PHYSIOLOGICAL CORRELATES OF VISUALLY INDUCED SELF-MOTION PERCEPTION

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Abstract

A striking manifestation of visual-vestibular interaction in the central nervous system is the ability of large-field visual motion to induce the perception of contra-directional self-motion (vection) in a stationary observer. The work of this thesis investigated the presence and nature of changes in several physiological and perceptual markers correlating with the subjective perception of visual motion as object- or self-motion.

During circularvection, the beating field of torsional as well as horizontal optokinetic nystagmus was found to deviate in the direction of perceived self-motion. This anticipatory deviation is present at several stimulus velocities as well as body orientations with respect to gravity and presumably reflects a reorientation of spatial attentional resources in the direction of perceived self-motion.

Using fMRI, it was found that during rollvection early motion-sensitive occipital and parieto-insular vestibular cortex deactivated whereas higher-order temporo- and parieto-occipital areas maintained identical, elevated, activity levels as during object-motion perception. However, event-related analysis showed that these areas were activated transiently during perceptual transitions reflecting their potential involvement in perceptual switching. Reduced primary visual cortex excitability during circularvection was also found using pattern-reversal visually evoked potentials and is likely to be mediated by feedback processes originating in higher visual and multimodal cortical areas.

The measurement of cardiovascular activity identified a generalised pressor response following real self-motion in roll. Although of similar perceptual quality, no systematic autonomic adjustments were observed following the perception of circularvection demonstrating a differential effect of visual-vestibular interaction on conscious perception versus autonomic regulation.

Measuring perceived postural verticality, it was confirmed that optokinetic stimulation in roll biases the perceived direction of gravity towards the direction of stimulus motion. However, no differential perception of postural verticality was obtained across perceptual states which can be explained by a functional segregation of visual-vestibular subsystems in the brainstem processing the perception of tilt and rotation.

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Abbreviations

ANOVA	analysis of variance
BA	Brodmann area
BP	blood pressure
CV	circularvection
DAP	diastolic arterial blood pressure
DM	dorsomedial occipital cortex
ECG	electrocardiography
EEG	electroencephalography
EOG	electrooculography
EP	evoked potential
ERP	event-related potential
fMRI	functional magnetic resonance imaging
MST	middle superior temporal area
M-system	magnocellular system
MT	middle temporal area
NOT	nucleus of the optic tract
N70	negative inflection of the VEP at about 70 ms
O_1, O_2, O_Z, F_Z	scalp electrode locations (10-20 system)
OM	object-motion
P100	positive inflection of the VEP at about 100 ms
PET	positron-emission tomography
PIVC	parieto-insular vestibular cortex
PO	parieto-occipital cortex
P-system	parvocellular system
SAP	systolic arterial blood pressure
SEM	standard error of the mean
ST	superior temporal cortex
V1 – V5	visual cortical areas 1 – 5
V5a	accessory V5 / MST
VEP	visually evoked potential
VIP	ventral intraparietal area
VOG	videooculography

1 Introduction

Most higher organisms possess the ability to perform complex perceptual and behavioural functions that are well adapted to three-dimensional space. In order to interact successfully with the environment, an individual must be able to determine the orientation of its own body as well as the position of its limbs and other motile units with respect to the body. In the human and in all other vertebrates, information relevant for spatial behaviour is acquired by the remote senses and is processed by the central nervous system. The principal sources of information about the relation between the body and the environment stem from the visual and vestibular systems. Additional sensory systems involved are the somatosensory, proprioceptive, auditory and, in humans only to a very limited extent, the olfactory systems. Hence, it is essential for the organism to analyse and integrate an abundance of multimodal sensory information at any point in time. However, in order to investigate the individual contributions of a single sensory system and the interactions between systems systematically in laboratory experiments, it is necessary to reduce the number of stimulated modalities and to control the type and intensity of the stimulation employed.

One of the many interactions between sensory systems that has been studied extensively in the past is that between the visual and the vestibular system (Dichgans and Brandt, 1978). The numerous investigations conducted can be classified according to several aspects. One distinction can be made with respect to the sensory modality that is being stimulated – vestibular, visual, or both modalities. Another way of dividing them is according to the perceptual or behavioural consequences induced by the sensory stimulation, for instance an impaired perception of primary spatial axes, of object-motion, or the perception of self-motion.

All experiments presented in this thesis are concerned with the study of perhaps the most compelling perceptual manifestation of visual-vestibular interaction – visually induced self-motion perception.

