson, 1975).

This hypothesis was obviously aimed at movements in the same plane. The neural integrator for horizontal eye movements was never thought to be the same as that related to vertical eye movements. This was indeed recently confirmed experimentally. Injection of muscimol in the interstitial nucleus of Cajal induced a failure of the vertical and torsional gaze holding but spared the horizontal gaze holding (Crawford *et al.* 1991). Analysis of the behaviour of the neurones of the interstitial nucleus of Cajal also showed that the involvement of this nucleus in the generation of the eye position signal was selective for vertical movements (Fukushima, 1987; Fukushima, Fukushima, Harada, Ohashi & Kase, 1990). Consequently the hypothesis of a common neural integrator is concerned either with vertical and torsional movements or with horizontal movements. It should be understood, however, that this framework does not exclude the possibility of the nucleus prepositus hypoglossi playing a role in co-ordination between vertical and horizontal eye position signals (Cheron, Mettens & Godaux, 1992).

Restricting our attention to horizontal movements, it must be realized that, in spite of persuasive theoretical evidence in favour of the hypothesis of the common integrator (Robinson, 1975), it is not trivial to test it experimentally. Indeed, at least one type of horizontal eye movement, the vergence movement, does not share an integrator with the other types of movement. Mays & Porter (1984) found that the eye position sensitivity during vergence movements and the eye position

sensitivity during conjugate movements were not matched at the level of individual abducens neurones. Thus for horizontal eye movements, the common neural integrator hypothesis is concerned only with the versional eye movements.

Methods for measuring eye position sensitivity and eye velocity sensitivity of the abducens motoneurones

Experimental testing of the validity of Robinson's hypothesis necessitates that we investigate whether the value of K (coefficient of sensitivity to eye position) for any neurone related to eye position is independent (or not) on the mode by which the eye is driven to any position. In this study, we analysed the behaviour of the pool of abducens motoneurones that is the output pathway of the neural integrator(s). The two versional movements that we studied were fixation during the intersaccadic periods (in the light) and the VOR (in complete darkness). During each intersaccadic fixation period, eye position remains stable and eye velocity is zero. During the VOR, both eye position and eye velocity vary. In order to assess a neurone's sensitivities during the VOR, the portions of the firing rate related to eye position and to eye velocity must be separated. Until now, three methods have been used: the subtraction method, the multivariate regression analysis and ours.

A subtraction procedure was used by Skavenski & Robinson (1973) and by Tomlinson & Robinson (1984) in the monkey and by Delgado-Garcia *et al.* (1986) and by Berthoz, Droulez, Vidal & Yoshida (1989) in the cat to obtain the sensitivity to eye velocity during the slow phase of vestibular nystagmus. These authors first established the firing rate–eye position relationship during intersaccadic periods (K_f). This relation was then used to calculate the portion of the discharge rate observed during vestibular responses that was related to eye position. The velocity-dependent discharge rate during the VOR was then obtained by subtracting the calculated position-dependent discharge rate from the observed rate. This procedure, however, assumes that the rate–position relationship established for fixation also holds during vestibular stimulation. In other words, such a procedure already assumes that the oculomotor neural integrator is common. Hence, the authors using the subtraction procedure do not measure the value of K_v.

In two recent studies, one in the goldfish (Pastor, Torres, Delgado-Garcia & Baker, 1991) and the other in the monkey (Fuchs, Scudder & Kaneko, 1988), K_f and K_v were measured by independent methods. K_f was obtained by measuring the slope of the linear regression fitted on the data of the relationship between discharge rate and position during fixation. K_v and R_v were calculated by multivariate regression analysis, according to the first-order approximation of the relationship between discharge rate and eye movement proposed by Skavenski & Robinson in 1973.

$$D = K(E-T) + R\frac{dE}{dt},$$

where D is the discharge rate, E is the eye position and T is the threshold or eye position at which a particular motoneurone is first recruited into activity. Computation of K and R by a multiple regression analysis assumes that K and R are constants independent of eye position and eye velocity. Unfortunately, this is

not the case. As illustrated in Fig. 10, R_v varied with eye position. This phenomenon, observed on nine out of our thirty-one motoneurones, was described previously by Delgado-Garcia *et al.* (1986) (see their Fig. 13). Such a variation cripples the multiple regression analysis as a suitable method for comparing K_f and K_v at the level of individual neurones.

The method developed in this paper does not presuppose that the integrator is common and takes into account the variation of R_v as a function of eye position. Moreover, K_v is calculated by an interpolation procedure at null eye velocity. Hence the situation is very similar to that seen in intersaccadic fixation where the eye velocity is null during each analysed period. Our method has, however, two limitations. First, higher threshold motoneurones could not be accurately analysed as the available data were insufficient for the computer program to operate. Secondly, no attempt was made here to take into account hysteresis in the firing rate described by others during intersaccadic intervals (Delgado-Garcia *et al.* 1986; Goldstein & Robinson 1986; Berthoz *et al.* 1989; Pastor *et al.* 1991).

