

COUPLING SENSORY INPUTS TO THE APPROPRIATE MOTOR RESPONSES: NEW ASPECTS OF CEREBELLAR FUNCTION

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INTRODUCTION

It is known that postural control is maintained through the integration of somatosensory, visual and vestibular signals (16, 30, 31), which inform the central nervous system about any deviation from the intended body position and generate postural reflexes appropriate to re-establish the original body orientation. The control of trunk, where most of the body mass is located, is crucial for this purpose. Several studies have emphasized the nearly linear interaction of the reflex effects induced by the different sensory signals in limb muscles activity (22, 29, 43) and body sway parameters (13, 19). In particular, vestibular and neck reflexes elicited by changes of head-in-space and body-to-head position, respectively, lead to changes in the limb extensor tone which are appropriate to stabilize the position of the body in space (22, 29, 36, 43). However, most of the receptors that elicit postural responses are located on moving segments of a multiarticulated body. As a consequence of this fact, it may happen that an identical input signal may be elicited during body displacements occurring in different directions. For instance, identical patterns of activation of vestibular receptors are generated when a subject, whose head and gaze are oriented straight ahead (condition A), sways forward in the sagittal plane, as well as when a subject, whose head and gaze point towards his left shoulder (condition B), sways to the left in the frontal plane. However, in order to maintain body position, different spatiotemporal patterns of muscle activation must be generated in the two conditions considered. Conversely, different input signals can be coupled to body displacements in the same direction. This is the case when we compare a subject who sways forward, while looking ahead (A), to a subject swaying in the same direction, but looking over his left shoulder (B). In this instance it is appropriate that the two different sensory signals elicit the same postural response. It can be postulated, therefore, that the relation between sensory signals and reflex responses is not univoque. There is indeed evidence that the pattern of muscle activation elicited by stimulation of vestibular (7, 18, 23, 32), neck (18) and visual (44) afferents is modified by the relative position of the different body segments and of the eyes in the orbit. These modifications seem to be appropriate to the goal of stabilising the position of the body in space.

At present, very little is known about the neurophysiological mechanisms underlying these phenomena. The present report tries to partially fill this gap, by sum-

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marizing the results of recent experiments obtained in decerebrate cats. It was known that, in this preparation, the forelimb extensor muscle triceps brachii displays spatially tuned responses to the labyrinthine input, being maximal activated during animal tilts oriented perpendicularly to the transverse axis (25, 43). Labyrinthine volleys may also reach the Purkinje (P)-cells of the cerebellar anterior vermis, which show preferred response directions uniformly distributed all over the horizontal plane (26, 34). The functional inactivation of this region greatly depresses the amplitude of the triceps brachii responses to animal displacement, whatever the orientation of the stimulus could be (25). The data described in the present report documents that, in decerebrate cats, i) the relative "body-to-head" position finely tunes the spatial organization of vestibulospinal (VS) reflexes (27), so to adapt them to the requirements of body stability, ii) this effect is reduced or abolished by functional inactivation of the vermal cortex of the cerebellar anterior lobe (27) and iii) it seems to be attributable to the changes induced by the neck input in the vestibular responses of the corresponding P- cells (24, 28).

METHODS

Basic information about methodological aspects of the described studies are given in the Results section (see the original papers for further details about animal preparation, stimulation procedure, data collection and population vector analysis (ref.s: 24-28, 34) All this experimental work was performed in collaboration with Prof. O. Pompeiano.

RESULTS

1. Neuronal responses to spatially oriented labyrinthine stimuli: evaluation of response vectors.

Head tilt in space is an appropriate stimulus for activate vestibular receptors. In particular, each otolith afferent, due to its functional polarization, will be particularly sensitive to tilts in a given, "preferred" direction (42). The same will held true for ampullar afferents, which are maximally activated when the tilt gives rise to a rotation in the plan of the corresponding semicircular canal (42). Afferent responses to animal tilt can be described by a single response (sensitivity) vector (S_{\max}), characterized by gain (G_{\max} , in imp/sec/°), direction (θ_{\max} , in °) and temporal phase (ϕ_{\max} , in °) components (1, 38). θ_{\max} , G_{\max} and ϕ_{\max} represent the direction of tilt giving rise to the maximal response, the response gain obtained for this preferred direction and the corresponding response phase, respectively. The afferent response to a sinusoidal tilt in a given direction can be evaluated by projecting the response vector along the stimulus direction. The discharge modulation obtained during a tilt of 1° corresponds to:

$$a) G_{\max} \times \cos(\theta_{\max} - \alpha) \times \sin(\omega t + \phi_{\max}) \quad (36),$$

where α is the direction of tilt, while $\omega = 2\pi \times$ frequency of tilt. Obviously, the response amplitude of an afferent will be maximal for a tilt in the direction of S_{\max} and equal to zero in the perpendicular direction, while the response phase will be

identical for all the tilt directions. A neuron behaving as the afferents described above is considered a one-dimensional, "narrowly tuned" unit (3, 4, 8). In order to determinate its response vector it is necessary to record its responses to stimuli oriented in a wide range of directions (1, 8) or, alternatively, to more complex "wobble" stimuli (39, 4). During wobble, a mixture of pitch and roll rotations (39), a tilt of constant amplitude is imposed to the animal, whose direction rotated, at uniform speed, over the horizontal plane (39), either in clockwise (CW), or in a counter-clockwise (CCW) direction. The components of the S_{\max} vector can be estimated by analyzing the responses to both CW and CCW stimuli (28, 34, 39, 4, 26). It has to be pointed out that narrowly tuned units are affected by wobble in both CW and CCW direction (bidirectional units) with similar response amplitude.

