

The Role of Vision in the Control of Posture During Linear Motion

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The purpose of this paper is to review some findings concerning the role of vision in the control of posture which have been obtained in recent years. We shall first present a short summary of the main ideas which were proposed by other authors and then describe some results obtained in our laboratories concerning more specifically the effect of vision on postural control during linear horizontal or vertical motion of either body or visual surround.

FREQUENCY DOMAIN OF THE INFLUENCE OF VISION IN POSTURAL CONTROL

The role of vision in the control of stance, locomotion, and compensation of various sensory defects such as labyrinthectomy has been known since the pioneer works of early researchers such as Flourens, Purkinje, De Cyon, Magnus etc. It was also described by neurologists such as Thomas (1940) at the beginning of this century. These early works have been reviewed recently (Dichgans and Brandt, 1978; Courion and Jeannerod, this volume, chapter VC4). The specific role of vision in the control of upright posture was demonstrated by many authors (Travis, 1945; Edwards, 1946; Rademaker and Ter Braak, 1948; Wapner and Witkin, 1950; De Haan, 1959) and it was suggested to contribute to locomotory pattern (Davis and Ayers, 1972). In the last ten years methods of frequency analysis of biomechanical parameters of balance, together with recordings of muscular activity, have helped to obtain information concerning the precise dynamics of visual-postural interaction (Baron and Litvinenkova, 1968; Gurfinkel and Elner, 1971; Cernacek and Jagr, 1972; De Wit, 1972; Gantchev et al., 1973; Litvinenkova and Hlavacka, 1973; Walsh, 1974; Bles and De Wit, 1975).

We owe to Gibson (1952, 1958, 1966) a most stimulating theory integrating vision in the overall function of proprioception. In line with this theory the stabilizing role of whole field complex visual scenes was elegantly demonstrated by Lee and his collaborators (Lee and Aronson, 1974; Lee and Lishman, 1974) who showed: a) that small movements of a swinging room surrounding a standing human induce postural oscillations unnoticed by the subject which are particularly great in infants (a finding later confirmed by Brandt et al., 1976, for roll motion, with the additional information that the effect peaks around 3–4 years of age, decreasing up to 16 years); and b) a

clear difference between active and passive relative motion between subject and visual surround.

The importance of visual cues was also evaluated by Amblard and Cremieux (1976). In standing humans, destabilization could be induced by stroboscopic illumination at low frequency (3 Hz). This result was interpreted according to the hypothesis that when visual cues are available, they dominate other vestibular or proprioceptive cues. Velocity information is required, however, to efficiently stabilize posture. Stroboscopic light at low frequency only provides position cues, hence, inducing a poor spatial reference.

A major contribution to these problems was offered by an extensive series of experiments performed by Dichgans with several coworkers, who studied thoroughly the stabilizing or destabilizing role of vision for circular movements. These authors placed this problem in the frame of visual-vestibular interaction proposing that "vision improves the speedometer function of the labyrinth in the low frequency range" (Dichgans et al., 1973).

A convenient method to describe the dynamic contribution of vision is to induce body oscillations by moving sinusoidally visual scenes in various directions. This frequency analysis was performed by several groups. Fig. 1 shows a summary of data obtained by authors who compared the subjective sensation of self motion (vection) induced by such scenes with the objective measure of body oscillations induced by

