RESEARCH ARTICLE

Coding of self-motion signals in ventro-posterior thalamus neurons in the alert squirrel monkey

Vladimir Marlinski · Robert A. McCrea

Abstract The firing behavior of 47 ventro-posterior thalamus neurons was studied in two alert squirrel monkeys during rotations of whole body, head and trunk. A total of 27 of these neurons (57%) were sensitive to spatial motion of the head irrespective of the mode of motion. These neurons responded similarly when the head moved simultaneously with the trunk, and when the head voluntarily or involuntarily moved on the stationary trunk. These neurons did not respond to rotation of the trunk when the spatial position of the head was fixed. Five neurons (11%) responded only to involuntary movement of the head produced by external force, but were insensitive to voluntary spatial head movement. They also did not respond to spatial motion of the trunk. Totally 15 neurons (32%) were sensitive to spatial motion, which included rotation of the trunk. These neurons responded when the trunk moved alone, and when the trunk moved simultaneously with the head, but were not responsive to spatial movement of the head while the trunk was stationary. We suggest that the vestibulo–thalamo–cortical pathway comprises two distinct functional channels. In one of these channels, cephalokinetic, spatial motion of the head is coded. In the other channel, somatokinetic, motion of the body in space is coded. Each of these channels further consists of two divisions. In the principal division the motion signal is conveyed continuously, irrespective of the behavioral context of motion. In the other auxiliary division the signal only codes movement caused by externally applied force.

V. Marlinski (✉) · R. A. McCrea
Department of Neurobiology,
Pharmacology and Physiology,
University of Chicago, 947 E. 58th Street,
MC0926, Chicago, IL 60637, USA
e-mail: vmarlinski@gmail.com

Introduction

Besides extensive connections with the oculo-motor nuclei and the spinal cord, the vestibular nuclei have ascending projections to the thalamus (Lang et al. 1979; Nagata 1986; Shiroyama et al. 1999). The ascending pathways that originate in the vestibular nuclei, and extend to the thalamus and further to the cerebral cortex are the neural substrate for conscious perception of spatial self-motion (Liedgren et al. 1976; Büttner and Lang 1979; Mergner et al. 1981, 1991; Grüsser et al. 1990; Bremmer et al. 2002; Gu et al. 2006).

The vestibular system evolved for the detection of inertial and gravitational forces. These forces are nearly constant on the surface of the earth, and one can expect constancy in the vestibular perception of spatial motion. However, results of psychophysical studies show that perception of self-motion varies depending on the behavioral context of the motion (Mergner et al. 1991; Jürgens et al. 1999; Marlinsky 1999a, b, c; Becker et al. 2002; Stevens and Earhart 2006).

Spatial motion signals originating in the vestibular sensory organs are significantly transformed within the vestibular nuclei. Many neurons in these nuclei receive visual, proprioceptive and efference copy inputs in addition to vestibular signals (Waespe and Henn 1977; Marlinsky 1992, 1995; Scudder and Fuchs 1992; Cullen et al. 1993; Gdowski and McCrea 2000; McCrea and Gdowski 2003; Roy and Cullen 2004; Beraneck and Cullen 2007). Due to the interaction of signals from different sources, the firing behavior in many vestibular nuclei cells can undergo dramatic changes depending on the context and circumstances of spatial self-motion. For example, neck proprioceptive

signals can alter the responses of vestibular nuclei neurons such that they code for movement of the body in space rather than movement of the head in space (Gdowski and McCrea 1999, 2000; McCrea and Gdowski 2003). Similarly, signals carrying the efference copy of motor commands can render vestibular neurons to become insensitive to voluntary head movements (McCrea et al. 1999; Roy and Cullen 2001; Cullen and Roy 2004).

In the present study, we investigated how self-motion signals are coded by neurons located in the ventro-posterior (VP) thalamus of the alert squirrel monkey. We found that thalamic neurons, which convey self-motion signals, are divided into separate groups according to their responses to spatial motion of the head or the trunk. We propose that these neurons are the part of a vestibulo–thalamo–cortical pathway, which is composed of two distinct functional channels. One of these, the cephalokinetic channel, codes for the spatial motion of the head. The other, the somatokinetic channel, codes for the motion of the body in space. Each of these channels further consists of two divisions. In the principal division the motion signal is always relayed, regardless of the behavioral context of motion. In the auxiliary division, only movements caused by externally applied forces are signaled. Preliminary results of this work have been presented in abstract form (Marlinski and McCrea 2005).

Methods

Surgery and animal care

Experiments were carried out in two adult squirrel monkeys (*Saimiri sciureus*) that were prepared for chronic recording of eye and head movements, and single cell activity. Protocols were approved by the University of Chicago Institutional Animal Care and Use Committee, and were in compliance with the National Institutes of Health guidelines for the care and use of animals in research.

The surgical preparation has been previously described in detail (Gdowski and McCrea 1999; McCrea and Gdowski 2003). All surgery was carried out in aseptic conditions, using initial ketamine and subsequent isoflurane general anesthesia. Analgesics and antibiotics were administered post-operatively.

Detailed description of experimental arrangements, stimulation technique, data analysis that were used in this study are presented in another, related paper (Marlinski and McCrea 2008).

