HUMANS use vestibular head-in-space information when redirecting gaze towards remembered target location in space. This study shows that neck input is also involved. Normal subjects performed saccades towards remembered locations in space of a previously seen target following passive horizontal rotations of the head or trunk. Saccades based on vestibular input alone fell short at low stimulus frequencies. Addition of neck input modified the responses, making them more accurate when the head was rotated on the stationary trunk. The results support a concept according to which vestibular input is channeled via proprioceptive coordinate transformations through the haptically perceived body support before yielding a sense of head motion in space. The loop is also involved in the saccadic gaze mechanism. *NeuroReport* **9**: 1469–1473 © 1998 Rapid Science Ltd.

Vestibular memory-contingent saccades involve somatosensory input from the body support

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Introduction

After a body-in-space movement, sensory information from different modalities is needed to redirect gaze to the location where an object was previously seen. Retinal signals provide us with a notion of the object's position relative to the fovea and an oculomotor efference-copy signal gives the eye's position in the head. However we also need to know head position in space. An abstract description of the problem would be to formulate coordinate transformations from a retinotopic via a craniotopic into spatiotopic reference frames, respectively.[1] It is generally accepted that the information on head motion in (inertial) space and on the head's orientation with respect to the earth vertical is mainly derived from vestibular cues. In fact, it has been shown that vestibular input is used when human subjects match the amplitude of a saccade to that of a preceding body rotation, when looking back to where a visual target had previously appeared.[2,3] In this 'vestibular memory-contingent saccade paradigm' the vestibular information is stored in, and retrieved from, working memory before being used to direct gaze in space.

However, psychophysical work on the human perception of head motion in space suggests that the vestibular input is complemented by proprioceptive inputs which signal relative motion between head, trunk and legs.[5,6] From this work, a 'down- and up-channeling' concept was formulated,[7] according to which (i) a version of the proprioceptive input is used to perceptually link the vestibularly derived space reference to the body support and (ii) a different version of the proprioceptive input links the head to the support. Both steps together yield a sense of head motion in space. The concept allows specific predictions to be made, one of which is that the proprioceptive effects only become evident in the low frequency range or at velocities where the signal transfer in the vestibular channel deteriorates (see Discussion). The present study addresses the question of whether the concept applies equally to the head-in-space information which is used for directing gaze. To assess this, we applied horizontal head and trunk rotations to normal subjects and studied the effect of vestibular and neck proprioceptive stimulation on memory-contingent saccades.

Material and Methods

Subjects: Six normal right-handed volunteers gave their informed written consent to participate in the study (four males, two females; mean age 36 ± 7.3 years). The experimental protocol was approved by the Ethics Committee of the Freiburg University Clinics and experiments were conducted in

accordance with the Declaration of Helsinki. Integrity of vestibular function was tested by conventional rotational tests in the clinical electronystagmography laboratory.

Stimulus and recording parameters: Subjects were seated on a Bárány chair with their heads fixed by means of a bite board to a head rotation device mounted on the chair. The set-up allowed horizontal rotations of each subject's trunk in space (TS) and, superimposed on this, of the head relative to the trunk (HT). While HT provided the neck proprioceptive stimulus, the sum of trunk-in-space and head-on-trunk rotations was used to generate the vestibular stimulus, i.e. head in space (HS = TS + HT). Four rotational stimulus conditions were applied: (i) Vestibular only (VEST): whole body rotation (HS = TS, HT = 0°), (ii) neck only (NECK): trunk rotation exactly matched by a counter-rotation of the head (TS = –HT) so that the head remained stationary in space (HS = 0°), (iii) 'synergistic' combination (VEST + NECK): rotation of the head on the stationary trunk (HS = HT, TS = 0°), and (iv) 'antagonistic' combination (VEST–NECK): superposition of head counter-rotation on a trunk rotation of double amplitude (HS = –HT, TS = –2HT).

Rotations of 16° amplitude were applied either rightwards or leftwards with the position profile of a smoothed ramp. The underlying velocity profile corresponded to a raised cosine function.[5] The dominant stimulus frequency was 0.1, 0.4 or 0.8 Hz (duration: 10, 2.5 or 1.25 s; peak velocity: 3.2, 13 or 26°/s, respectively). Four rotational conditions in the two directions and at the three different frequencies produced twenty four stimuli altogether, which were repeated four times for each subject on different days.