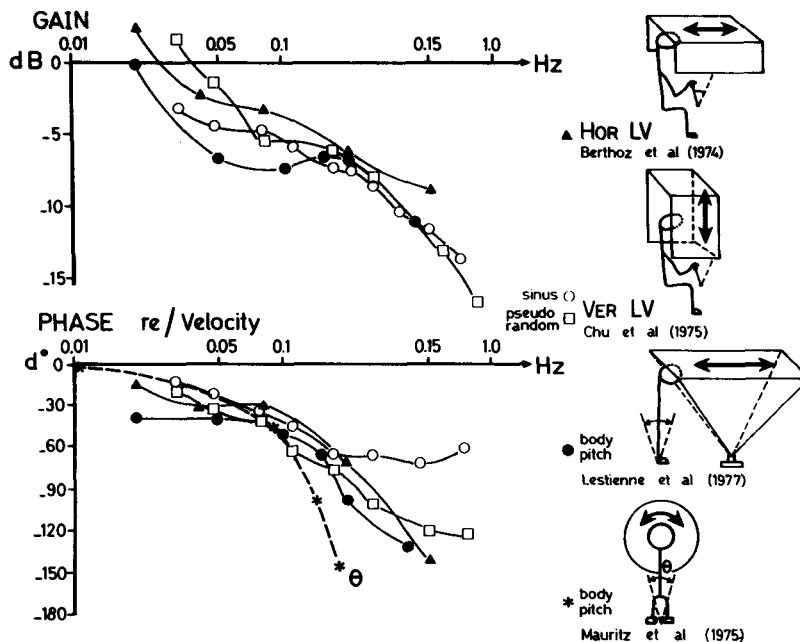


Fig. 1. Comparison between the frequency response curves for linear vection and for postural oscillations induced by moving visual scenes. Gain and phase of linear vection (LV) induced by horizontal and vertical sinusoidal (or pseudo-random) motion of the visual surround. Gain is the ratio between subjective magnitude estimation of LV and visual surround velocity. (From Berthoz et al., 1974; and Chu and Young, 1975.) These subjective evaluations of LV are compared with body pitch induced by visual scenes moving in the horizontal plane (Lestienne et al. 1977) or around the line of sight (Mauritz et al. 1975). In this case the gain is the ratio between body angle θ and visual surround velocity.

visual surround motion. The magnitude estimation curves for horizontal linear vection induced by horizontally moving visual scenes obtained in a seated subject (Berthoz et al., 1975), are plotted and compared with those obtained by Chu and Young (1975) with both sinusoidal and pseudo-random visual surround velocity. Gains have been plotted on an arbitrary scale in order to show the general shape of the slope. In both cases gain and phase indicate vection magnitude estimates vs. image velocity. The two sets of curves are strikingly close although they do not account for a number of important features such as forward-backward or up-down asymmetries which have also been reported by these authors.

It is interesting to note that the curves which represent body pitch induced by linearly moving visual surround (Lestienne et al., 1977) fall very close to the vection curves. This coincidence does not however preclude a dissociation between the two effects (pitch and vection) and subjects may also report vection without postural change, or change their posture without reporting vection. The phase curve obtained by Mauritz et al. (1977) for body pitch induced by roll vection has been plotted for comparison. It also falls within the same range supporting the *general statement of a role of vision in the low frequency range (0–0.2 Hz)* which has been suggested both by linear and circular vection experiments.

Similar conclusions have been reached by Talbott (1974) and Talbott and Brookhart (1976, 1978) by studying the postural response of the dog to horizontal fore and aft motion of visual surround and of the platform on which the animals were standing. They also conclude that the visual component of sensory information may play a dominant role in balance. Inducing a dynamic conflict between information derived by visual pathways and that derived via other sensory pathways by submitting the dog to conflicting visual and body motion, they found a “variable visual gain.” For instance, if visual field motion is at 0.3 Hz and platform motion is at 1 Hz, the 0.3 Hz component of the dog’s destabilization is more than 10 times that which would be expected on the basis of the response to a 0.3 Hz motion of visual surround given in isolation. In a recent series of papers which are still in press, these authors have demonstrated that peripheral vision is essential in these effects as indicated by both studies using lesions of visual cortex (Mirka et al., 1978) and selective occlusion of parts of the visual field.

In our laboratory the difference between visual field motion given in isolation and/or in combination with linear acceleration has been investigated in standing humans and we shall now describe briefly the essential conclusions of this work.

DYNAMIC EFFECT OF VISION ON LOW FREQUENCY PERTURBATION OF POSTURE

In a previous series of experiments (Lestienne et al., 1977) we have studied the effect of moving visual scenes on the control of posture. These experiments have demonstrated that linear motion of a visual scene induced, in standing humans, postural readjustments observable as a body pitch in the direction of image velocity. The amplitude of the change in body “vertical” was related to the velocity of the visual scene, but also more surprisingly, to its spatial frequency. We suppose that these visual effects may be of even greater magnitude during combined body and visual motion.