Vestibular and neck proprioceptive stimulation

Motion actuator for vestibular stimulation used in experiments consisted of two rotary motors (Kollmorgen DDR)

and a linear sled (T3D, Trilogy Systems). One rotary motor was positioned on the floor, and another one was mounted to the ceiling. Vertical axes of both rotary motors were aligned with each other. Translational axis of the sled was in the horizontal plane. The linear sled was mounted on the top of a rotary motor positioned on the floor.

During experiments the animal was seated on a perch in a harness that allowed free movements of the limbs, but restraint of the trunk. The perch was situated on a platform that was mounted on the linear sled. The monkey's head was attached to a vertical rod placed within double bearing races. The rod could rotate freely, could be locked in position, or could be connected to the ceiling motor.

We allowed the monkey to voluntarily rotate its head around the vertical axis, or we rotated the monkey's head using the ceiling motor. Thus, we could compare neuronal activity during voluntary and involuntary head rotations in the yaw plane. Rotation of the head on the trunk evoked both vestibular and neck proprioceptive signals. To distinguish between the two, we rotated the whole animal and produced a vestibular only signal, and we rotated the animal's trunk while keeping the head stationary, thus activating only neck afferents. These rotations were produced with a rotary motor positioned on the floor. The rotational stimuli throughout the study were sinusoids of 0.5 Hz, with a peak angular velocity of 40 deg/s. The ceiling motor was driven by similar sinusoidal stimuli or by a waveform stimulus command that reproduced previously recorded voluntary head rotations. Involuntary head rotations reproducing voluntary head movements were used if quality of recording from the neuron was still satisfactory after presentation of sinusoidal forced head rotations and other motion stimuli.

Motion profile commands were constructed using the Spike-2 (CED 1401) software, which controlled inputs to the servomotors.

Stimulating and recording techniques

A scleral search coil was implanted in one eye, and another coil was attached to the head, for monitoring the movements of the eye and the head, respectively, using a magnetic search device (Angle-Meter NT, Primelec).

Silver wire electrodes were implanted chronically in both temporal bones for stimulation of the VIII cranial nerve (VIIIn) (for details see Minor and Goldberg 1991).

Single cell recordings were made with tungsten electrodes (5 MΩ, A-M Systems) that were connected to a motorized microdrive (FHC), which was mounted on the head-holding frame during experiments. After two-stage amplification and 10^2–10^4 Hz band-pass filtering of the microelectrode recording, the spikes were discriminated with a dual window discriminator (Bak). Trigger pulses

generated by the discriminator were sent to the event channel of the CED 1401 device.

Rotational velocity of the platform mounted on the turntable was recorded with an angular velocity sensor (Watson).

Analogue signals were low-pass filtered with 6 pole 7 kHz Butterworth filters (Frequency devices), digitized at 992 Hz with a CED Power 1401, and saved on a computer for off-line analysis. In addition, unfiltered microelectrode recordings were sampled at the rate of 55.6 kHz, and were used for field potential analysis and checking the fidelity of spike discrimination.

Identification of neurons

During recordings the electrode position in the thalamus was determined in coordinates of a cranial stereotaxic system corresponding to Clarke's principles (Emmers and Akert 1963). In the course of surgical preparation, when animal's head was held with a stereotaxic instrument, a head-holding acrylic frame was oriented in parallel to the cranial basic-horizontal plane and attached to the scull. A reference pin was secured to the frame, and stereotaxic coordinates of the pin were measured. The anterior-posterior and medio-lateral coordinates of the penetration, as well as vertical position of the electrode were calculated relative to the pin.

The recording sites within the thalamus were identified using a combination of techniques described in detail elsewhere (Marlinski and McCrea 2008). The location of vestibular sensitive neurons in the thalamus was estimated with respect to the lateral geniculate nucleus, which was recognized by evoked responses to light flash. Their location was also calculated with respect to the medial geniculate nucleus, which was recognized by field potentials evoked by VIIIn electrical stimulation. Finally, their location was also estimated with respect to the VP nuclei of the thalamus, which were recognized by cells that were strongly sensitive to stroking of the skin or to gentle pressure on muscles. Reconstruction of locations of identified neurons and evoked field potentials is shown in Fig. 1.

Neurons were considered vestibular-sensitive if their firing rate (FR) was altered during whole animal yaw rotation in the dark. Neurons that responded to animal's movement exclusively in the illuminated room were regarded as sensitive to visual input only.

Sensitivity of the neuron to eye movements was assessed during simultaneous monitoring of the neuronal discharge rate, and horizontal and vertical eye positions. The discharge rate of neurons analyzed in this paper was not altered with the change of eye position in the absence of head movement.

Care was taken to discriminate neuronal responses to vestibular stimulation from responses to somatosensory stimuli associated with spatial motion of the animal. Somatosensory sensitivity of every neuron was examined with gentle touch of hair and skin, and pressure of muscles of the head, the trunk, extremities and the tail. When the neuron responded to any of these stimuli, the somatosensory receptive field was localized. If mechanical stimulation of such a field could not be excluded because of the animal's body motion relative to the harness during vestibular stimulation, the neuron was considered sensitive to somatosensory input only, and discarded from further analysis.

Number of synapses between VIIIn and vestibular-sensitive neurons was not assessed.