When vestibular signals endowed with different spatial *and* temporal properties converge at the level of single units (spatiotemporal convergence), the behavior of these neurons can be described by two vectors, S_{\max} and S_{\min} , spatially and temporally orthogonal (3, 4, 8). The response of these cells to a sinusoidal tilt in a given direction is then obtained by summing the projections of both vectors along the stimulus direction. These bi-dimensional, "broadly tuned" units display a maximum sensitivity for stimuli in the direction of S_{\max} , a minimum, nonzero sensitivity for stimuli in the direction of S_{\min} and a response phase which changes progressively with the stimulus direction, the minimal response leading the maximal response by 90° . Gain, direction and temporal phase of both S_{\max} and S_{\min} can be obtained from the analysis of neuronal responses to CW and CCW stimuli (28, 34). In particular, the direction of S_{\min} (θ_{\min}) can be oriented 90° clockwise or counter-clockwise to S_{\max} . Finally, $\varphi_{\min} = \varphi_{\max} + 90^\circ$. These neurons are affected by both CW and CCW stimuli (bidirectional units), but with different response amplitudes.

A quantitative measure of the two-dimensional spatial sensitivity is represented by the "tuning ratio" (8) which indicates the gain ratio of the minimum over the maximum sensitivity vector (G_{\min}/G_{\max}). Units are considered as narrowly or broadly tuned when their tuning ratios are lower or higher than 0.1, respectively (8). The units showing equal gain components of their S_{\max} and S_{\min} vectors and a tuning ratio equal to 1.0 (3, 4) respond only to wobble in one direction (unidirectional units). Their response to tilt stimuli display the same sensitivity, irrespectively of the stimulus direction, while their phase changes linearly with stimulus orientation (3), being 0° at the direction of the maximal discharge obtained during the effective CW or CCW rotation.

2. Spatial organization and cerebellar control of VS reflexes.

It has been shown that, when the body is aligned to the head, the forelimb extensor triceps brachii is maximally activated during whole animal tilts oriented perpendicularly to the longitudinal body axis, the peak activity occurring near to the extreme side-down position (25, 43). This reflex can in part be attributable to the transfer of information from the labyrinth to the spinal circuits through VS and reticulospinal pathways (6, 20, 39). The cerebellar lobules IV and V (culmen), which correspond to the "forelimb region" of the anterior vermis (17, 35), may represent an additional side-path in the VS reflex: in fact, the corresponding P-cells receive infor-

mations from the labyrinth (11, 26, 34) and control the activity of both VS and reticulospinal neurons (17, 35).

When the simple spike discharge of P-cells was analyzed during whole animal wobble stimuli (28, 34), it appeared that these neurons showed spatially selective responses. Most of the cells, however, were broadly tuned and unidirectional unit could also be found. Thus, convergence of vestibular signals endowed with different spatial and temporal properties, seems to be a rule, rather than an exception, within the cerebellar cortex.

The directions of maximal and minimal sensitivity vectors of these cells were uniformly distributed all over the four quadrants of the horizontal plane (in the reference system utilized, directions of 0° , 90° , 180° , and -90° corresponded to side-down, nose-down, side-up and nose-up tilts, respectively, side-down and -up positions being referred to the recording side). On the other hand, the temporal phase of S_{\max} , calculated with respect to table position, ranged between -90° (lag) and 90° (lead) (34). Moreover, units with different spatial and temporal properties were not segregated within the explored cerebellar region (34), whose functional inactivation, by a local injection of the GABA_A muscimol, greatly depressed the amplitude of the VS reflexes elicited by tilts oriented in all the possible directions (25). On the basis of these findings, it was postulated that P-cells with the same preferred direction represented functional units, facilitating the postural response elicited by similarly oriented stimuli.

It is a matter of fact, however, that most of P-cells, although spatially tuned, can be affected by tilts in a wide range of directions. On the other hand, a specifically oriented stimulus would activate neurons with different spatial properties. How could this pattern of recruitment give rise to a precise coding of stimulus direction, leading to the development of the appropriate postural response? The activation of P-cells by spatially oriented stimuli reminds the condition observed by Georgopoulos and collaborators (14) within motor cortical areas, where each motor cortical neuron is tuned to a particular (preferred) direction of arm movement performed within the workspace. These authors have proposed that the simultaneous changes occurring in the activity of all these cells during an arm movement represent a neuronal signal which effectively codes for the direction of that movement. Each cell gives a vectorial contribution to the population coding. The direction of the contribution corresponds to the preferred direction of the neuron, while its amplitude is the change in activity observed during the movement. Individual contributions summate vectorially, thus generating a population vector, whose direction corresponds to that of the movement. The model proposed by Georgopoulos was adapted to the response characteristics of spatially tuned corticocerebellar units, which show maximal and minimal response directions. These neurons were assumed to contribute to the population response with two vectors, V1 and V2 oriented along θ_{\max} and θ_{\min} , respectively (further details about the contribution given to the population vector by the few recorded unidirectional cells, which are not spatially tuned, can be found in ref. 24 and 34). The length of V1 and V2, i.e. the strength of the neuronal signalling, corresponded to the changes in neuronal activity generated by each vector during the specific tilt considered, i.e. to their projections along the direction

of the stimulus. Therefore, the amplitudes of V1 and V2 were sinusoidally modulated during the tilt (see equation a).