The experimental set-up which was designed to verify this assumption is shown in

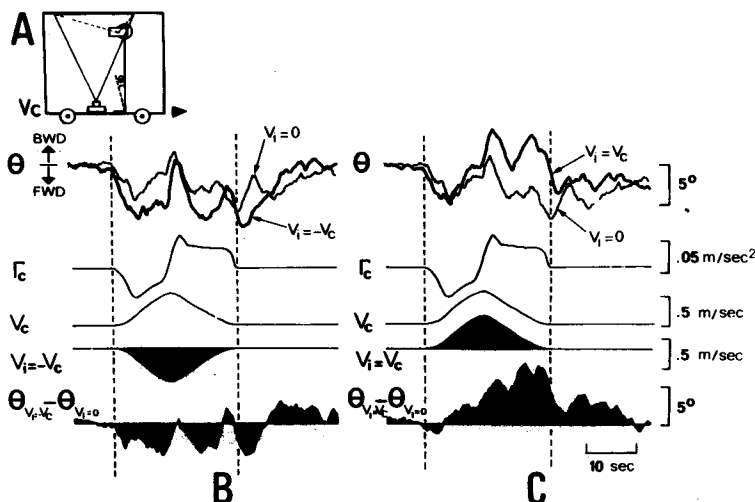


Fig. 2. Influence of linear motion of visual surrounds in response to postural perturbation. A) Experimental set-up: The subject stands erect on a moving platform. The angle of head and body pitch is measured by a potentiometer fixed to the head by means of a rod and crank attachment. An image moving at velocity V_i is projected on the screen which is placed horizontally above the subject as described in Lestienne et al. (1977). Lightweight cardboard blinders obliterate the lateral and inferior aspects of the visual field and permit the subject only a view of the screen S. This ensemble is placed on a cart which can move at velocity V_c . Triangular analog signals are used to drive the cart. The traces in B and C show the average pitch θ of 8 subjects in three experimental conditions. In all three conditions the cart moved in the backward (BWD) direction with a peak velocity $V_c = 0.05 \text{ m/sec}$ and peak acceleration $\Gamma_c = 0.05 \text{ m/sec}^2$. The light traces in B and C were obtained when the image was stationary with respect to the cart ($V_i = 0$). The dark trace in B was obtained when velocity was in a direction opposite to cart velocity ($V_i = -V_c$) and thus stationary relative to the ground. The dark trace in C, when image velocity was in the same direction as cart velocity ($V_i = V_c$). The difference of pitch θ in the two conditions for B and the two conditions for C are shown (lower records). (From Soechting and Berthoz, 1979.)

Fig. 2A. The subjects stood erect on a platform attached to a mobile cart which was driven by servo-controlled torque motors. It was enclosed on all sides. The subject wore lightweight cardboard blinders which blocked the lateral and inferior aspects of their visual field and permitted only restricted views of the cart's ceiling. Details concerning this method are given by Soechting and Berthoz (1979). The visual scene consisting of a black-and-white checkerboard pattern was projected on the ceiling using a film projector and mirror. Accurate control of both image and cart velocity allowed a very precise definition of these stimuli. The subject's pitch angle forward or backward was calculated by potentiometric methods assuming that for these small angles the body was equivalent to an inverted pendulum. This hypothesis was discussed in Lestienne et al. (1977) and has been shown to be a rough but sufficient approximation in the perspective of this work.

Fig. 2B shows records of body pitch θ when the cart accelerated suddenly backward (see acceleration trace Γ_c) which was induced by a triangular waveform of velocity V_c . Three conditions of visual surround motion were used. In the first case the velocity of visual images was zero ($V_i = 0$). The visual surround was moving together with the cart, which is equivalent to riding inside a closed illuminated vehicle. This condition was used as a control by comparison with the case when the visual scene motion was a)

opposite to cart velocity ($V_i = -V_c$) as in "natural" motion (Fig. 2B), and b) equal to cart velocity ($V_i = V_c$) which is a "conflict" situation (Fig. 2C). The records of θ in Fig. 2B, which are averaged curves, show that a clear difference (statistically significant), exists between the two visual conditions $V_i = 0$ (thin lines) and $V_i = -V_c$ (dark lines), although in both cases θ seems to follow the general waveform of acceleration Γ_c .