Data analysis

Analysis was done with a laboratory-developed program using the IGOR Pro software package (WaveMetrics). To evaluate the sensitivity of the neurons to vestibular and neck proprioceptive inputs, we analyzed their responses to whole body and trunk sinusoidal rotations. Averages of the motion stimulus velocity and of the unit responses were fitted with sinusoidal function, and corresponding amplitudes and phase shifts were estimated. The ratio of the response amplitude to stimulus peak velocity gave an estimate of the sensitivity (spikes/s/deg/s). A difference between calculated phase shifts of the stimulus velocity and of the response modulation gave an estimate of the response phase relative to angular velocity. To quantitatively examine and compare neuronal responses to rotations of any velocity profile, the FR was modeled with a linear function $FR = K0 + K1 \times H_s' + K2 \times H_s'' + K3 \times H_t + K4 \times H_t' + K5 \times H_t''$, where $K0$ was the cell's background discharge rate, $K1$ was the cell's sensitivity to the head angular velocity in space (H_s'), $K2$ was the cell's sensitivity to the angular head acceleration in space (H_s''), $K3$ was the cell's sensitivity to the head position relative to the trunk (H_t), $K4$ was the cell's sensitivity to the head angular velocity relative to the trunk (H_t'), and $K5$ was the cell's sensitivity to the head angular acceleration relative to the trunk (H_t''). For analysis of neuronal responses during voluntary head movements, the recording fragments, 0.5–2 s in duration, with the head velocity close to the peak velocity of our standard sinusoidal stimulus were selected. The accuracy of fit was assessed by the coefficient of determination (R^2) between the experimental data and regression model.

Results

We recorded the activity of 107 vestibular-sensitive neurons in the VP thalamus neurons of two squirrel monkeys. In 47 of these neurons the duration of recording was long

Fig. 1 Reconctruction of recordings from the left (**a**) and right (**b**) thalamus of one animal, and the right thalamus of another animal (**c**). Left column (panels with index 1) shows saggital views, and right column (panels with index 2)—frontal views of recording sites. Identified neurons and field potentials are indicated with symbols: *black circles*—neurons responding with similar sensitivity to whole body and head on the trunk rotations, *black diamonds*—neuron sensitive to whole body rotations and involuntary only head on trunk rotations, *black squares*—neuron responsive to rotations of the whole body and the trunk, large *gray circles*—vestibular-sensitive neurons, *gray circles*—neurons sensitive to somatosensory stimuli, *gray triangles*—neurons sensitive to visual stimuli, *gray diamonds*—field potentials evoked by flash illumination, *gray squares*—field potentials evoked by VIII cranial nerve stimulation. *LG* lateral geniculate body, *MG* medial geniculate body, *PuI* nucleus pulvinaris inferior, *PuL* nucleus pulvinaris lateralis, *PuM* nucleus pulvinaris medialis, *VL* nucleus ventralis lateralis, *VPL* nucleus ventro-posterior lateralis, *VPM* nucleus ventro-posterior medialis
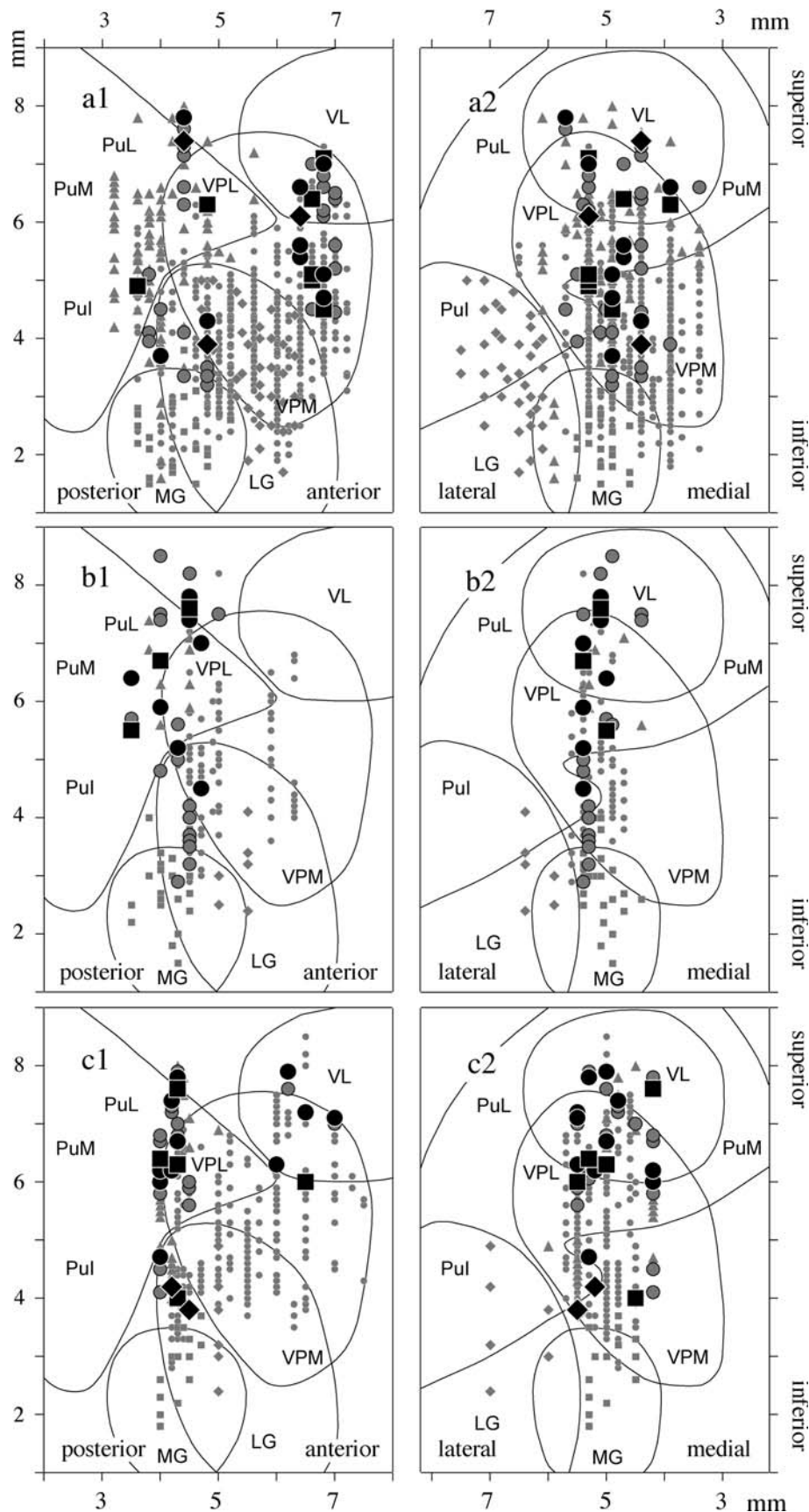
enough to compare the firing behavior across different movements of the whole body, head and trunk. According to their responses to rotations of the whole body, to voluntary and involuntary movements of the head on the stationary trunk, and to rotations of the trunk with the head held stationary, these neurons could be divided into separate groups. In another paper we reported that vestibular-sensitive neurons in the VP thalamus were distributed in three clusters on the anterior and posterior borders of somatosensory nuclei (Marlinski and McCrea 2008). Neurons of different groups described here were present in all clusters located in the VP thalamus (Fig. 1).