Instructions and experimental procedures: Figure 1 shows the experimental paradigm used for, in this particular case, a NECK stimulus. A light spot, subtending 0.2° of visual angle, was projected onto a cylindrical screen surrounding the chair. The spot could be moved horizontally at eye level by a mirror galvanometer. First, the spot was stepped 10° to either side by a computer generated signal fed into the galvanometer input and the subject was asked to set it straight ahead by means of joystick (second galvanometer input). Then the spot blinked twice, signaling the position in space to be remembered, and the galvanometer input was switched to a HS signal (electronically generated from potentiometer signals of chair and head rotation devices) so that the spot would remain aligned with the head. Prior to application of the rotational stimulus the spot was re-illuminated. Subjects fixated it while it was rotated together with the head, thereby suppressing reflexive eye movements in response to the rotational stimulus. When the rotation ended, the spot was extinguished and subjects had to redirect gaze to the remembered location where the spot blinked. Finally, subjects were rotated back to primary position in the dark without receiving feedback about their performance. The other rotational stimuli were applied in an analogous way. Two experimental series were performed: (a) 'Head-fixed target' series, the spot was illuminated during the rotational stimuli (as in Fig. 1), and (b) 'darkness' series; the spot was extinguished and subjects were rotated in complete darkness.
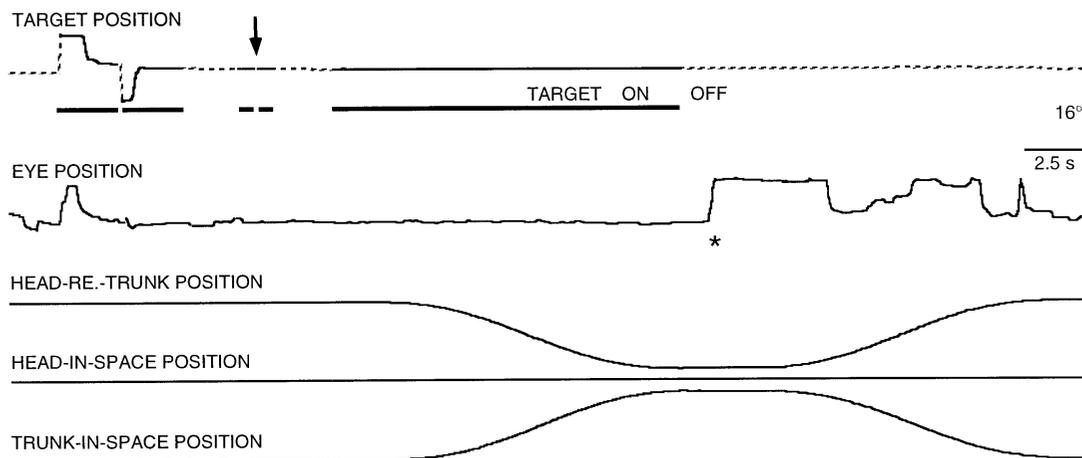

FIG. 1. Experimental paradigm (memory-contingent saccade paradigm). Example of a NECK stimulus trial from one subject (stimulus duration: 10 s, corresponding to a dominant frequency of 0.1 Hz). The subject remembers a target position in space (two target blinks; arrow), then is rotated while fixating the re-illuminated target which is kept aligned with the head during the stimulus (head-fixed target series), and finally, after stimulus end and extinction of the target, redirects gaze towards its previous location in space. Note that the rightward trunk in space rotation (upward) is matched by a counter-rotation of the head relative to the trunk, so that the head remains stationary in space, as does the target; the rightward saccadic response (asterisk) therefore is erroneous. Further details in text.

Horizontal right eye position was recorded using an infrared reflection technique (Iris System, Skalar, Delft, The Netherlands). Eye position calibration was performed with ±8° and ±16° steps of the light spot at the beginning and end of each recording session as well as after each fourth trial. This allowed any non-linearities in the eye recordings to be controlled and corrected.

Data acquisition and analysis: The positions of eye, chair, head rotation device, galvanometer (all in degrees) and the on–off signal of the light spot were sampled at 200 Hz by computer and stored on hard disk for off-line analysis. For analysis, eye position after the saccadic response (including correction saccades) was compared with eye position 300 ms after the spot blinked (difference taken as overall eye response) and with eye position immediately prior to the saccade (difference taken as saccadic eye response). Statistical significance was tested by analysis of variance (models specified below). Since no statistically significant difference was found for stimulus direction, the data for both directions were pooled. Statistics were performed on signed errors, which were defined as the difference between the actual and ideal responses. Precision of subjects' performance for a particular stimulus was defined as the s.d. across the four trial repeats.