The results of this analysis indicated that, during a dynamic head tilt, the direction of the population vector corresponded to the tilt direction, while its amplitude was proportional to that of tilt (24, 34).

3. Effects of body-to-head rotation on the spatial organization of VS reflexes and P-cell responses to labyrinthine stimuli.

Effects of body-to-head rotation on the response vector of the forelimb extensors: role of the cerebellum.

As reported above, when the body was aligned to the head, the direction of the S_{\max} vector of the triceps brachii was close to the transverse axis, pointing toward the recording side. However, body-to-head rotation around a vertical axis passing through C1-C2, induced a displacement of the response vector in the same direction and by the same amplitude as the body (27). The overall effect of body displacement was highly significant (ANOVA, $P < 0.0001$). This finding indicates that, in decerebrate cats, when head and body are not aligned, the preferred response direction of triceps brachii to head tilt is kept orthogonal to the *body* and not the *head* axis.

Only in few instances significant changes could be induced in the temporal phase of the response vector, in its gain or else in the tuning ratio. Since the angle of vector rotation induced by body-to-head displacement was significantly reduced by about 40% in experiments where the first and second dorsal root were cutted bilaterally, or the dorsal neck muscles were infiltrated with novocaine, it is likely that neck information entering the spinal cord at C1-C2 level contributed to the observed effects.

In some of these experiments, a microinjection of the GABA_A agonist muscimol was performed into the lobules IV-V of the cerebellar vermal cortex (1-2.2 mm lateral to the midline), ipsilaterally to the recording side (27). In these instances, before cerebellar injection, a body rotation of 30° towards the recording side induced a displacement of the triceps response vector in the same direction (average angle of vector rotation: 30.7 ± 11.5 , SD, °). The injection always induced an increase in the extensor tonus of the ipsilateral forelimb, as would have been expected following removal of P-cells inhibition upon VS neurons (35).

In addition, cerebellar injections also led to a prominent and significant reduction in the rotation of the response vector.

The effectiveness of cerebellar inactivation was greater in those animals which showed the largest vector rotations following body displacement. Cerebellar inactivation could affect the rotation of response vector induced by body displacement without modifying the gain of the response vector.

Effects of body-to-head rotation on the response vectors of P-cells: average modifications.

In decerebrate cats, the response vectors of P-cells located in the lobules IV and V were evaluated while the body was aligned to the head and following 15-30° of

body displacement either towards or away from the recording side. The statistical significance of the changes observed in the different parameters of the response vectors was then evaluated at single unit level. Moreover, the average modifications observed at the level of the whole population of recorded units were correlated to both amplitude and direction of body-to-head rotation (28).

Body-to-head rotation affected the response vector(s) of a large proportion (87%) of the recorded neurons. Changes in the direction of the response vector(s) were most often observed, but gain and phase components could be affected too. Many units also showed prominent changes in tuning ratio, thus indicating that body-to-head rotation could modify the spatiotemporal convergence of vestibular signals at single unit level. In few instances, bidirectional patterns of response could be reversed to unidirectional. Modification in base frequency were rarely observed. The average changes in θ_{\max} were clearly related to both amplitude and direction of body displacement. As shown in Fig. 1 (filled symbols), the median values of the changes in the directions of S_{\max} obtained for body rotations of -30° , -15° (away from the recording side), 15° and 30° (towards the recording side) corresponded to -27° , -19° , 9° and 30° , respectively. The correlation between vector and body rotation was highly significant ($r = 0.99$, $P < 0.005$) and the corresponding regression line ($y = 0.93x - 1.46$) was close to the line $y = x$. The amplitude of vector rotation was independent upon the values of θ_{\max} obtained in the control position.

The changes in ϕ_{\max} as well as those in G_{\max} , G_{\min} and tuning ratio, evaluated within the whole population of tested units, were independent on both direction and amplitude of body rotation. Moreover, all the observed modifications did not depend upon changes in the base frequency.

Effects of body-to-head rotation on population coding.

The modifications in unit response properties induced by body displacement affected the population coding of head tilt direction (24). When the body was aligned to the head, the population vector always pointed to the direction of head (and thus of body) tilt. The average directional difference between population response and stimulus corresponded, for the eight tilt direction analyzed (0° , 45° , 90° , 135° , 180° , -135° , -90° , -45°), to $0.0 \pm 1.8^\circ$. The assumption was made that body displacement modified the amplitudes but not the directions of neuronal contributions to the population vector: in other words, the directional information coded by the individual neurons was considered invariant with respect to the relative body-to-head position. From this point of view the distribution of the directions of maximal and minimal response evaluated in the control position represented an "invariant" reference frame for coding the stimulus direction.