One group contained neurons that responded to spatial motion of the head in space, produced both by whole body rotation and by rotation of the head on a stationary trunk. This was the most numerous group, and consisted of 27 cells (57% of the sample). The majority of these neurons (22/27, 81% of the group) were of type II according to the classification scheme of Duensing and Schaefer (1958), and the remaining cells (5/27, 19%) were type I. The firing behavior of one of these neurons during various rotational stimulations is shown in Fig. 2. The neuron responded nearly identically to involuntary sinusoidal whole body rotations and to involuntary rotations of the head on the stationary trunk (Fig. 2a, c). The responses of the neuron to voluntary head motion were similar to the responses to involuntary head motion (Fig. 2d). The linear model of the $FR = 30 - 0.25H_s'$, satisfactorily approximated responses to rotation of the whole animal ($R^2 = 0.88$), and responses to involuntary ($R^2 = 0.82$) and voluntary ($R^2 = 0.81$) movements of the head on the stationary trunk. Thus, the rotational sensitivity of the neuron was not altered across different modes of spatial head movements. None of neurons of this group responded to rotation of the trunk while the position of the head was fixed (Fig. 2b), and therefore were insensitive to neck proprioceptive signals.

Another group consisted of neurons responsive only to involuntary head movements in space, which were produced either by rotation of the whole animal, or by rotation of the head on the stationary trunk. This was the smallest group consisting of five neurons (11% of our sample). Three of these were of type II (60%), and two were of type I (40%). The responses of one of these neurons to involuntary sinusoidal whole body rotations are shown in Fig. 3a. These responses could be approximated with a polynomial equation that included sensitivity to the angular head velocity and acceleration in space: $FR = 30 - 0.3H_s' - 0.05H_s''$, $R^2 = 0.69$. When the animal was allowed to make voluntary head saccades the discharge rate of the neuron was not altered (Fig. 3d). Firing behavior of the neuron during voluntary head movements was very different from that predicted by the neurons's sensitivity to head motion during involuntary whole body rotations ($R^2 = 0.1$). When
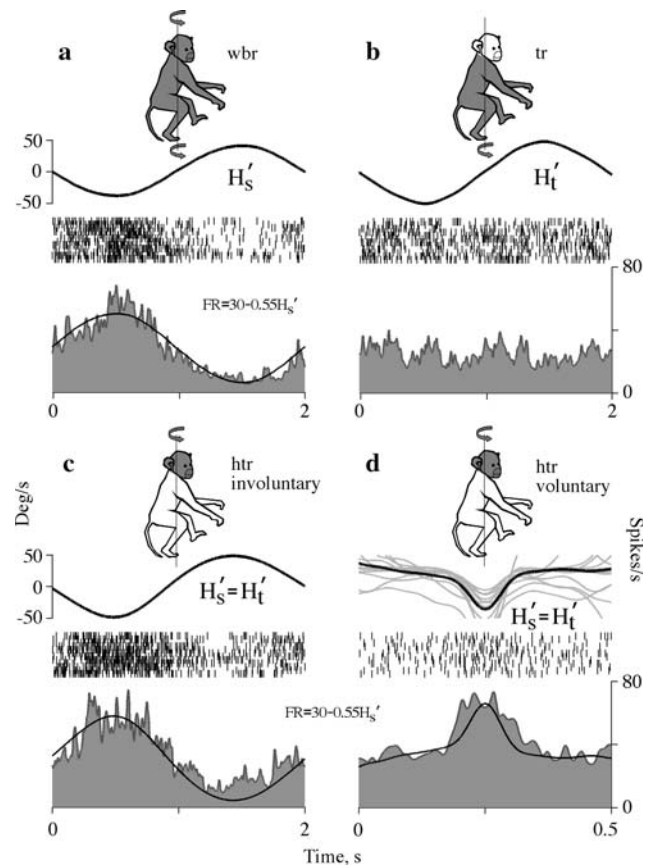