The difference between the two traces has been plotted in the lowest curve ($\theta_{V_i = -V_c} - \theta_{V_i = 0}$). It is in the direction of visual image motion (compare dark triangle of image velocity V_i with darkened surface of curve). A similar comparison was made when a conflict was induced between image and cart motion. Fig. 2C shows records obtained when $V_i = 0$ and $V_i = V_c$. The influence of visual surround motion is very striking and once more in the direction of image motion. Statistical calculations and precise quantitative measures of peak body pitch have revealed that the effect of visual surround is about twice as great when visual surround and body motion are combined, a finding very much in accordance with the results of Talbott and Brookhart (1976, 1978).

The frequency spectrum of cart and image velocity stimuli given in this series of experiments did not exceed about 0.2 Hz. Consequently, the conclusions drawn from these results are in keeping with the general idea that vision plays a stabilizing, or destabilizing role in the low frequency range. We shall now however, describe some results which have challenged this conclusion and suggest that during rapid postural movements vision may be an essential component of the sensory systems contributing to adequate motor activity.

CONTRIBUTION OF VISION TO RAPID MOTOR REACTIONS DURING POSTURAL PERTURBATIONS

An experiment has been designed to demonstrate conclusively that manipulation of the visual surround, at the time of a rapid postural perturbation, could induce changes in early motor responses which were not predicted by most authors (Nashner and Berthoz, 1978).

The main idea of the experimental set-up, which is shown schematically in Fig. 3, was to suppress visual cues about body motion selectively and only at the very precise moment of a transient backward acceleration of a platform (cart) on which human subjects were standing. For this purpose a sliding box providing a visual surround was fixed to the frame of the cart. The velocity and position of the box could be controlled so that it could either a) move together with the cart, in this case subjects had normal (N) visual cues concerning motion of their body inside the cart (this is equivalent to situation $V_i = 0$ in Fig. 2), or b) be stabilized (S) with respect to the head through a servo-controlled motor so that at the time of onset of the acceleration, minimal relative motion would occur between head and box, thus suppressing visual motion cues.

Surprisingly visual stabilization induced a striking increase in body pitch and a strong decrease in the earliest motor reaction measured by electromyogram in the triceps surae. This result was at odds with all previous results obtained during free fall in man (Matthews and Whiteside, 1960; Greenwood and Hopkins, 1976, 1977; Melvill-Jones and Watt, 1971), in the monkey (Lacour et al., 1978), or in the cat

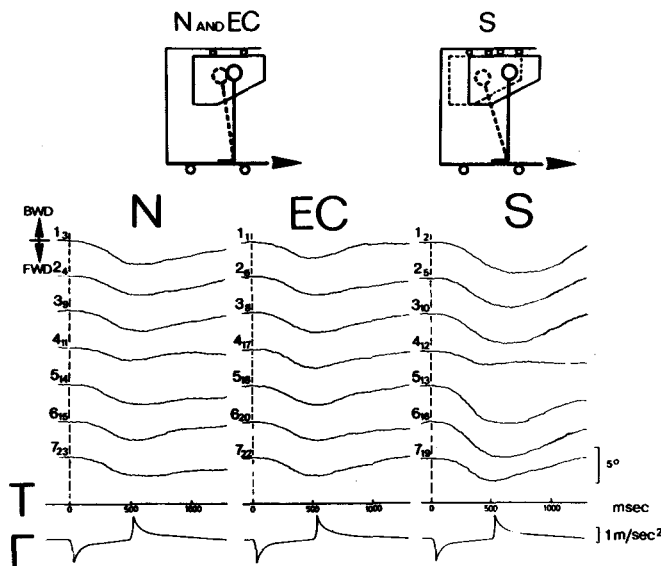


Fig. 3. Influence of stabilized visual surround on body pitch following a perturbation of posture. The experimental set-up has been described by Nashner and Berthoz (1978). The subject is standing on a moving platform which accelerates backward with an acceleration profile Γ . The visual surround is the inside of a sliding box with a high spatial frequency pattern, which is also controlled by a motor and can be either moving together with the cart (N) or translating together with the head (stabilization of visual surround with respect to head) (S). A potentiometer records horizontal fore and aft head motion and controls the movement of the box. A computer and a drive and hold device synchronizes platform (cart) and box motion so that in the case of stabilized condition S, the visual information about body motion is only suppressed at the onset of the perturbation. Body pitch, (backward: BWD; forward: FWD) measured by the potentiometer, is shown in the normal (N), eyes closed (EC) and stabilized (S) conditions. Numbers on each record give the order of the randomized presentation in the experimental sequence. Note the small increase in body pitch in EC condition and the large destabilizing effect of visual stabilization. (From Vidal et al., 1979b.)