1.1 Visually Induced Self-motion Perception

Although suprathreshold vestibular stimulation is the principal sensory event to induce the perception of self-motion, the peripheral vestibular system is only sensitive to acceleration stimuli. Since vestibular receptor organs are not stimulated by steady-state rotation or translation, they do not contribute to the perception of self-motion in an observer moving at a constant velocity and the brain needs to extract the information about the body being in motion from sources other than vestibular sensation. In this context, one of the most potent stimuli to induce the perception of self-motion in a stationary observer is coherent motion of a large proportion of the visual environment. It must be noted that sustained rotation at a constant velocity results in radially directed centripetal forces acting as linear acceleration on those parts of the body that are located eccentrically of the axis of rotation which could theoretically be picked up by some of the peripheral vestibular receptor organs. However, during naturally occurring motion profiles this acceleration is small in magnitude and unlikely to be sensed by the vestibular receptors. Also, due to their radial direction with respect to the axis of rotation, centripetal forces could only be used to extract information on the existence, velocity and plane of constant-velocity rotation but bear no value for the detection of its direction. Rotation-induced linear acceleration is therefore presumably of little, or no, use for the central nervous system to construct the perception of self-motion at a constant angular rate. In a natural environment, the vestibular and visual systems act in a mutually corroborative manner in mediating the perception of self-acceleration but the sustained perception of self-motion at a constant velocity is almost exclusively based upon visual motion information (Brandt et al., 1973; Dichgans and Brandt, 1978). The lack of visual input results in the fact that deceleration from sustained self-motion in darkness will inevitably be perceived as acceleration in the opposite direction, a perception in accord with the relativistic nature of acceleration. In the same way, uniform motion of the visual environment allows for two different perceptual interpretations when there is no corroborative vestibular stimulation present simultaneously. Apart from the "correct" interpretation as motion of the environment with respect to the stationary observer, the same visual stimulus can equally be attributed as originating from contra-directional self-motion in a stationary environment. An everyday example of this phenomenon can frequently be experienced during travel on railway trains. When sitting on a train that is stationary in a train station, the sight of another train starting to move on the adjacent track often induces the illusory perception that one's own train is accelerating. Similarly, watching a river from the top of a bridge or the motion of clouds in the sky have been reported to elicit the perception of self-motion in a motionless observer (Brandt, 1991).

The earliest scientific investigations on the phenomenon of visually induced self-motion perception were conducted by the Physicists Ernst Mach (1875) and Hermann von Helmholtz (1896). Helmholtz explained the observed perceptual phenomena with a postulated psychological mechanism he termed "Urteilstäuschung", or deception of judgement. He assumed that illusions of self-motion perception would arise from an explicit or implicit assumption of a stable environment that is based on experience. Consequently, the perception of environment motion would need to be interpreted as resulting from contra-directional self-motion (Dichgans and Brandt, 1978). Tschermak (1931) introduced the term "vection" for the perception of self-motion.

The stimuli used for the laboratory investigation of visually induced self-motion perception commonly consist of real or projected patterns covering a large proportion of the visual field that either are rotated around an observer or are moved linearly along him, usually in a lateral, antero-posterior or vertical direction. The stimulation device most frequently used to elicit the perception of self-rotation along one's longitudinal axis is the so-called "rotating drum". It is pivoted on a motor-driven vertical axis and contains a regular alternation of black and white vertical stripes on its interior side. The perception of self-rotation elicited by rotatory visual stimulation has been termed "Zirkularvektion", or circularvection, by Fischer and Kornmüller (1930). In an equivalent manner, the term "Linearvektion", or linearvection, was used for the perception of self-translation along a straight line induced by viewing a pattern that is displaced linearly with respect to an observer. Other frequently used terms to distinguish between environment- and self-motion perception are "egocentric" and "exocentric" motion perception, respectively.

As mentioned above, during both perceptual states the visual stimulus remains unchanged and only consists of relative motion between the observer and the visual environment. Hence, in order to perceive this relative motion as arising from a moving environment it is necessary to assume one's own body to be a stationary point of reference. This location of stationary reference is called egocentric. In analogy, the perception of vection requires the assumption of a stable environment and has therefore been called exocentric by Fischer and Kornmüller (1930).

The phenomenon of vection has not only been reported following visual motion stimulation but also in response to stimulation of other sensory modalities. Marme-Karelse and Bles (1977) induced audiokinetic CV by presenting their subjects with a sound source rotating around their longitudinal axis. Proprioceptively induced vection has also been reported. Brandt et al. (1977) and Brandt and Büchele (1978) asked their subjects to extend their arm horizontally and passively rotated it around their longitudinal axes. The self-rotation perception induced by this manoeuvre was termed arthrokinetic CV. In a similar manner, Bles and Kapteyn (1977) induced the perception of self-motion in their subjects by letting them walk actively on a treadmill-style, but rotating, platform under exclusion of visual or vestibular stimulation. The observation that self-motion perception can be induced by a moving tactile stimulus has been reported by Dichgans and Brandt (1978) as "haptokinetic" vection.

As will be explained in more detail later, the optokinetic pathways largely utilise the same neural structures as the vestibular system. Convergence of visual motion signals and vestibular inputs occurs as early as in the vestibular nuclei, the entry point of the vestibular projection into the central nervous system. A large number of central vestibular neurones are modulated in an equivalent manner in response to sole optokinetic stimulation as they are as a consequence of vestibular stimulation which further emphasises the functional synergy with which both types of signals are processed in the brain (Henn et al., 1974; Waespe and Henn, 1977; Waespe and Henn, 1979).

Wertheim (1994) suggested that the central nervous mechanisms involved in determining to what extent coherent visual motion is caused by object-motion or by contradirectional self-motion are based on a functional convergence of retinal, extraretinal and vestibular signals. Since motion of the visual environment is inherently ambiguous, the central nervous system needs to incorporate an element of information about self-motion in space. According to Wertheims (1994) model, this reference signal is an estimator of retinal surface velocity in space and is hypothesised to arise from the vestibular nuclei. The reference signal consists of an oculomotor efference copy (von Holst and Mittelstaedt, 1950) estimating the eye velocity in the orbit and a vestibular element estimating head velocity in space. This signal is subsequently compared to the retinal image velocity of the optokinetic stimulus. When these signals are identical, retinal slip is concluded to arise from self-motion and when they differ, object-motion is perceived. That the perception of vection can be induced solely by optokinetic stimulation is explained by visual motion signals being able to access the reference signal. When their influence builds up, the reference signal increases and the perception of self-motion arises whilst the perception of object-motion ceases concurrently. It is therefore important to note that the contrasting perceptual states of object-motion and vection are not mutually exclusive but can indeed perceptually coexist. During optokinetic stimulation, the perception of vection often develops gradually with a simultaneously perceived slowing of object-, or environment-motion (see e.g. Wertheim, 1994). Despite of this gradual build-up, all experiments in this thesis require subjects to decide in a binary, or all-or-nothing, manner whether they perceive optokinetic stimulation as originating from environment- or from self-motion and is then referred to as a perceptual switch, although this switch actually corresponds to the a subject's individual decision to report the perception of self-motion from then on. This design was decided in order to ensure observers were given a simple and intuitive task as well as to enable statistical analysis of the perceptual effects as a categorical variable.