Fig. 2 Firing behavior of the neuron responding with similar sensitivity to whole body and head on trunk rotations: whole body rotation (wbr) (**a**), trunk rotation with the head stationary (tr) (**b**), involuntary head on trunk rotation (htr involuntary) (**c**), voluntary head on trunk rotation (htr voluntary) (**d**), these were head movements selected from a several minute record. *Shaded area* of the monkey picture indicates the part of the body in motion, *curved arrows* indicate rotational motion of that body part. In each panel the *upper curve* is angular velocity of the head relative to space (H_s') or relative to the trunk (H_t'). In panel **d** the *gray lines* represent individual head movements, while the *black line* is their average. The *rasters* in the middle represent spikes generated during the corresponding period of time. The *bottom histogram* represents the average discharge rate. A *curve* superimposed on each histogram represents a linear model of the firing rate (FR), an equation expressing that *curve* is shown above the histogram. The left ordinate is the angular velocity, deg/s; the right ordinate is unit discharge rate, spikes/s; the abscissa is time, s

records of voluntary head movements were used to command the ceiling-mounted motor, giving the same motion profile to involuntary head movements, the neuron was responsive (Fig. 3c). This response corresponded to that predicted from the sensitivity of the neuron to involuntary whole body rotation ($R^2 = 0.62$). Neurons of this type, similarly to neurons of the former group, were insensitive to trunk rotation, and therefore did not receive neck proprioceptive input (Fig. 3b). Cancellation of the vestibular motion signal during voluntary head movements can be attributed neither to interaction with the neck afferent input, nor with the visual input.
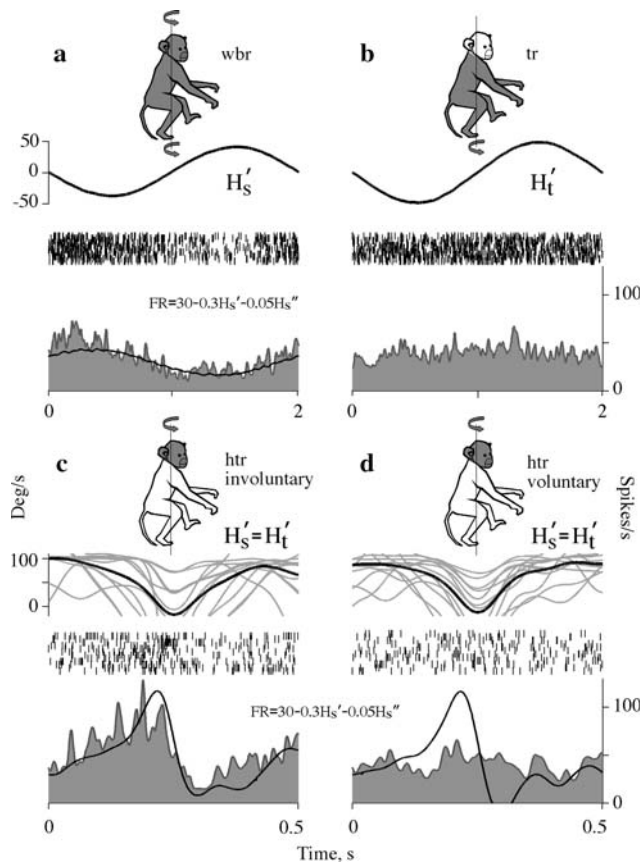
Fig. 3 Firing behavior of the neuron sensitive to involuntary head movements only: whole body rotation (**a**), trunk rotation with the stationary head (**b**), involuntary head on trunk movements (**c**), voluntary head on trunk movements (**d**). Traces on panels, symbols, ordinates and abscissa are the same as in Fig. 1

Fig. 4 Firing behavior of the neuron responsive to rotations of the whole body (**a**) and the trunk (**b**). During head rotations when the trunk was stationary, the neuron had no response, whether the head movement was involuntary (**c**) or voluntary (**d**). Traces on panels, symbols, ordinates and abscissa are the same as in Fig. 1