(Watt, 1976). All of these authors had compared motor responses occurring previous to, or at the time of landing, and had concluded that there was an absence of vision contribution because repeating the experiments with both eyes closed or in darkness induced similar responses.

In order to study more precisely this question we have recently repeated (Vidal et al., 1978, 1979a, b) our experiments and compared the three conditions as defined above: normal (N), eye closure (EC) and stabilized vision (S). We shall now summarize briefly the main findings of these experiments.

Fig. 3 shows recordings of head displacement (forward and backward) used as a rough estimate of body pitch during a sudden backward acceleration of the cart on which the subject is standing. When the subject has his eyes closed, a small increase of destabilization is evidenced. During visual surround stabilization (S) a striking increase of body pitch occurs.

Quantitative evaluation in which difference in maximum body pitch in the three conditions, N, EC, and S, gives about 5% mean difference (SD, 13%) between N and EC and about 40% difference between S and N (SD, 2%). The underlying muscular response was measured in the triceps surae by standard surface electromyography (EMG). Some example of records are shown on Fig. 4 in which detected and inte-

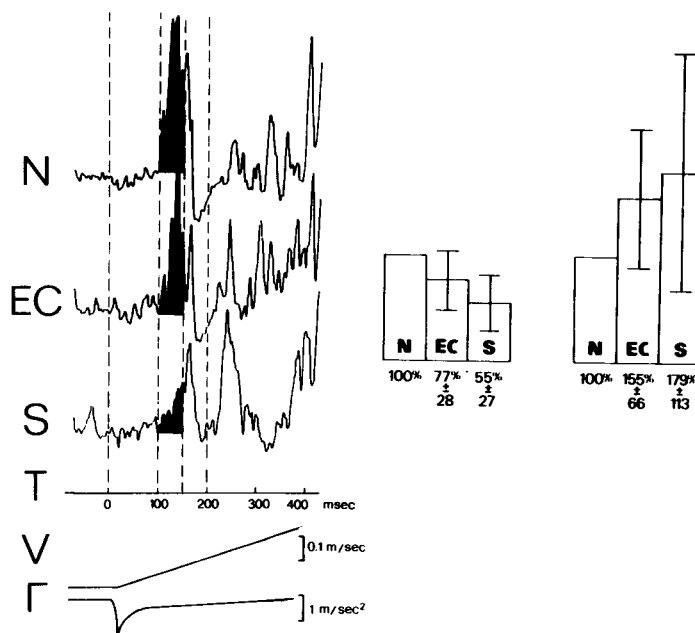


Fig. 4. Influence of stabilization of visual surround on muscle response to a sudden perturbation. Standing subjects are placed in the experimental situation described in Fig. 3. The records show the integrated electromyographic (EMG) activity in the extensor of the ankle (triceps surae), before and immediately after a sudden backward motion of the cart on which the subject is standing (mean value for 3 trials of one subject). The parameters of motion are given by the time scale (T), the velocity of the cart (Vc) and its acceleration (Γ). N, EC and S refer to "normal", "eyes closed" and "stabilized" conditions as defined in Fig. 3. The mean and SD of the surface EMG between 100 and 150 msec (histogram) after the onset of the linear acceleration are shown on the right for 7 subjects. Values are given for each trial and each subject by comparison with the value in the N case (From Vidal et al., 1979b).

grated EMG was obtained in the three conditions, N, EC and S, in the same experimental conditions as those of Fig. 3. Eye closure does not change significantly the first motor response which occurs at a latency of about 100 msec. This large phasic response which is necessary for an efficient maintenance of posture following the perturbation is indeed similar in both cases and most authors have taken argument of this result to negate any role of vision at this early stage. However, as shown by Nashner and Berthoz (1978), and exemplified again in the bottom record of this figure, when visual information about head motion is selectively removed, this early motor reaction is decreased and in this case nearly suppressed.