Under this assumption, it was observed that, following $\pm 30^\circ$ of body displacement, the direction of the population vector showed significant deviations from the direction of head tilt (24). These deviations were not observed for $\pm 15^\circ$ of body displacement. The average directional differences between population response and stimulus, evaluated at 30° and -30° of body displacement are illustrated in Fig. 1 (open symbols) and corresponded to $-26 \pm 10^\circ$ and to $37.8 \pm 18.3^\circ$, respectively (ANOVA, $P < 0.001$). These findings indicate that, at this

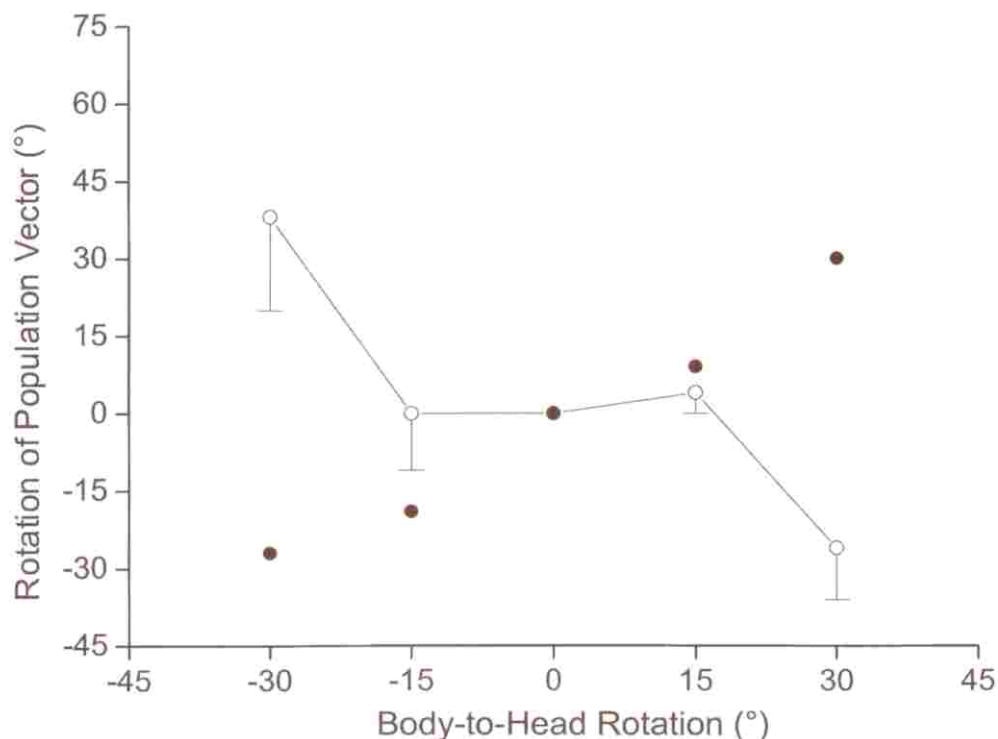


Fig. 1. - Average changes in the orientation of S_{max} and in the population coding of tilt direction induced by body-to-head rotation in the cerebellar vermis.

Filled symbols represent the medians of the angles of S_{max} rotation observed following body displacement in the neuronal population analyzed.

Open symbols corresponds to the average differences between the direction of the population vector and that of tilt (rotation of population vector). Each point is the mean of the values obtained at eight different tilt directions (0° , 45° , 90° , 135° , 180° , -135° , -90° , -45°). In this and the following figures error bars represent S.D.

Positive and negative values on the abscissas represent body displacements towards and away from the recording side, respectively.

amplitude of body displacement, a precise correspondence exists between the deviation of the population vector from the direction of head tilt and the relative body-to-head position.

Effects of body-to-head rotation on the response vectors of P-cells: patterns of changes at single unit level.

Units studied following body displacement in both directions could show three different patterns of directional changes (24). On the whole, 88% of these units showed significant changes in θ_{max} following body displacement in at least one direction. In some units (Fig. 2A), the S_{max} response vector rotated in opposite directions following body displacements towards and away from the recording side ("slope" units). In other neurons, vector rotations of comparable amplitude and identical direction were

observed following body displacements towards and away from the recording side (Fig. 2B, filled symbols) (“triangular” neurons). Finally, (Fig. 2B, open symbols), the