Results

Overall eye response, head-fixed target series: Figure 2 presents in the left hand panels the raw data obtained for each frequency (6 subjects × 2 directions × 4 repeats; $n = 48$), separately for the four stimulus conditions. Following body rotation to the right (VEST), subjects made a saccade back to the left, thereby bringing gaze close to the spatial location of the previously seen target. Eye responses undershot the ideal value of 16° by a small amount at 0.8 Hz, by slightly more at 0.4 Hz and clearly more at 0.1 Hz. The corresponding mean values are shown in the panel on the right (full lines). Following rightwards NECK stimulus, subjects made saccades which were small and scattered about the primary position (the ideal value) at 0.8 Hz, but became larger and directed to the left at 0.4 Hz, and even more so at 0.1 Hz. Eye responses following VEST + NECK to the right were similar to those obtained for VEST, but did not show the undershoot at low frequency. Eye responses following VEST–NECK (Hs to the right, HT to the left) were directed correctly to the left at 0.8 Hz and 0.4 Hz, as with VEST and VEST + NECK, but were clearly shifted to the right at 0.1 Hz. Response precision averaged 2.8° across
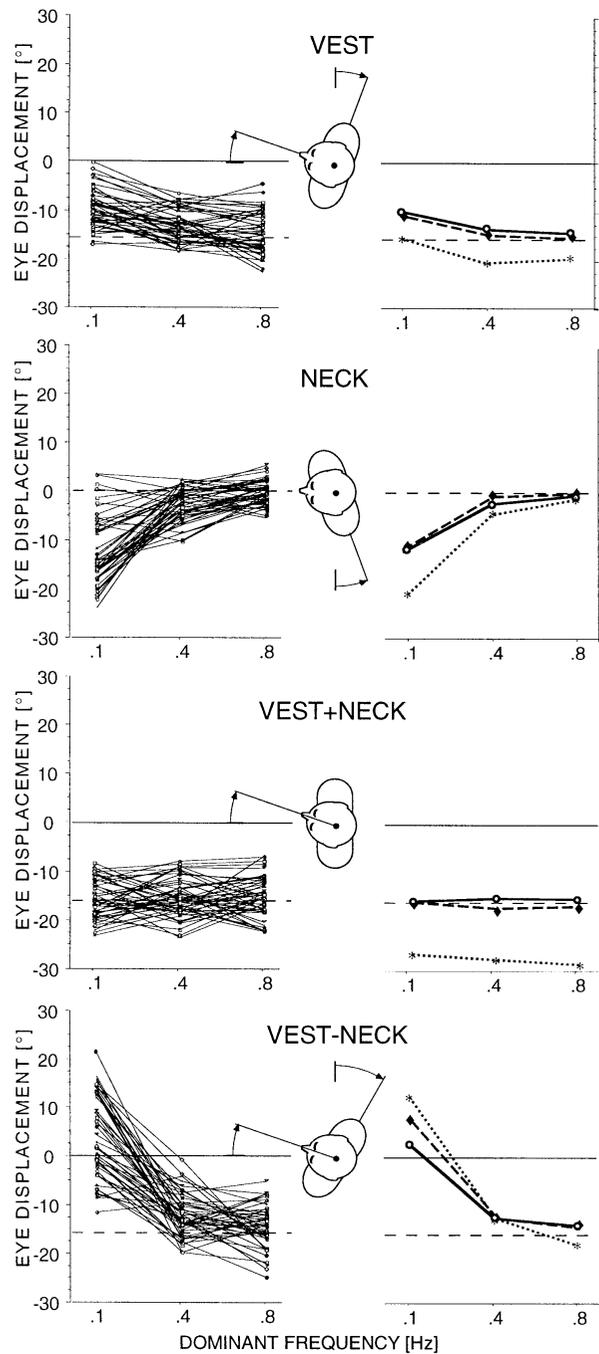

FIG. 2. Eye displacement in the four different stimulus conditions (VEST, NECK, VEST + NECK, VEST–NECK) as a function of stimulus frequency. The data are normalized with respect to stimulus direction (rightward VEST and NECK). Left panels show the individual overall eye responses for the head-fixed target series. The corresponding mean values are given in the right panels by full lines, together with those of the darkness series (overall eye responses, dashed; saccadic eye responses, dotted). Horizontal dashed lines give ideal (correct) responses. Insets give stimulus conditions in the form of pictographs (subject from above).