1.2 Vestibular System

1.2.1 Labyrinth

The vestibular receptor organs are embedded in the bony labyrinth of the inner ear. The receptor organ consists of two cavities - the utricle and the saccule - and the semicircular canals. Both, utricle and saccule are located in the vestibule of the bony labyrinth with the three semicircular canals originating from the utricle. Utricle and saccule communicate via the utriculosaccular duct. The osseous labyrinth is lined with the membraneous labyrinth which contains endolymphatic fluid. The space between osseous and membraneous labyrinth is filled with perilymphatic fluid. The ionic composition of the endolymph is similar to that of intracellular fluid whereas that of the perilymph is comparable to the electrolytic relations of the cerebrospinal fluid with both being of low protein concentration and a specific gravity close to that of water (Wilson and Melvill Jones, 1979; Junqueira et al., 1992).

1.2.2 Semicircular Canals

Each labyrinth comprises three semicircular canals consisting of an anterior, posterior and horizontal semicircular canal. Although these are in an approximately orthogonal orientation with respect to each other they are not aligned with the three major spatial axes of the head but instead are tilted posteriorly by about 30° and laterally by about 45°. The canals join together in the utricle which, therefore, contains endolymph common to all three semicircular canals. Distal to the point of joining into the utricle, each canal possesses a widening of its lumen, called ampulla membranacea, that contains the sensory epithelium, crista ampullaris. The crista ampullaris is composed mainly of connective tissue that contains numerous nerve fibres and protrudes into the endolymphatic space. Its surface contains the sensory cells, hair cells, that are embedded in supporting cells to which they are fixed via desmosomes

(Junqueira et al., 1992). On its apical surface, each hair cell contains 60 to 100 stereocilia (Barnes, 1983). In addition, each hair cell contains one kinocilium that is located more laterally on the apical surface, of greater length and width than all other stereocilia and, although its name suggests differently, is now thought not to be motile. The length of the stereocilia increases the further away from the kinocilium they are located. Distally, stereocilia and kinocilium are attached to the cupula. The cupula, a gelatinous layer of glycoproteins, covers and occludes the crista ampullaris in a manner resembling a diaphragm. As a result of this mechanic coupling, displacement of the cupula moves the kinocilium and stereocilia which in turn transmits shearing forces onto the apical hair cell membrane where the mechanoneural transduction takes place. The mechanical shearing presumably changes the state of membrane ion channels. Shearing of the stereocilia towards the kinocilium results in a depolarisation of the hair cell, movement in the opposite direction hyperpolarises the cell (Trincker, 1957).

The cupula is of the same specific weight as its surrounding endolymph. Therefore the relative position between the cupula and the hair cells is not influenced by linear accelerations and forces like gravity. The adequate stimulus to induce motion of the cupula and subsequent shearing of the stereocilia is therefore a flow of the endolymph with respect to the surrounding epithelium of the membraneous labyrinth. Under physiological circumstances this flow results directly from rotational acceleration of the head in space as a consequence of the endolymph's inertia. For clinical testing, however, endolymph flow mainly of the horizontal semicircular canal can be induced by cold or hot water irrigation of the outer ear canal. Furthermore, some pharmacological interventions like the consumption of alcohol beyond moderation might affect the specific weight of the cupula and therefore lead to unphysiological stimulation of vestibular receptors with all known consequences (for review, see Brandt, 1991).

For a long time it was believed the cupula would resemble a "swing-door" that is only hinged to the crista ampullaris (Steinhausen, 1931; Steinhausen, 1933). McLaren and Hillman (1979), however, demonstrated that the cupula is fixed to the epithelium along the whole circumference of the semicircular canal in a manner similar to a diaphragm.

The sensory hair cells of the cristae ampullares are arranged in an orderly manner. The kinociliar poles of all hair cells in the horizontal semicircular canal are oriented towards the utricle. The preferred direction for depolarisation of these is therefore achieved by a utriculopetal flow of the endolymph. In the anterior and posterior semicircular canals the hair cell poles are pointing away from the utricle resulting in a hyperpolarisation of these during utriculopetal endolymph flow (Hudspeth and Corey, 1977; Löwenstein and Wersall, 1959).

1.2.3 Otolith Organs

The otolith or macular organs are located in the lining of the utricle and the saccule. They contain supporting cells and innervated hair cells and form shallow protrusions into the lumen. Like the sensory cells of the semicircular canals' cupulae, the hair cells of the otolith organs express numerous stereocilia as well as one kinocilium on their apical surface. These protrude into the statoconial membrane, a viscous layer of glycoproteins presumably secreted from the supporting cells. The surface of this layer contains the otoliths, crystallised sediments that largely consist of calcium carbonate and are deposited in calcite form. The embedding of otoliths into the statoconial membrane increases its specific weight to 2.71 times that of the surrounding endolymph (Carlström et al., 1953). Hence, linear acceleration acting on the head induces shearing of the statoconial membrane which, in turn, stimulates the sensory hair cells in the same way as in the cupulae.