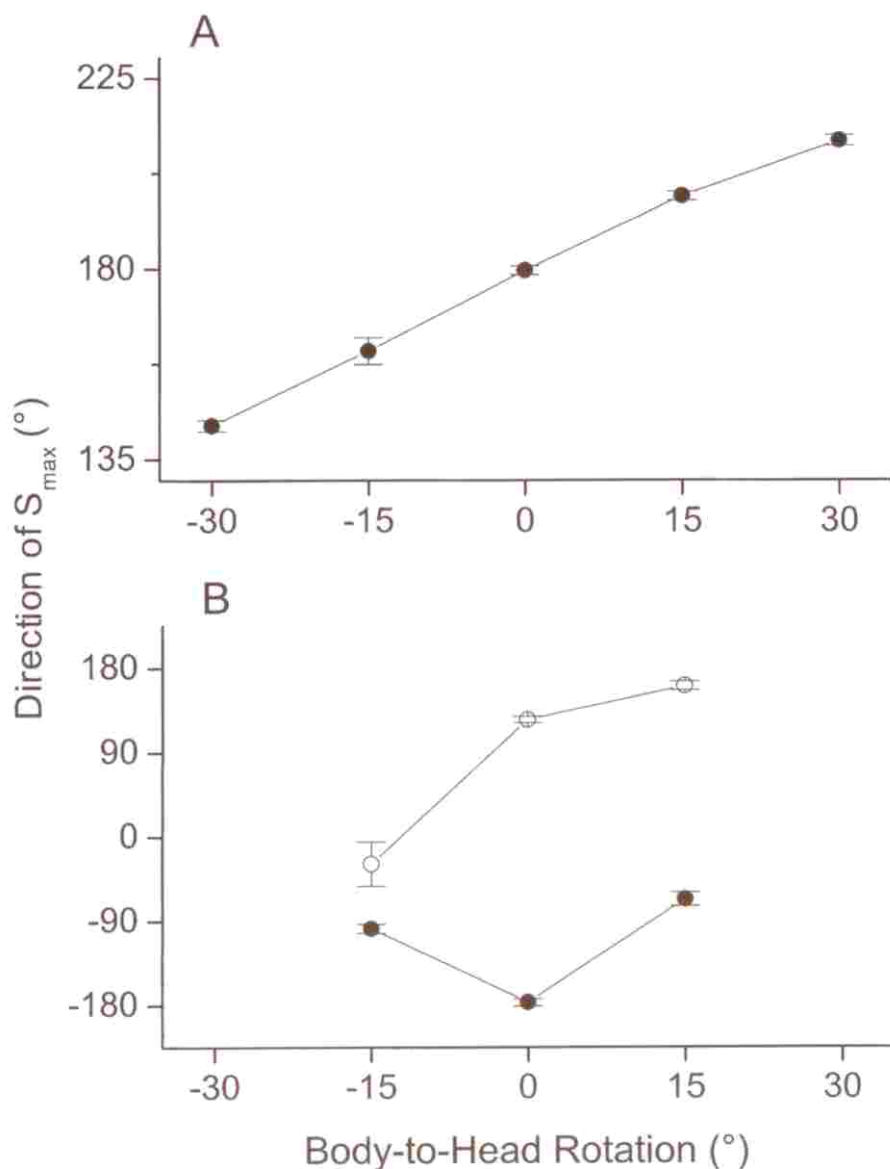


Fig. 2. - Changes in the direction of the S_{max} vector induced by opposite directions of body rotation in three different P-cells.

A. Unit showing a typical “slope” pattern of changes in the S_{max} directions. B. Examples of a “ramp” (circles) and a “triangular” (dots) unit. Both in A and B positive and negative values on the abscissas represent body displacement towards and away from the recording side. Each point is the mean of 16 evaluations of the S_{max} direction.

changes in S_{\max} orientation induced by opposite directions of body displacement could be opposite in sign, but of quite different amplitude ("ramp" neurons) and often the smaller change did not reach the level of statistical significance.

Qualitatively similar pattern of changes were also observed for ϕ_{\max} , G_{\max} , G_{\min} and tuning ratio. In particular, 68% of the units showed modification in ϕ_{\max} . Typical units with "slope" and "triangular" patterns of changes in ϕ_{\max} are shown in Figure 3A and B, respectively (filled symbols). With respect to the changes in ϕ_{\max} , the directional modifications (open symbols) observed in a given unit could follow the same (Fig. 3B) or a different pattern (Fig. 3A). Changes in G_{\max} and G_{\min} were observed in 52% and 61% of the units, respectively. They could occur in the same unit and, most often, they followed a triangular or a ramp pattern. Others neurons, however, displayed selective changes in gain for one of the two response vectors. Finally, the modifications in the amplitude of S_{\max} and S_{\min} induced by body-to-head rotation led to significant tuning ratio changes in 61% of the individual neurons. Ramp or triangular response patterns were most often observed.

A given unit could show any combination of modifications in response properties. On the whole, there was little obvious correlation between the changes in the different parameters: for instance the changes in gain, phase, and tuning properties observed in a given unit could show a different pattern with respect to the directional modifications, when the latter were present (Fig. 3A).

DISCUSSION

Changes in the spatial organization of vs reflexes induced by body-to-head rotation: neurophysiological mechanisms

Cerebellar mechanisms.