subjects, similarly for all stimuli, with the exception of NECK and VEST–NECK at 0.1 Hz where it amounted to 7.2° and 6.8°, respectively. Signed errors (mean values ± s.d. given in Fig. 3A) were compared

by a 4 × 2 × 3 ANOVA with condition (VEST, NECK, VEST + NECK, VEST–NECK), direction (left, right), and frequency (0.1, 0.4, 0.8 Hz) as the within-subject repeated measures factors. There was a highly significant difference for condition (F = 29.7, p = 0.0001) and for the interaction of the factors condition and frequency (F = 39.9, p = 0.0001).

Overall eye response, darkness series: The responses closely resembled those in the previous series. The mean response values are shown in Fig. 2, right panels (dashed lines). The same deterioration of precision and signed error values was seen at 0.1 Hz. Statistics on signed errors revealed no difference with respect to the head-fixed target series (p = 0.99).

Saccadic eye response, head-fixed target series: The results (not shown) were essentially identical to those obtained for the overall eye response in this series,
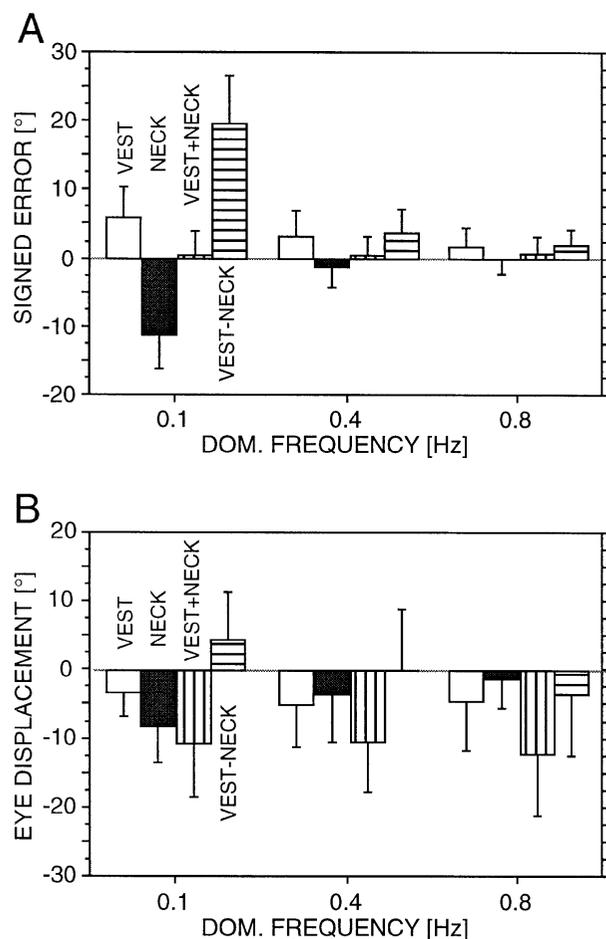
because subjects fixated the head-aligned spot during the rotation as required, thereby maintaining eye-in-head position approximately constant until immediately before initiating the saccade.

Saccadic eye response, darkness series: The saccadic eye response data (mean values in Fig. 2, left panels, dotted lines) clearly differed from the overall eye response data in this series (compare dashed curves) by a consistent amount across frequencies for VEST and by a larger amount for VEST + NECK. These differences were due to the net effect of slow and fast phases of reflexive vestibular and/or cervical nystagmus occurring during the rotational stimuli. Despite the fact that nystagmus modified the eye position, the subsequent saccades still reached their goal (the remembered target location), and the overall eye response was essentially the same as that in the head-fixed target series in which nystagmus was suppressed (see above). Thus, the nystagmic changes in eye position were accounted for by a corresponding change in saccadic amplitude. Mean values (± s.d) of presaccadic eye displacement are given in Fig. 3B; the largest displacement is found with VEST + NECK (statistical significant difference for condition, p = 0.01; ANOVA design as above).

Discussion

If the coordinate transformation from a craniotopic to a spatiotopic frame of reference in the memory-contingent saccade task depended solely on vestibular input, then proprioceptive stimulation at levels below the head should have no effect. However, our experiments clearly demonstrate that neck input does modify gaze shifts to remembered target locations in space, as we have postulated on grounds of the down- and up-channeling concept mentioned in the Introduction.