In the saccule the macula is located on its inferior wall, whereas the utricular macula is situated on the lateral wall. Therefore the two maculae are positioned orthogonally and, according to the positioning of the semicircular canals, tilted approximately 30° backward from the horizontal plane of the head.

The macular hair cells are also arranged in an orderly manner but, in contrast to the cupulae, not all poles are pointing in the same direction. The macular surface possesses a curved longitudinal structure, called striola, that subdivides each macula into two areas. The striola of the utricular macula has the shape of a crest whereas that of the saccular macula forms a protrusion. The utricle's hair cells are oriented in a way that the hair cell poles on either side of the striola are pointing towards the crest. The saccular hair cell poles are oriented distally from the protrusion. Because the striolae do not follow a straight line and since the maculae are not flat but possess a three-dimensional curvature, linear acceleration in any direction stimulates at least a small number of hair cells of each otolith organ, given the acceleration is sufficiently strong (Wilson and Melvill Jones, 1979).

1.2.4 Central Projections

The first afferent neurone of the vestibular projection is a bipolar cell whose cell bodies form the vestibular ganglion in the vicinity of the internal auditory meatus. Their dendrites synapse onto the hair cells of the semicircular canals and otolith organs, the axons form the vestibular branch of the VIIIth cranial nerve. The fibres enter the brainstem on the level of the cerebello-pontine angle and are relayed onto the second vestibular neurone whose cell bodies are located in the vestibular nuclei on the floor of the fourth ventricle. Semicircular canal afferents mainly project onto the superior and medial vestibular nuclei. Fibres from the otolith organs are mainly relayed to the inferior vestibular nucleus. The lateral vestibular nucleus receives only little primary vestibular innervation but obtains primarily proprioceptive information via cerebellar afferences and is occasionally regarded as external cerebellar nucleus (Nieuwenhuys et al., 1988). A small proportion of labyrinthine efferences forms a direct and unrelayed projection to the ipsilateral vestibulocerebellum, the gigantocellular reticular nucleus of the reticular formation and to the lateral cuneate nucleus.

Apart from primary vestibular afferences, the vestibular nuclei receive projections from the cerebellovestibular and spinovestibular tracts as well as collateral projections from the spinocerebellar and accessory optic tracts. In addition, fibres from the reticular formation and from several oculomotor nuclei innervate the vestibular nuclei. Apart from the lateral vestibular nucleus, the vestibular nuclei also form numerous reciprocal connections via ipsi- and contralateral commissural fibres. A detailed review of the afferences and efferences of the individual vestibular nuclei and their functional roles is given in Carleton and Carpenter (1983), Graf and Wilson (1989) and in Nieuwenhuys et al. (1988).

Nieuwenhuys et al. (1988) divide the efferences from the vestibular nuclei into three classes. Fibres belonging to the first class project to the vestibulocerebellum either directly as mossy fibres or, after relay in the inferior olive, as climbing fibres. Those of the second class form a descending projection into the spinal cord as medial and lateral vestibulospinal tract or ascend to subcortical oculomotor nuclei. As will be seen below, these projections form part of the vestibulo-ocular reflex pathways. The last class of vestibular nuclei efferences ascends to the ventral posterolateral, posterior inferior and lateral thalamic nuclei (Lang et al., 1979). The thalamus relays projections to the neocortex of all but the olfactory sensory systems. Thalamocortical vestibular projections, which are likely to be responsible for the generation of conscious vestibular perception, terminate in the somatosensory Brodmann area 2v and 3a (Friberg et al., 1985), in the multimodal parieto-insular vestibular cortex (PIVC) described by Grüsser et al. (1982) and in frontal cortical areas (White and Brinkman, 1988).

1.3 Visual System

1.3.1 Retina

The sensory epithelium of the eye, the retina, is ontogenetically part of the diencephalon. Its precursor is present before closure of the neural tube and differentiates further during embryonic and foetal development to eventually form part of the eye. The transduction of light entering the eye into neuronal signals takes place in the retinal receptor cells, cones and rods. The different structure, physiological properties and placement of these cells gives rise to functional specialisation in the visual system. Cones are concentrated in the fovea, are spectrally tuned, thereby subserving colour vision, and possess low sensitivity but high acuity. Rods, in contrast, are concentrated in the retinal periphery, are monochromatic and very light sensitive but have lower temporal and spatial resolution. Three neuronal layers are contained in the retina and initial stages of visual processing take place not only through feedforward connections but also via horizontal and amacrine cells mediating contrast enhancement by lateral interactions. The first afferent neurones of the optic projection are the retinal bipolar cells which con- and diverge onto retinal ganglion cells, the second-order neurones of the visual system. Ganglion cells fall into two morphological categories that also form different functional entities. The parvocellular ganglion cells (P- or Pβ-cells) possess a smaller cell body and give rise to the so-called P-system which is largely responsible for the ability to see colour and static form of a stimulus. The M-system originates in the larger-bodied magnocellular ganglion cells (M- or Mα-cells). Its principal purpose is to mediate the perception of motion and dynamic form (Livingstone and Hubel, 1987, 1988).