A third group included neurons that, in contrast to those described above, responded not only to the whole body rotation, but also to trunk rotation when the head was held stationary. This suggests that these neurons receive neck proprioceptive input in addition to vestibular input. We recorded the activity of 15 neurons of this type, comprising 32% of the total sample. Ten of these neurons (67%) had type II responses, and 5 of them (33%) had type I responses. An important feature of the responses to vestibular and neck proprioceptive stimulation was their reciprocity in phase. An example of this can be seen in the firing behavior of the neuron shown in Fig. 4. In this neuron, during whole body rotation, when the head and trunk moved together, an increase in the discharge rate followed rightward head velocity in space. During rotation of the trunk with the head stationary in space, an increase in the discharge rate followed trunk rotation to the right, when the velocity of head movement in relation to the trunk was directed leftward. The response of the neuron to whole body rotation could be approximated with the model FR = $22 + 0.5H_s' + 0.03H_s''$ ($R^2 = 0.84$), while the response to
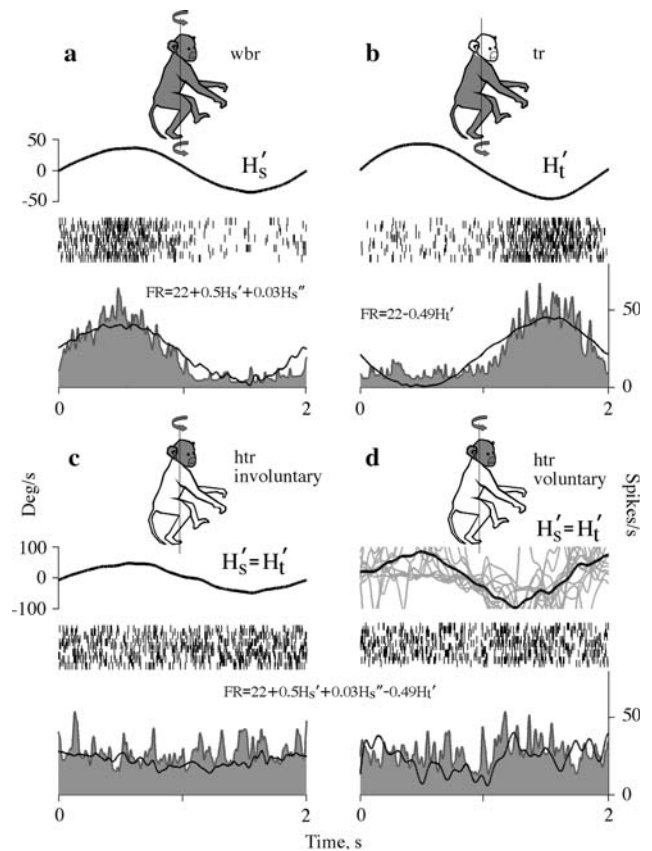
trunk rotation could be approximated with the model FR = $22 - 0.49H_t'$ ($R^2 = 0.76$). The sensitivity of this neuron to vestibular stimulation was nearly similar in magnitude, but opposite in phase to the sensitivity to proprioceptive stimulation. During rotation of the head on the stationary trunk, i.e. when the head changed position in space and simultaneously changed position relative to the trunk, no alterations in the discharge rate were seen. This was true during both involuntary and voluntary movements of the head on the trunk (Fig. 4c, d). The absence of modulation of the cell's discharge rate during head-alone rotation could be predicted as a result of linear summation of the responses to vestibular (Fig. 4a) and to neck proprioceptive (Fig. 4b) stimulation: FR = $22 + 0.5H_s' + 0.03H_s'' - 0.49H_t'$, where the H_s' stimulus profile was identical in amplitude, but opposite in phase to the H_t' stimulus profile.

In the neurons receiving both vestibular and neck proprioceptive inputs, the responses to head on trunk rotations could be cancelled either completely, as in the cell described in Fig. 4, or just partially, as in the one described next. In the latter case, the resulting alteration of activity

could be seen as an attenuated response related to only one of the two inputs. An example of such a neuron that was more sensitive to vestibular than to neck proprioceptive stimulation is given in Fig. 5. For this cell the response to whole body rotation could be approximated with the model $FR = 50 + 0.9H_s' + 0.04H_s''$, $R^2 = 0.71$ (Fig. 5a), and the response to trunk rotation could be approximated with the model $FR = 50 - 0.7H_t'$, $R^2 = 0.74$ (Fig. 5b). During head on trunk rotation the activity of the neuron was modulated, and this modulation was in phase with the response to whole body rotation, but reduced in amplitude. The response to the head movement could be predicted as the result of linear summation of responses to vestibular and neck proprioceptive inputs: $FR = 50 + 0.9H_s' + 0.04H_s'' - 0.7 H_t'$. Using this model, the predicted responses to voluntary ($R^2 = 0.61$) and involuntary ($R^2 = 0.49$) head movements, which are shown in the Fig. 5d and c, were comparable with the actual responses of the neuron.