Eye position sensitivities of the abducens neurones during distinct types of movements

The major finding from the present study is that the eye position sensitivity of identified abducens motoneurones is the same during intersaccadic fixation (in the light) and during the slow phase of vestibular nystagmus (in complete darkness). In this section, we will examine the significance of this result in relation to the hypothesis of a common neural integrator.

Whatever the command triggering the horizontal eye movements, the transformation from velocity signals to position signals takes place in the prepositus–vestibular nuclear complex (Cheron *et al.* 1986; Cannon & Robinson, 1987; Cheron & Godaux, 1987). If there were separate integrators within this complex, one might expect that their outputs on individual motoneurones would have some variability and that K_f would be different from K_v at least for a few motoneurones. However, K_f and K_v values would also be similar for each motoneurone if two separate integrators would project onto the same motoneurone pool with the same local synaptic density. Therefore, identity of K_v and K_f at the level of individual motoneurones is a necessary, though not sufficient, condition to establish that there is a common integrator.

In fact, versional ocular movements can be triggered by the four following command signals, individually or in partnership: (1) a signal from the saccade generator (Van Gisbergen *et al.* 1981), (2) a vestibular signal (Fernandez & Goldberg, 1971), (3) an optokinetic signal (Cohen, Matsuo & Raphan, 1977; Lisberger, Miles, Optican & Eighmy, 1981) and (4) a pursuit signal (Lisberger & Westbrook, 1985; Lisberger, Morris & Tychson, 1987). In the cat, only the first three command signals are effective (Evinger & Fuchs, 1978). Any test of the common integrator hypothesis necessitates comparing two ocular movements that are not triggered, even in part, by a common signal. For instance, comparison of the behaviour of a neurone during saccades made in the light and during vestibulo-ocular reflex elicited in the light, would be inappropriate. In our study, we compared the behaviour of the abducens motoneurones when integration was elicited either by saccades in the light (signal No. 1 in Fig. 1) or by the vestibulo-

ocular reflex in darkness (signal No. 2 in Fig. 1). We did so because alertness, which strongly influences the sensitivity of neurones to eye position (Delgado-Garcia *et al.* 1986; Berthoz *et al.* 1989), was difficult to maintain in the cat held still in complete darkness.

Comparisons with previous studies

The value for the K_f of 7·50 spikes s^{-1} deg^{-1} obtained in the present study agrees reasonably well with those of some previous studies in the cat, e.g. 5·3 spikes s^{-1} deg^{-1} (Goldberg, 1980), 8·7 spikes s^{-1} deg^{-1} (Delgado-Garcia *et al.* 1986), and 4·4 spikes s^{-1} deg^{-1} (Berthoz *et al.* 1989). Furthermore, there is no major interspecies difference as the value of K_f ranged from 3·5 to 5·9 spikes s^{-1} deg^{-1} in the monkey (Fuchs & Luschei, 1970; Skavenski & Robinson, 1973; Mays & Porter, 1984; Fuchs *et al.* 1988; Gamlin, Gnadt & Mays, 1989) and was recently measured to be 4·8 spikes s^{-1} deg^{-1} in the goldfish (Pastor *et al.* 1991). None of these previous studies was specifically designed to investigate whether there was a common neural integrator. In the only two previous studies that measured K_f and K_v without presupposing the uniqueness of the neural integrator (see above), the mean values of K_f and K_v were matched. In the monkey, the mean values of K_f and K_v were respectively 5·3 and 6·2 spikes s^{-1} deg^{-1} (Fuchs *et al.* 1988). In the goldfish, the mean values of K_f and K_v were respectively 4·8 and 4·2 spikes s^{-1} deg^{-1} (Pastor *et al.* 1991). Neither study compared the values of K_v and K_f at the level of the individual motoneurones. Moreover such a comparison would not have been meaningful as K_v and K_f were both measured during movements guided by vision (see above).

Conclusion

The major finding of this paper is that, at the level of the individual abducens motoneurones, the sensitivity to eye position measured during intersaccadic fixation in the light is equal to the sensitivity to eye position measured during vestibulo-ocular reflex elicited in complete darkness. If this had not been the case, even for occasional motoneurones, the hypothesis of the uniqueness of the neural integrator would have been ruled out. The observed behaviour matches that which would be detected if the neural integrator was actually shared by the different subsystems for versional horizontal movements

We thank Christiane Busson for secretarial assistance. We acknowledge Marie-Pierre Dufief for excellent technical assistance during experiments and in histology. We thank Emilie Daubry for help in histology and Sally and Gordon Petrequin for revising the English text. We thank Michel Baligniez and Bernard Foucart for taking care of the mechanical and electronic equipment. We thank Joël Deconinck who designed the appropriate way to process our data statistically. This research was supported by the Fonds National de la Recherche Scientifique (Belgium) and by the Commission of the European Communities, Contract No. SC1*-CT91-0649.

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