The studies reported above have clearly shown that, in decerebrate cat, the spatial organization of VS reflexes is tuned by the relative body-to-head position, so that the maximal activation of the triceps brachii always occurs for tilt oriented perpendicularly to the longitudinal axis of the body, whatever the relative orientation of the stimulus with respect to the head could be. This finding is remarkable, since the VS reflexes are driven by displacement of the head and not of the body in space. In other words, the VS reflexes result spatially organized within a body-centered, rather than head-centered reference frame. The observed effects can be at least in part attributed to cervical afferents, entering the cord through several dorsal roots. These experiments are consistent with those performed in standing human subjects, in which the direction of body sway induced by unilateral galvanic stimulation of the labyrinth rotates by the same angle and in the same direction as the head over the body (23), the effect being due to parallel modifications of the electrically driven muscle responses (7, 32). A reduced animal model is therefore well suited to investigate the neurophysiological mechanisms by which VS reflexes are tuned by the neck input, thus becoming adequate to stabilize body position in space. In this respect, the present data give us two important informations. First of all, this tuning of VS reflexes

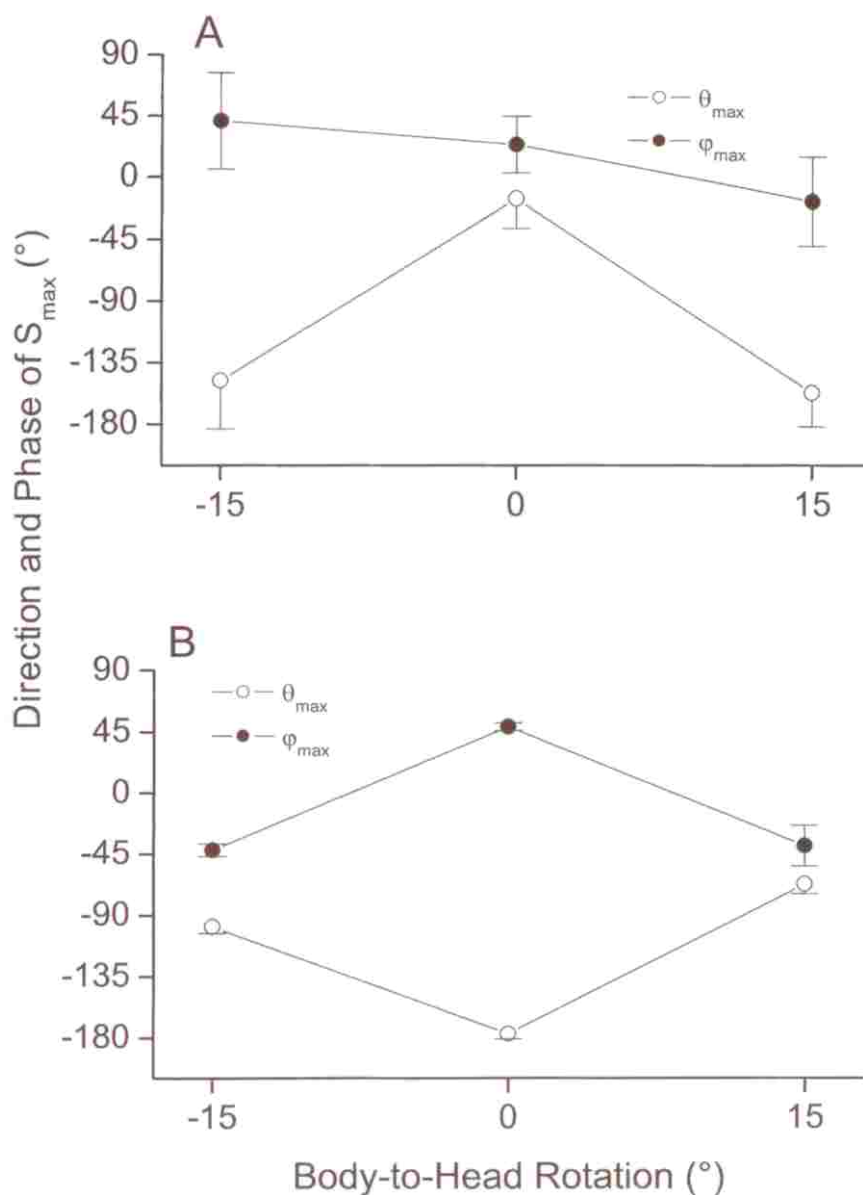


Fig. 3. - Changes induced by 15° of body-to-head displacements towards and away from the recording side in the temporal phase (dots) and in the direction (circles) of the S_{max} vector of two different corticocerebellar units (A and B).

A. Unit showing a "slope" pattern of phase change (dots) and a triangular pattern of directional modification (circles) following body displacement.

B. Unit showing "triangular" patterns for both phase (dots) and directional changes (circles). Positive and negative values on the abscissas indicate body displacements towards and away from the recording side.

Both in A and B, each point represents the mean of 16 values.

takes place with a great accuracy even in the absence of supratentorial structures. Second, it requires the functional integrity of the vermal cortex of the cerebellar anterior lobe.