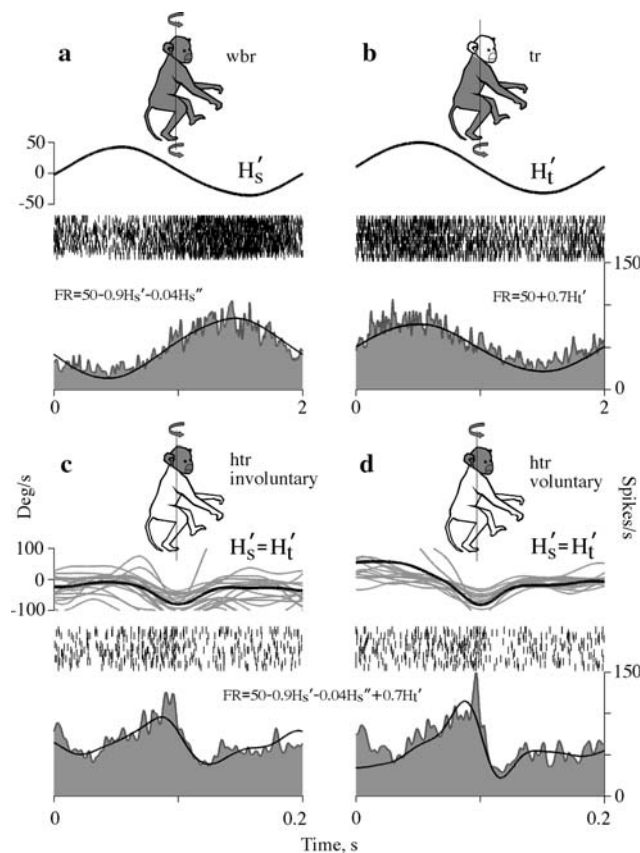To characterize processing of vestibular and neck proprioceptive signals in the group of neurons receiving both inputs, we analyzed their population responses. The population responses to vestibular and neck proprioceptive stimuli were calculated in polar coordinates of a mean vector (Batschelet 1981). To simplify analysis, we did not distinguish between type I and type II neurons, but assigned vestibular responses to be in the same direction, while neck afferent responses as related to the vestibular responses. The mean population response to the vestibular input had rotational sensitivity of 0.43 spikes/s/deg/s, and was practically in phase (0.1° phase lead) with angular velocity. The mean population response to the neck proprioceptive input had sensitivity of 0.24 spikes/s/deg/s, and was in phase opposite to angular velocity (180.2°). The mean population response to both inputs acting together was negligible: rotational sensitivity was 0.07 spikes/s/deg/s, and the phase of remaining response was −0.8° relative to angular velocity. This result signified that irrespective of individual differences in sensitivity to one of the two inputs, the population response to simultaneously activated vestibular and neck proprioceptive inputs was nullified. As a consequence, neurons of this type did not transmit signal during spatial movement of the head on the stationary trunk, but only during simultaneous movement of the head and trunk. On the contrary, these neurons generate the signal when the trunk moved in space either alone or simultaneously with the head. This suggests that these neurons do not code for spatial movement of the head, but for spatial movement of the body.

Discussion

Perception of self-motion in space is a complex sensory event that includes perception of spatial movement of the head—cephalokinesthesia, and perception of spatial movement of the body—somatokinesthesia. The results of our present study of self-motion sensitive thalamic neurons lead us to suggest that cephalokinetic and somatokinetic signals are conveyed to the cortex through functionally distinct vestibulo-thalamic channels. A proposed functional organization of these channels is illustrated schematically in Fig. 6.

A cephalokinetic signal is forwarded to the cerebral cortex through the channel composed of neurons sensitive to head motion only. These were the neurons shown in Figs. 1 and 2 that generate signals related to movement of the head in space, which were similar whether the head moved on the trunk, or the head and trunk moved together. A fraction of these cephalokinetic neurons, similar to the neuron represented in Fig. 2, generated signals only during involuntary movements of the head in space, and were not responsive to voluntary self-generated movements of the head. The absence of head motion signals during voluntary movement could not be attributed to cancellation by neck
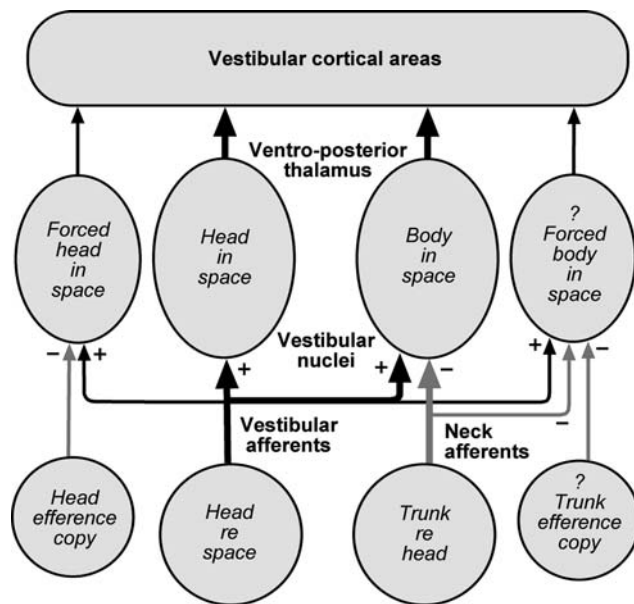

Fig. 5 Firing behavior of the neuron with different sensitivities to whole body (**a**) and trunk (**b**) rotations. The neuronal response to head rotation when the trunk was stationary was equivalent to an attenuated response to whole body rotation (**c**, **d**). Traces on panels, symbols, ordinates and abscissa are the same as in Fig. 2

Fig. 6 Self-motion signals are processed in two distinct vestibulo–thalamo–cortical channels. One of them, cephalokinetic, which is shown on the left, originates in vestibular nuclei neurons, which receives signals of head motion in space from primary vestibular afferents. The head motion signal is forwarded to the thalamus, and from there finally to areas of the cerebral cortex responsible for encoding spatial motion. Within the principal division of this channel, the head motion signal is conveyed unperturbed irrespective of the behavioral context of motion. In the auxiliary division of this channel, only the signal of head motion produced by externally applied force is transmitted due to the addition of an efference copy of a head motor command, which acts to cancel the vestibular signal during voluntary head movement. Another, somatokinetic channel, which is shown on the right, originates in those vestibular nuclei neurons that receive, in addition to spatial head motion signals, signals of trunk motion relative to the head. Due to the convergence of these two inputs, the qualitatively new signal representing movement of the body in space is constructed. This signal is conveyed to separate neurons in thalamus, and further to the cerebral cortex. A hypothetical division of this channel carries only the signal of involuntary body movement in space, while the signal of voluntary body motion is cancelled due to addition of efferent copy of the command initiating voluntary movement of the trunk

afferent inputs, or by visual inputs. The other likely source of signal cancellation would be an efference copy of a motor command, which we suggest was involved (Holst von and Mittelstaedt 1950; McCrea et al. 1999; Roy and Cullen 2001, 2004; Cullen and Roy 2004).