The statistical measurements shown in the right part of the figure show the average amplitude of the decrease in early EMG component (100–150 msec) which is measured by calculating the surface of integrated EMG. Notice that parallel with this decrease, an increase in amplitude of the subsequent EMG appears in the S condition. This finding is to be compared with the results of Amblard and Crémieux (1976) who, in steady state low frequency stroboscopic illumination, obtained a strong destabilization. The essential point of our result is that visual cues about body motion are only removed at the onset of the perturbation and that other changes in visual parameters are modified.

Having thus demonstrated that visual motion cues have a not yet fully understood, but definitely powerful role in the release of an adequate motor pattern in these conditions of dynamic equilibrium, we were tempted to see whether a similar modification could be induced during free fall. As the basic characteristics of motor activity during free fall had been established in the baboon by Lacour et al. (1978) we designed an experiment to verify whether visual stabilization could also modify early motor responses to which had been attributed a pure vestibular (otolithic) origin.

MODIFICATION OF EARLY MOTOR RESPONSES BY VISUAL STABILIZATION DURING FREE FALL IN THE MONKEY

The experimental set-up for the study of free fall in the baboon (*Papio-Papio*) is shown in Fig. 5. Total height of the fall was 90 cm. The details of the experiments are described in Lacour et al. (1978). In addition the head of the monkey could be placed in a box which could either provide total darkness, or be illuminated by a small light bulb. A checkerboard pattern of black and white squares whose properties had been studied in Lestienne et al. (1977) was placed inside the box. Fig. 5, modified from Lacour et al. (1978), shows the basic pattern of muscular activity encountered in the extensors of the leg during the fall with normal visual cues (monkey falling in the laboratory without box). It must be emphasized that in this case no landing occurs and mainly vestibular, visual and probably also pressure tactile cues are signalling perti-

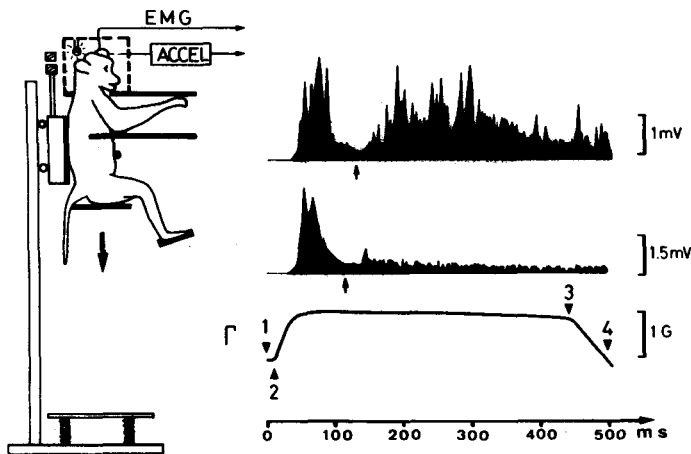


Fig. 5. Experimental set-up and basic responses for the study of motor reactions in the baboon during free fall. A) Experimental set-up: the monkey (*Papio-papio*) is seated on a chair which can slide down on rails. The chair is maintained in an initial position by electro-magnets. The head is restrained by four hard plates preventing major lateral or vertical head movements and the body is in a plaster cast. The fall occurs either when the monkey is: a) viewing the laboratory (normal condition (N)), b) when a box is surrounding the head (complete darkness (D)), c) when a light illuminates the inside of the box which is covered with a high spatial frequency checkerboard pattern. (Visual surround is stabilized with respect to the head (S).) Landing is smoothed by elastic springs. B) Typical detected and integrated electromyogram from the soleus muscle during free fall (average of . . . trials for . . . monkeys). The records show the responses obtained during the first (top record) and the 10th (bottom record) fall of an experimental session. Γ is the vertical acceleration record. Arrows indicate initial trigger (1) actual release of the chair (2), and deceleration (3,4). (Modified from Lacour et al., 1978.)