1.3.2 Central Projections

The parvo- and magnocellular ganglion cell axons leave the retina at the optic disc from where they are myelinated and project as optic nerve and, postchiasmatically, optic tract to the lateral geniculate body of the posterior thalamus. Since the optic chiasm relegates fibres originating in the nasal hemiretina to the contralateral hemisphere, the lateral geniculate body contains a representation of the contralateral visual field. The lateral geniculate body consists of six histologically distinct cell layers that reflect the inputs from the different eyes and retinal ganglion cell types. Its cell bodies are arranged retinotopically according to the location of their receptive fields. Counted from ventrally, layers 2, 3 and 5 receive input from the nasal hemiretina of the contralateral eye whereas layers 1, 4 and 6 receive projections originating in the temporal hemiretina of the ipsilateral eye. The innermost layers 1 and 2 contain large-bodied neurones and, hence, are named magnocellular. The major source of their afferents stems from retinal Pα ganglion cells. Layers 3 to 6 have smaller, parvocellular, cell bodies and are innervated by retinal Pβ ganglion cells (Zeki, 1993; Mason and Kandel, 1991).

The axons of lateral geniculate body neurones form the optic radiation and terminate in layer 4 of the primary visual cortex, V1 or, according to Brodmann's cytoarchitectonic classification, area 17 (Brodmann, 1909). Possessing the highest degree of laminar differentiation in human neocortex, layer 4 can be histologically subdivided into three sublayers. Geniculofugal fibres of the M-system predominantly terminate in layer 4Cα, whereas those of the P-system mainly project onto layers 4Cβ. Layer 4B receives its major input from fibres of cortical origin and is the site of projection from magnocellular system neurones of striate cortical layer 4Cα (Mason and Kandel, 1991).

From there on, the magnocellular system projects to the so-called thick stripes of area V2 and then on to area V3, both in Brodmann area 18. Fibres from there form parallel pathways to area V5 of Brodmann area 19 that, in primate, is also referred to as middle temporal area (MT) and is engaged in the processing of motion and spatial stimulus properties as well as the generation of stereopsis. Originating there, further connections project to ventral intraparietal (VIP) cortex, middle superior temporal (MST) cortex and to parietal cortical area 7a (DeYoe and Van Essen, 1988).

Two subdivisions within the parvocellular system exist in visual cortex. The parvocellular interblob system, sensitive to the orientation of visual stimuli, projects from neurones in layer 4Cβ of area V1 to the so-called interblobs of primary visual cortex layers 2 and 3. From there projections arise to the pale stripes of area V2 and, via V4 to the inferior temporal lobe. The parvocellular blob system, concerned with the processing of colour, projects directly from the lateral geniculate body to the so-called blobs of striate cortex layers 2 and 3 and then to the thin stripes of area V2 (Tootell et al., 1988). After relay in area V4 in Brodmann area 19 the projection reaches inferior temporal cortex (DeYoe and Van Essen, 1988).

Based upon the neuroanatomical location of the visual cortical areas involved, the motion-processing pathway outlined above has been referred to as dorsal stream by Mishkin et al. (1983) and contrasts the more form- and colour-sensitive ventral stream. The ventral stream is engaged in the identification of stimuli in the visual field and has therefore also been termed "what system". As outlined above, it projects through more ventral occipital areas and terminates in inferior temporal association areas. The motion-sensitive projection, also engaged in the localisation of stimuli ("where system") occupies a more dorsal location and eventually projects into parietal association areas.

1.3.3 Extrageniculate Pathways

Apart from the principal visual pathway whose first relay location distal from the retina is in the lateral geniculate body, additional retinofugal projections exist that terminate in the thalamic pulvinar. Further important pathways exist that do not possess any direct connection with the thalamus. In one of these, axons of retinal ganglion cells terminate in the superior colliculus and synapse onto neurones whose axons project to the pulvinar. From there, ascending fibres connect to striate and extrastriate visual cortex – Brodmann area 17 to 19 (Nieuwenhuys et al., 1988).

Additional subcortical nuclei exist that receive axons mainly stemming from ganglion cells of the contralateral eye but that are not part of a primary corticopetal projection. These are located in the pretectal region that contains the nucleus of the optic tract (NOT), the pretectal olivary nucleus and the anterior, medial and superior pretectal nuclei. The accessory optic system is formed by ganglion cell axons that lie in the optic tract, leave it distally of the lateral geniculate body and terminate on neurones of the dorsal, medial and lateral terminal nuclei of the optic tract. These terminal nuclei possess reciprocal connections with the nucleus of the optic tract which plays an important role in the generation of certain eye movements. Furthermore, the terminal nuclei of the optic tract send axons to the dorsal ramus of the inferior olivary nucleus from where climbing fibres project into the cerebellum.

1.4 Oculomotor System

The eyes are connected to the orbit via three pairs of extraocular muscles. Individual muscles within these pairs are oriented antagonistically with respect to their direction of pull, so that, in primary position, they cause movements of the eyeball in opposite directions. The lateral and medial rectus muscles exclusively mediate horizontal abduction and adduction of the eye. All other extraocular muscles, however, mediate simultaneous vertical and horizontal eye movements. The third cranial, or oculomotor, nerve innervates the superior, inferior and medial rectus muscles as well as the inferior oblique muscle. The superior oblique muscle is innervated by the fourth cranial, or trochlear, nerve. The abducens nerve (sixth cranial nerve) innervates the lateral rectus muscle. These cranial nerves contain the axons of the α- and γ-motoneurones whose cell bodies lie in the respective brain stem nuclei.

The biological purpose of eye movements is twofold. Firstly, they enable the organism to actively position the projection of a visual stimulus of interest onto the retinal fovea where highest visual acuity is ensured. Secondly, they allow the observer to maintain this foveal projection and a stable retinal image of the visual environment during simultaneous motion of the visual stimulus, the observer's head, or of both. This purpose is accomplished through five different principal classes of eye movements for each of which a dedicated neuronal control system has evolved. These are vestibular, optokinetic and saccadic eye movements as well as smooth pursuit and vergence movements. Since the oculomotor experiments of this thesis only modulate the first two types of movements, only these shall be explained in more detail.