According to the concept, gravito-inertial forces on earth activate both vestibular receptors and somatosensory receptors (at the body site where ground reaction forces act) and the resultant sensory signals are linked to each other by proprioceptive coordinate transformations (in our experimental condition linkages are between head and trunk). Described in a simplified form, the down-channeling transformations first yield an internal representation of the trunk in space, ts = λHS – λHT (λHS reflects the magnitude of the vestibular signal, with λ representing the non-ideal vestibular transfer characteristics; λ < 1 at low frequencies/velocities. λHT stands for a version of the neck proprioceptive signal which centrally has been given the vestibular characteristics λ).[4,7] The subsequent up-channeling then yields an internal representation of the head in space which

FIG. 3. (**A**) Signed errors of overall eye displacement in the head-fixed target series for the four stimulus conditions (VEST, NECK, VEST + NECK, VEST–NECK) and the three stimulus frequencies (0.1, 0.4, 0.8 Hz). Note that error is largest with VEST–NECK (antagonistic stimulus combination) at 0.1 Hz. (**B**) Presaccadic eye displacement resulting from vestibular and cervical nystagmus (net effect across slow and fast components). The largest displacements are found with VEST + NECK. Mean values ± s.d.

can be measured in the form of the perception $\Psi HS = ts + HT$ (HT is ideal). It follows that $\Psi HS = (\lambda HS - \lambda HT + HT = \lambda HS + (1 - \lambda)HT$. From this equation the following predictions can be made: VEST yields $\Psi HS = \lambda HS$, NECK $\Psi HS = (1 - \lambda)HT$, VEST + NECK $\Psi HS = HT$, and VEST − NECK $\Psi HS = (1–2\lambda)HT$. Note that ΨHS is veridical across all frequencies only for VEST + NECK, whereas all other stimulus conditions yield results which contain an error at low frequency/velocity due to λ. When extending the concept to a standing subject, this would mean that, in the normal situation of a stationary body support (ground), perception of body motion in space is veridical despite the non-ideal vestibular signal.

It has been shown that the concept, in the form of a dynamic model, can describe experimental findings on human object motion perception,[8] the updating of object localization through vestibular and proprioceptive stimuli,[9] and is also applicable to human postural control.[7] Our results show that it also applies to the head in space signal that is used by subjects when they redirect gaze towards remembered target locations in space, since the above predictions were confirmed. Noticeably, vestibular–neck interactions in the model are linear, but it does contain non-linear elements (detection thresholds)[4] and the perceptual measurements suggest that attentional mechanisms are also involved,[9] which may account for the fact that the errors observed for VEST and NECK at 0.1 Hz (Fig. 3A) had different amplitudes. Previous work[11] has already demonstrated that the neck input in the VEST + NECK condition improves the accuracy of memory-contingent saccades compared with the VEST condition, but could not elucidate the role of the neck input, because the NECK condition was tested in a trunk relative to head rather than in the head in space (spatiotopic) task. However, these studies[10,11] showed that, with the trunk relative to head task, saccades in the NECK condition are independent of stimulus frequency/velocity, a finding which is in line with the above concept (ideal HT signal in the up-transformation).

An additional finding was that subjects (unconsciously) take momentary eye position into account when redirecting gaze; errors in the head-fixed target series were essentially the same as those in the darkness series for all conditions, despite the fact that eye position immediately prior to the saccadic response had changed in the darkness series due to eye reflexes. The eye displacement is due to the fact that fast and slow nystagmus phases differ somewhat in amplitude, especially in the condition VEST + NECK (net eye position shifted in the direction of head displacement).[12] This finding is in line with previous work which showed that extraretinal eye position signals are taken into account in delayed gaze shift tasks, if eye position is intermittently changed.[13–15] Our findings show that suppression of vestibular and cervical ocular reflexes is not a prerequisite for a successful performance of the memory-contingent saccade paradigm.

Conclusion

These experiments show that the addition of neck proprioception can improve the accuracy when subjects use vestibular input to redirect gaze towards remembered target locations in space. The neck contribution is part of a complex proprioceptive mechanism which links vestibular input to somato-sensory information about the body support. A further result is that the current eye in orbit position is also taken into account in this gaze directing mechanism.

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