The majority of head movements in space are voluntary, and the cephalokinetic signaling would be reduced in those circumstances in freely moving subjects. When head movements are induced by external forces, all of the head motion sensitive neurons will respond. In this context, the cephalokinetic signal would be augmented. Indeed, it is known from human psychophysical studies that cognitive perception of self-generated head motion is reduced in comparison to perception of motion produced by externally

applied force (Jürgens et al. 1999; Marlinsky 1999a; Stevens and Earhart 2006).

A somatokinetic signal is constructed in the vestibular nuclei neurons by the addition of the signal of the head displacement relative to the trunk to the signal of the head movement in space (Gdowski and McCrea 1999, 2000; Marlinski and McCrea 2006). The principal source of the signal of the head displacement relative to the trunk is neck proprioception. Sensitivity of the vestibular nuclei neurons to neck afferent stimulation is well known and described in details (Boyle and Pompeiano 1981; Anastasopoulos and Mergner 1982; Marchand et al. 1987; Kasper et al. 1988; Wilson et al. 1990). It should be mentioned that an efferent copy of the motor command controlling neck muscles could contribute to construction of this signal, though techniques used in our study were not effective to investigate this possibility. The somatokinetic signal is forwarded to the cortex through thalamic neurons that are sensitive to simultaneous movement of the head and trunk, and to movement of the trunk alone. In these somatokinetic neurons, both involuntary and voluntary movements of the head on the stationary trunk yielded no response (Fig. 3).

We did not study the firing behavior of thalamic neurons during voluntary trunk motion, and so do not have evidence for the cancellation of neck proprioceptive responses due to the addition of an efference copy of voluntary trunk motion command. However, such cancellation of afferent somatosensory signals by the efference copy of voluntary body motion command has been described in another species—the mormirid fish (Bell and Grant 1992; Mohr et al. 2003). We hypothesize that a fraction of somatokinetic neurons receives both afferent trunk motion signals and an efference copy of motor commands initiating this motion. The somatokinetic neurons, which we found to be specialized for coding only passive spatial motion, could permit discrimination between intended motion and unexpected perturbations of the body for the purpose of generating appropriate compensatory postural responses, and for calculation of heading direction during complex body movements, such as running or walking on uneven terrain.

The different vestibulo–thalamic channels carry signals that can provide complementary estimates of head and body motion. The construction of a coherent estimation of self-motion is essential for both effective motor control and for cognitive percepts of the motion in the visually perceived environment. Pathological changes in the posterior-lateral thalamus and in the superior-temporal and insular cortex cause postural disbalance and perceptual disorientation in human patients (Dieterich et al. 2005). It is noteworthy that spatial orientation in these patients could be disrupted across two distinct cognitive levels: one being a mismatch between perceived head position and visual vertical, and the other being an alteration of perception of body

posture in relation to gravity (Brandt and Dieterich 1994; Karnath et al. 2005).

In our study of vestibular sensitive thalamic neurons we had found that they are confined in separate clusters in the VP thalamus (Marlinski and McCrea 2008). Location of these clusters matched termination sites of ascending vestibulo-thalamic fibers labeled with anterograde tracers injected into the vestibular nuclei (Lang et al. 1979; Nagata 1986; Shiroyama et al. 1999). Position of the anterior cluster in the area bordering VP lateral and ventro-lateral nuclei corresponded to termination sites of fastigial and interposed cerebellar nuclei neurons, which are responsive to vestibular stimuli (Stanton 1980; Asanuma et al. 1983; Büttner et al. 1991; Shaikh et al. 2005; Meng et al. 2007). These neuronal clusters might correspond to separate sources of projections from the thalamus to various cortical areas involved in the processing of vestibular signals, which were described by Grüsser et al. (1990) (Akbarian et al. 1992). We examined a possible correlation between different clusters of vestibular sensitive thalamic neurons and their functional preferences. Our data did not provide evidence for specialization of these clusters for conveying signals of spatial movement of the head and of the body: cephalokinetic and somatokinetic neurons were evenly distributed over the area of VP thalamus explored in our experiments. This presumes that different cortical areas receive both cephalokinetic and somatokinetic signals for spatial motion. Indeed, it had been found in experiments in macaque monkeys that the majority of vestibular sensitive neurons in the retro-insular cortex received neck proprioceptive input (Grüsser et al. 1990), and a third of vestibular sensitive neurons in the ventro-parietal cortex were responsive to neck proprioceptive stimulation (Klam and Graf 2003). We can speculate that cephalokinetic and somatokinetic signals entering posterior insular vestibular cortex, which is proposed to be the "core vestibular cortex" (Guldin and Grüsser 1998), could provide for distinct perception of spatial motion of the head and the body based primarily on the vestibular cue. Cephalokinetic and somatokinetic signals reaching other cortical areas that are principally related to other sensory modalities, such as somatosensory cortical area 3a (Guldin et al. 1992), or visual ventral parietal and medial superior temporal cortex (Bremmer et al. 2002; Gu et al. 2006), will contribute to the multimodal subjective representation of space in accordance with spatial movement of the head or spatial movement of the body.

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