1.4.1 Vestibulo-ocular Reflexes

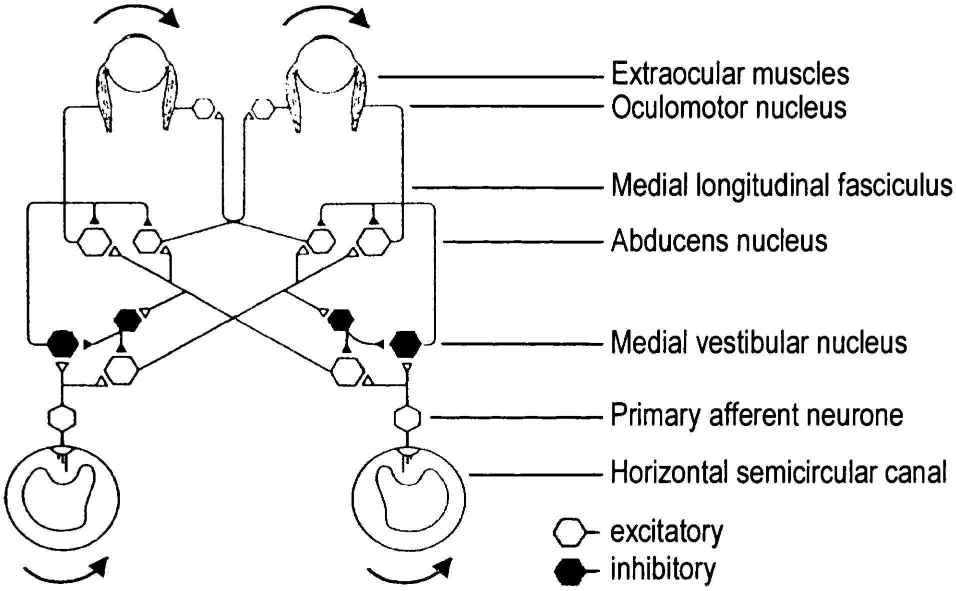


__Figure 1.1__ The principal neural pathways involved in the generation of the slow phase eye movement of the horizontal rotational vestibulo-ocular reflex. See text for further explanation. After Curthoys and Halmagyi (1995)

Vestibular eye movements occur as a consequence of, active or passive, motion of the head in space that stimulates the peripheral labyrinthine receptor organs. These eye movements are involuntary and it is usually not possible to fully suppress them in darkness without the presence of a (real or imaginary) fixation target. The vestibulo-ocular reflex compensates a displacement of the eye in space caused by a head movement by initiating a slow eye movement in the opposite direction. During larger-amplitude or longer-lasting head movements, the slow eye movement is followed by a rapid saccadic repositioning of the eye in the orbit in the same direction of that of the head movement. This mechanism prevents the eye reaching an end point in the orbit and ensures the maintenance of pursuit of the visual environment. The rhythmic alternation of slow and fast phase eye movements as a result of maintained vestibular stimulation is referred to as vestibular nystagmus. The efficiency at which the vestibulo-ocular reflex operates is underlined by its onset latency that can be as short as 14ms (Lisberger, 1981).

The basic neural substrate of vestibular eye movements is a three-neuronal reflex arc and shall be detailed with the example of the horizontal vestibulo-ocular reflex (Figure 1.1). During leftwards acceleration of the head around the longitudinal axis, hair cells of the right semicircular canal's cupula hyperpolarise and those of the left labyrinth depolarise. This depolarisation increases the firing rate of those primary vestibular afferents that terminate in the left vestibular nuclei, synapsing onto excitatory and inhibitory interneurones that, as a consequence, become depolarised. The axons of the excitatory interneurones cross the midline and project to the contralateral abducens nucleus depolarising motoneurones of the right lateral rectus muscle. Another set of excitatory commissural interneurones originate in this place which synapse onto motoneurones of the left medial rectus muscle. In order to induce a compensatory eye movement it is not sufficient to only contract the agonist muscles but it is also necessary to decrease contraction of the antagonists. Therefore, inhibitory interneurones of the left medial vestibular nucleus project to motoneurones of the left abducens nucleus and, in consequence, inhibit the lateral rectus muscle of the left eye. In addition, excitatory commissural interneurones that project to the right oculomotor nucleus are inhibited which decreases the tonic firing rate of right medial rectus motoneurones. The hyperpolarisation of neurones innervating the right horizontal semicircular canal gives rise to an inverted, and synergistic, pattern of excitation and inhibition of the contralateral neuronal and muscular structures (Carpenter, 1988; Leigh and Zee, 1991).

In the same way as endolymph flow in the horizontal semicircular canals elicits the horizontal vestibulo-ocular reflex, compensatory eye movements are carried out in response to the stimulation of other pairs of canals. In addition to rotational accelerations, compensatory eye movements can also be elicited by linear acceleration of the head, one example being the conjugated counterrolling of the eye following lateral head tilt relative to the direction of gravity. Linear accelerations along the naso-occipital, or x-axis, induce vergence movements of the eyes. Lateral head translation is compensated by horizontal eye movements and vertical eye movements are carried out in response to longitudinal translation (Gresty and Bronstein, 1992a; Gresty and Lempert, 2000).