nent information concerning the fall (practically no neck flexion or extension was allowed by restraint). The top record shows two components of EMG. The first one was shown by Lacour et al. (1978) to be composed of two subcomponents. The long-lasting second component disappears when repeating the fall (lower record is taken after repetition of the fall). It is probably related to the preparation of landing and is suppressed by the monkey. The first rapid component was shown to disappear with bilateral labyrinthectomy by Lacour et al. (1978) and consequently thought to be essentially of otolithic origin. Similar conclusions were drawn by Watt (1976) concerning the motor discharge in gastrocnemius of the cat which occurs about 70 msec after onset of free fall, by Melvill-Jones and Watt (1971) for the 75 msec latency discharge in human gastrocnemius after sudden release of subjects hanging to the ceiling, and Greenwood and Hopkins (1976, 1977) for the responses occurring at about 72 msec in quadriceps, 82 msec in soleus and 81 msec in tibialis of their human subjects during free fall. These last authors attributed the earliest response to a startle-like response as it also disappears when the subject makes a voluntary release. Influence of blindfolding after landing in the cat is studied by Lewis et al. (1979).

The results of comparison between free fall in normal (N) visual conditions, in total

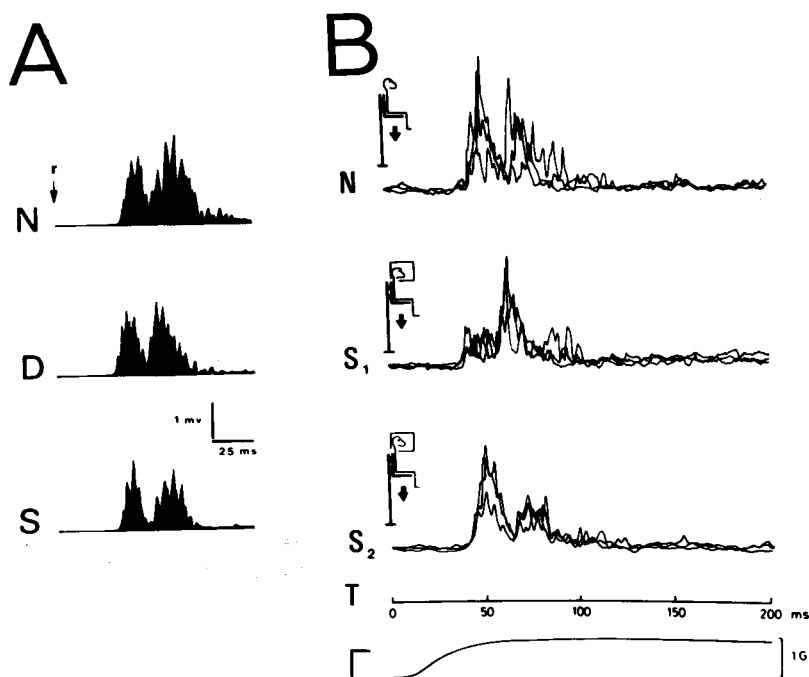


Fig. 6. Decrease of initial motor response in the soleus muscle of the monkey with visual stabilization. Detected and integrated electromyograms of the soleus muscle in the falling baboon (see Fig. 5 for methods) in three conditions: N: normal visual condition (falling in the laboratory); D: darkness; S: stabilized vision. A) Average records from one monkey (90 trials) showing the moderate decrease in the early response in darkness and the strong decrease in S condition. Arrow indicates instant of release which is about 4–8 msec before actual onset of acceleration. B) Typical records of soleus EMG in another monkey for three conditions: N: normal visual condition (falling in the laboratory); S1: three superimposed records in which the first component earliest peak of activity was nearly suppressed; S2: three superimposed records in which both components of earliest peak were decreased but the second was more clearly suppressed. Bottom trace indicates vertical acceleration record Γ . (From Vidal et al., 1979.)

darkness (D) and with visual stabilization are reported in Fig. 6. Recordings were made in various groups of muscles (splenius capitis, soleus, tibialis anterior, quadriceps femoris). In all of them a statistically significant decrease of amplitude (as much as 30%) of the earliest component occurs (Vidal et al., 1979a). An example concerning the soleus is shown in Fig. 6A. In complete darkness (D) the overall amplitude of the EMG response is also decreased although, in some instances, the response is not significantly different from the N condition.

Fig. 6B shows a detailed description of typical records in which the decrease of EMG during stabilization affected either the first or the second subcomponent of the response. This suppression is clearly as powerful as the one described above and in other publications (Nashner and Berthoz, 1978; Vidal et al., 1978b) for the standing man during postural perturbation.