The observation that, following body-to-head displacement, the P-cell S_{\max} vector rotated, on the average, by the same angle and in the same direction as the body, could explain why functional inactivation of the cerebellar vermis may greatly reduce the rotation of the response vector of the forelimb extensor triceps brachii observed following body-to-head displacement (27). Changes in the spatial properties of P-cell responses may, in fact, promote similar modifications at the level of VS and reticulospinal neurons, thus affecting the motor output (17, 35). While the average directional changes of the response vector were related to the amplitude and direction of body displacement, the changes in temporal phase, gain and tuning ratio were not. However, three basic patterns of modifications could be observed at single unit level for all the response parameters investigated. These findings suggest that all the response modifications due to body displacement may arise from a common neuronal mechanism and support the hypothesis that, in some way, the neck input modifies the gain of different vestibular input channels impinging on P-cells, thus finely tuning their responses to the labyrinthine input. It is of interest that body-to-head rotation could modify in a specific way the convergence on the same cells of vestibular signals endowed with different spatial and temporal properties, as indicated by the observed changes in tuning ratio. It may well be that the large degree of spatiotemporal convergence of vestibular signals on P-cells could represent a fundamental mechanism that allows the cerebellar cortex to modify the response pattern to afferent stimulation according to specific regulatory inputs.

When the animal's body and head are aligned along the same axis, the population response (vector) of vermal P-cells is a very good predictor of the tilt direction (26, 34). The changes in the response vectors of P-cells to labyrinthine stimulation, observed in the cerebellar cortex following 30° of body-to-head displacement, may effectively modify the information about the direction of head tilt coded by this neuronal population. In this instance, the direction of the population vector does not correspond to that of *head* tilt, but appears to be related to that of *body* tilt. This result was obtained under the assumption that a given spatially tuned P-cell (either broadly or narrowly tuned) would always signal the same direction of tilt (i.e. promote the same postural adjustment), whatever the relative body-to-head position could be. This hypothesis is physiologically meaningful, since it is likely that the content of directional information coded by a cerebellar unit will depend upon its pattern of connections to nuclear neurons, which should not be modified by body displacement.

Possible spinal mechanisms.

The changes in spatiotemporal characteristics of the P-cell responses to vestibular stimulation following body-to-head rotation seem to be critical for the change of reference frame (from head to body) occurring in the labyrinthine-induced motor response, which is strongly dependent upon the proprioceptive neck input.

It has been postulated that such changes could, in part at least, depend upon pre-cerebellar structures, such as the lateral reticular (21) and the central cervical nucleus (41), where convergence and interaction between neck and vestibular inputs occur. There is, in fact, evidence that small amplitude neck displacements powerfully affect the excitability of these precerebellar neurons (21), possibly modifying their ability to transmit vestibular information to the cerebellar cortex through mossy fibers.

A recent theoretical paper by Mergner and Rosemeier (31) has proposed that the human postural control can rely upon different frames of reference, which are implemented by a process of multisensory integration, according to the scheme illustrated in Figure 4A. In particular, the interaction of signals from the labyrinth (related to head movement in space) with those arising from the neck (head-to-body movement) leads to a body-in-space signal (box A), which can be further integrated in a cascade process (boxes B and C), with somatosensory and proprioceptive inputs signalling the relative position of the different body segments. This "down channelling" of information will ultimately lead to a neural signal related to the movement of foot (and related support) in space. Starting from information related to foot contact, this chain can be also followed in the opposite direction ("up channelling"), ultimately leading to signals related to the movement of the head with respect to the support. These signals can be relevant for postural stabilization. Figure 4B shows that this model may have a neurophysiological counterpart. As pointed out by Mergner and coll. (30, 31), at any level of the spinal cord VS volleys converge on crossed ascending spinoreticular neurons which project to the lateral reticular nucleus (LRN) (9) and receive volleys from flexor reflex afferents (15). These volleys utilize both group II and group III cutaneous and proprioceptive muscular afferents (12). Since the lateral reticular nucleus project to the cerebellar anterior vermis, including lobules IV-V (17), this cerebellar region could then receive vestibular signals which have undergone a transformation by interacting with proprioceptive volleys at all the levels of the spinal cord, thus becoming appropriate to the goal of body stabilization. Finally, this information can be fed back from the cerebellar cortex to the lateral vestibular and fastigial nuclei, which are "executive" relay stations for VS reflexes. The loop shown in Figure 4B may actually represent only one of several loops by which non-vestibular information is processed with the vestibular signals. The role of the cerebellum in these loops would be to bring together the various pieces of sensory information in creating the appropriate spatial reference for the postural reflexes.

Role of the cerebellum in sensorimotor transformations.

As stated in the Introduction, vestibular, visual and proprioceptive neck signals, driving the postural reflexes aimed to body stability, bear only an indirect relation to body position. In other words, these sensory signals are coded in a reference frame, which do not correspond to that of the reflex response (40). In order to stabilize the body, a shift in the reference frame is therefore necessary in the flow of information from the sensory to the motor networks.