1.4.2 Optokinetic Eye Movements

This form of eye movements is elicited during uniform motion of the visual environment under absence of any correlated vestibular stimulation. A situation like this can arise when motion of the head occurs at constant velocity for a prolonged period of time which is the case during transportation on trains and cars or during steady-state rotation on a rotating chair. Since, as has been discussed before, neither the cupulae nor the otolith organs are displaced in response to head motion at constant velocities, any vestibulo-ocular compensatory eye movements will cease to be efficient in stabilising a retinal image shortly after a steady-state velocity has been reached. In such circumstances optokinetic reflexes ensure a continuation of the compensatory nystagmic eye movements. Optokinetic nystagmus consists of the same eye movement pattern as vestibular nystagmus, a rhythmic sequence of a slow phase eye movement during which the visual environment is being pursued and a rapid, contradirectional saccadic repositioning of the eye in the orbit.

Optokinetic reflexes largely use the same neuronal pathways as vestibulo-ocular reflexes. A relative displacement between a large proportion of the visual environment and an observer increases the firing rate of those neurones in the vestibular nuclei that would also be depolarised during comparable vestibular stimulation (Dichgans and Brandt, 1978). The relegation of visual inputs onto vestibular nuclei neurones is achieved firstly through descending projections from the accessory optic system by axons whose cell bodies are located in the pretectal nucleus of the optic tract. In addition, fibres originating in the terminal nuclei of the optic tract project to the vestibulocerebellum and especially efferences from the medial terminal nucleus have been demonstrated to innervate mainly the contralateral superior and medial vestibular nuclei (Simpson, 1984). A further source of visual motion input onto vestibular structures has been postulated to stem from motion-sensitive visual cortical areas (Straube and Brandt, 1987; Straube et al., 1987). To date, no direct connection between visual cortex and vestibular nuclei has been demonstrated but several indirect pathways exist via the paramedian pontine and the mesencephalic reticular formation. Part of their cell bodies receive afferent input from the visual cortex and send their axons to the vestibular nuclei (Carpenter, 1988). Cortical areas MT (V5) and MST give rise to descending fibres which terminate in the inferior olive. From there, direct projections to the vestibular nuclei exist but it is also the origin of the climbing fibre system which, amongst others, innervates the vestibulocerebellar flocculus and nodulus. The cerebellum also possesses afferent connections by mossy fibres via the pontocerebellar tract. The pontine nuclei in turn receive fibres from the superior colliculi and therefore indirect input from visual cortical areas 17 and 18 (Bjaalje and Brodal, 1983; Gibson et al., 1978). One point of termination of this network are the vestibular nuclei which also receive direct afferences from the vestibulocerebellum.

1.5 Vestibulo-autonomic Influences

Many spatial reorientations of an organism with respect to gravity incur changes in intravascular orthostatic pressure that require compensation. For example, standing up from lying supine in humans increases the orthostatic, or hydrostatic, column between the heart and the distal extremities by factor six (Yates, 1996a). The maintenance of a steady rate of blood flow, and therefore tissue oxygenation under the varying orthostatic demands that occur during changes of posture and movement necessitates the regulation of peripheral blood pressure as well as of cardiac output. For this purpose, efficient control systems have evolved that continuously measure blood pressure by means of baroreceptors regulating central autonomic nervous system activity and thereby mediating adjustments in peripheral vessel diameter as well as causing direct cardiac effects. It can, however, be conceived that regulation might not only occur through autoreception but also be mediated by the vestibular system because of its principal ability to detect changes in head orientation that demand the adjustment of circulatory mechanisms. In line with this hypothesis, it has been demonstrated that the vestibular system is indeed involved in regulating blood pressure during spatial reorientations, especially those threatening orthostatic hypotension, by acting predominantly on the sympathetic nervous system and generating a "pressor" response (Doba and Reis, 1974; Yates, 1992; Yates, 1996a; Yates, 1996b).

More recently, behavioural evidence in humans was obtained demonstrating the existence of vestibular influences on the regulation of blood pressure and heart rate during anterior-posterior linear acceleration and lateral translations (Yates et al., 1999; Radtke et al., 2000). The notion of an involvement of the vestibular system in the execution of cardiac responses to spatial reorientations is supported by numerous studies demonstrating an abolishment, or a reduction, of these responses after lesions of the vestibular nerve or the vestibular nuclei (Yates, 1992; Yates and Kerman, 1998).

There are several sites in the central nervous system where vestibular signals can functionally converge onto sympathetic circuitries. Many neurones mediating sympathetic outflow are located in the raphe nuclei of the caudal medulla (Morrison and Gebber, 1982; Morrison and Gebber, 1984; Morrison and Gebber, 1985) and in the reticular formation of the lateral and the rostral ventrolateral medulla (Barman and Gebber, 1985; Dampney et al., 1987) where pacemaker neurones are located that initiate tonic sympathetic activity (Sun et al., 1988). A large number of those neurones respond to stimulation of the labyrinth, preferentially to head rotation in the vertical plane (Yates et al., 1991; Yates et al., 1993). Using antero- and retrograde tracer techniques and electrical stimulation, it has further been demonstrated that neurones located in the vestibular nuclei project to the lateral and ventrolateral portion of the nucleus tractus solitarii which plays an important role in cardiovascular regulation (Yates et al., 1994; Balaban and Beryozki, 1994). The first synapse of the carotid sinus baroreflex pathway is located there and electrical stimulation leads to a reduction of sympathetic activity, presumably resulting from an inhibitory influence of the nucleus tractus solitarii on the rostral ventrolateral medulla (Biaggioni et al., 1998).

Neuroanatomical, neurophysiological and behavioural evidence are in agreement that vestibulo-autonomic pathways mainly influence blood pressure regulation through action on the smooth muscles in the blood vessels and appear to have little direct influence on the parasympathetic nervous system and on the vagal control of heart rate (Yates and Kerman, 1998) although they clearly affect cardiac action sympathetically (Radtke et al., 2000).