This result demonstrates that, even if there is an important otolithic contribution to the genesis of these early motor responses, the visual surround motion when eyes are open is an important factor in at least determining the gain of the released motor activity. It is not possible at this stage to determine more precisely the nature of this influence.

DISCUSSION

The above results suggest that during linear motion vision is essential not only to regulate the general tone of muscles in the low frequency range, but also to release adequate motor reactions during sudden changes in posture. They also show that the dynamic role of vision has to be studied in conditions when it is a relevant cue as discussed by Granit (1978) on a more general basis.

In spite of the extensive amount of interest raised by the study of postural control recently, the pathways and underlying mechanisms by which vision influences the general motor system are still mostly unknown although a number of possible pathways are suggested by animal investigations (see other contributions in this volume). Most of the available neuronal data concerning visual-vestibular interaction concerns angular rotation and little information has been obtained for linear motion except from the work of Daunton and Thomsen (1976).

The idea that changes in visual surround may modify efferent motor reactions within short latencies is confirmed in the present results, and is compatible with the known latencies after which visual stimulation can influence discharge of neurons in brain stem structures (Baker et al., 1976; Azzena et al., 1977; Keller and Precht, 1979).

It could be argued that the "stabilized vision" condition is artificial and places the subject or the animal in a discordant set of sensory inputs which leads to an unspecific "hold reaction" and a generalized suppression of motor activity. Although this is a possibility, we would rather prefer another interpretation and propose that at the time of the rapid selection of an adapted motor pattern, the release of the adequate motor synergies is dependent upon an expected pattern of congruent sensory inputs (Nashner and Berthoz, 1978). Thomas (1940) had proposed a theory by which once a motor pattern would be learned using a number of sensory cues, any of these would be sufficient to trigger this pattern. This theory would also predict that absence of an essential cue could prevent the onset of the reaction.

We know in vestibulo-ocular physiology, that the sudden appearance of a visual

surround, stable with respect to the head of man, monkey or cat, can induce a very rapid suppression of a previously existing vestibular nystagmus (Takemai and Cohen, 1974a, b), which is mediated by visual pathways which through the cerebellum exert a powerful inhibition of the vestibulo-ocular reflex. Our results on posture suggest the existence of a visuo-motor equivalent to the pursuit system which, in the case of eye movements, is responsible for this suppression.

Posture, in this frame, cannot be differentiated from movement and any posture would have to be studied as preparatory to a movement. The question of why the motor reactions have been found to be similar with eyes closed and eyes open cannot yet be precisely answered. It could be proposed that closing the eyes or blindfolding induces a change in the gains of the various segmental sensory motor loops, allowing the maintenance of the same motor performance, but with very different "settings" (see also Gurfinkel and Shik, 1973). However Greenwood and Hopkins (1976, 1977) have tested segmental reflex gains and found no significant difference between eyes open and blindfolding conditions. This point deserves further clarification but we would favor an interpretation which would hypothesize such reorganizations.

Granit has made, in the Sofia Symposium on motor control, a statement which seems particularly adequate to this point: "If a measured response is uninfluenced by the loss of one source of information, it is hardly possible to conclude that this particular source, under any circumstances, could not have contributed to it. Remaining pathways to the central interpreter suffice to throw sentient circuits into action." The logical error, so elegantly denounced in this text, was probably the cause of an underestimation of the role of vision in the rapid control of posture.

SUMMARY

A review of the main theories concerning the influence of visual surround motion on the control of posture is presented. Gains and phases obtained by measuring either linear vection or body pitch induced by sinusoidal motion of visual scenes are compared. These curves seem to confirm the general statement that vision contributes to postural stabilization in the low frequency range of body movements (0 to 0.1–0.2 Hz). However, new experimental findings are described which show successively:

1. Direction-specific influence of visual surround motion when visual and body motion are combined, demonstrating also the enhanced effect of vision when active postural tasks are used.
2. The action of vision on the early motor responses to postural perturbation (within 100–150 msec of onset of perturbation). In this study eye closure is compared with visual stabilization which induces a 40% increase in body pitch.
3. A strong decrease of early motor responses during free fall in the monkey, which is shown to occur with visual stabilization within 50–100 msec from the onset of the fall. These results are interpreted as implying a role of vision in the general setting of the parameters of motor responses during posture and movement.

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