Sensorimotor transformations characterized by changes in the reference frame

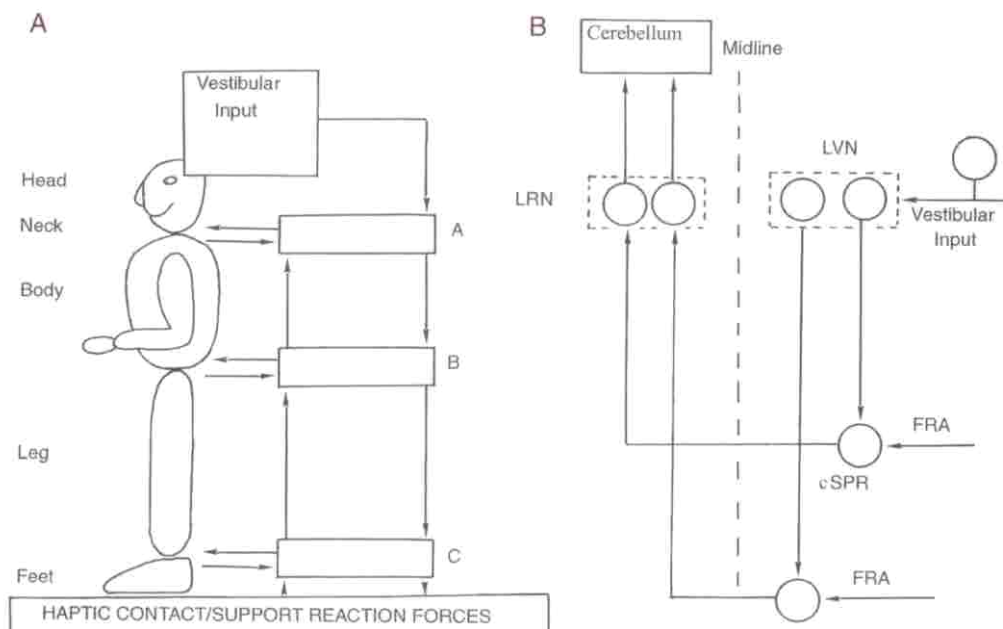


Fig. 4. - Postural control model proposed by Mergner and Rosemeier (A) and its possible neurophysiological counterpart (B).

A. Schematic form representing a four-segmented body. Horizontal arrows represent information arising from motion at specific joints and the efferent control of the same joints. Box A represents an integrative site for neck and vestibular signals. Boxes B and C are sites of further integration with proprioceptive information arising from lower joints.

B. Schematic illustration indicating convergence of vestibular and somatosensory information on neurons of the crossed spino-reticulo-cerebellar pathway. LRN: lateral reticular nucleus; LVN: lateral vestibular nucleus; cSPR: crossed spino-reticular neurons, FRA: flexor reflex afferent.

also occur in the context of oculomotor reflexes, such as the post-rotatory vestibular (2) and optokinetic (10) nystagmus. It appears, in fact, that when the orientation of the head in space is suddenly changed at the end of a constant velocity rotational stimulus acting in the horizontal plane, a reorientation of the direction of post-rotatory nystagmus may occur. In particular, the axis of eye rotation shifts, so as to realign itself with the vertical. In this case, while the semicircular canal's input is related to an head-centered reference system, the oculomotor response is organized in a reference frame aligned with gravity. This transformation seems to depend on otolith afferents (2). On the other hand, voluntary reaching movements, towards precise points of the surrounding space, can occur by means of proprioceptive eye and neck signals, which allow to relate retinal information to head and body position (37, 40). Theories about cerebellar function suggests that this structure is critical for the changes of reference frame occurring in the sensorimotor transformations related to voluntary movements (5, 33). It is known that, in the monkey, the macular input utilizes the vestibulocerebellum in order to transform the ampullar input, related to a

head-centered reference system, into an oculomotor response organized in a reference frame aligned with gravity (2). Finally, the results described in the present report indicate that the cerebellar cortex modify the reference frame for VS reflexes (27). On the basis of all these arguments we may put forward the hypothesis that the integrative process occurring within the cerebellum allows to establish the correct relation between sensory inputs and motor responses, both in the context of voluntary as well as of reflex movements. It is possible that this function is implemented through the fine tuning, by appropriate regulatory signals, of multiple input channels impinging upon P-cells. This process would modify the changes in activity of these neurons during voluntary and reflex motor behaviour, generating appropriate changes in the final motor output.

SUMMARY

It is known that proprioceptive signals modify the spatial organization of the postural reflexes, thus leading to body stability. The neurophysiological basis of this phenomenon are at present unknown. The present report documents that, in decerebrate cat, body-to-head rotation in the horizontal plane modified the preferred response direction to labyrinthine stimulation of the forelimb extensor triceps brachii. Such direction resulted always perpendicular to the longitudinal body axis of the animal, whatever its relative position with respect to the head could be. The rotation of the preferred response direction of the triceps was greatly reduced by functional inactivation of the ipsilateral cerebellar vermis. On the other hand, following body-to-head displacement, the preferred response directions of the corresponding P-cells tended, on the average, to rotate in the same direction and by the same angle as the body.

We propose that the neck input finely tunes parallel vestibular channels, endowed with different spatial and temporal properties, impinging upon P-cells, thus modifying their responses to animal tilt and, as a consequence, the spatial properties of VS reflexes. It is possible that, by a similar mechanism, the cerebellum may contribute to the changes in reference frame occurring in sensorimotor transformations of reflex and voluntary nature.

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