1.6 Aims of this Thesis

The topics of optokinetic stimulation and of visually induced self-motion sensation have received considerable research interest over the past decades. Numerous studies have been conducted identifying relevant stimulus parameters, studying several perceptual and a multitude of oculomotor effects. However, only few attempts have been made to systematically compare the two distinct and mutually exclusive perceptual interpretations of visual motion originating either from object-motion or from vection with respect to other behavioural, perceptual and physiological consequences.

At first glance, the transition from perceiving object-motion to perceiving circularvection during sustained and unchanged optokinetic stimulation might appear as a purely perceptual phenomenon. However, this perceptual shift ought to bear some important ecological relevance for an organism since a sudden onset of whole-body self-motion should require a number of compensatory, protective and predictive behavioural and attentional measures to be carried out in order to cope appropriately with a sudden reorientation in space.

The initial hypothesis of the present body of work was therefore that such a fundamental change in perception and cognition of the interrelations between one's own body and the environment might be accompanied by adaptive changes in a number of physiological variables. It was therefore the aim of this thesis to identify and subsequently quantify physiological changes that correlate with the perceptual states observers report during optokinetic stimulation.

An obvious starting point in this search was to study the reflex directly associated with full-field visual motion stimulation – optokinetic nystagmus. The first two experimental chapters present a number of experiments measuring torsional and horizontal optokinetic nystagmus and correlating various oculomotor parameters with whether observers were reporting the perception of object-motion or that of rollvection (Chapter 2) or yawvection (Chapter 3) at the time of recording.

Chapter 4 consists of two studies investigating the neural correlates of the perceptual states induced by torsional optokinetic stimulation. The first experiment used functional magnetic resonance imaging in order to determine changes in cerebral blood flow when subjects switched between perceptual states. The subsequent experiment was designed to further investigate the electrophysiological state of early occipital cortex during the differential states of motion-perception. Observers viewed a central checkerboard-reversal stimulus that was superimposed onto a large-field optokinetic stimulus and had their visually evoked potentials recorded whilst continuously indicating which perceptual state they were experiencing.

Chapter 5 presents the measurement of the autonomic nervous system parameters peripheral arterial blood pressure and tissue perfusion. The effects of real whole-body reorientation around the sagittal axis, achieved by tilting subjects in a flight simulator, were compared with those of illusory self-motion perception in the same direction, accomplished by inducing rollvection in the observers using torsional optokinetic stimulation.

In Chapter 6, torsional optokinetic stimulation was used to induce the illusion of whole-body tilt in observers who, seated in a flight simulator, had to indicate their perception of verticality as well as to report the perception of object-motion versus circularvection. The aim of this paradigm was to determine whether there is a correlation or dissociation between the perception of tilt and that of circularvection, both consequences of the same torsional optokinetic stimulus.

2 Oculomotor Correlates: Torsional Optokinetic Nystagmus

2.1 *Experiment 1: Upright Observers*

2.1.1 Introduction

Brecher (1934) was the first researcher to discover the presence of binocular torsional nystagmus under visual roll stimulation by observing conjunctive blood vessels of the subjects' eyes via a telescope. Since then, optokinetically induced torsional eye movements have been investigated by numerous groups with systematic variations of head and body position (Merker and Held, 1981; Morrow and Sharpe, 1993), in microgravity (Young et al., 1981; Cheung et al., 1995), with modifications of several stimulus features (Kertesz and Jones, 1969; Wade et al., 1991), at different stimulus velocities (Collewijn et al., 1985) and using stimuli rotating continuously or oscillating sinusoidally (Cheung and Howard, 1991; Cheung et al., 1995). A significant attribute of torsional optokinetic nystagmus is that it is involuntary since naive normal subjects have little voluntary influence over their torsional eye movements.

Few studies have examined whether the shift between the perception of visual motion as object-motion and self-motion coincides with changes in induced optokinetic eye movements. Finke and Held (1978) presented their participants with an optokinetic stimulus subtending 122° of visual angle and rotating at a constant velocity of 40°/s. They measured the elicited torsional optokinetic nystagmus with the afterimage method first described by Wells (1794, cited after Wade, 1996). Prior to the onset of optokinetic stimulation a stroboscope flash was used to induce a retinal afterimage in form of a horizontal bar. The subjects were presented with a line superimposed onto the optokinetic stimulus and were instructed to continuously align this with the retinal afterimage. The authors found eye movements and perceptual state to be "(...) relatively independent (...)" (ibid., p. 340) but this might be due to their chosen method of measuring torsional eye movements since the afterimage method is rather limited in its ability to detect dynamic oculomotor processes. Similarly, using scleral search coils, Cheung and Howard (1991) reported that they could find no correlation between the onset or offset of rollvection and changes in quality of torsional eye movement but did not provide quantitative evidence for this assertion. In view of this limited evidence, the object of the present experiment was to assess the behaviour of torsional eye movements related to the presence or absence of circularvection using 3-dimensional videooculography, a method that offers high spatial resolution at low levels of invasiveness and discomfort.

2.1.2 Materials and Methods

Subjects

Two women and six men, from 22 to 50 years of age (mean 34.3 years), without history of relevant neurological or sensory disease, consented to participate in the experiment. All had normal vision or were mildly myopic, and had no difficulty in fixating the stimulus without the need of corrective lenses. Informed consent had been obtained from all subjects prior to the start of the experiment.

Apparatus

The stimulus (see Figure 2.1) consisted of a cone whose maximum diameter was 58 cm with a depth of 25 cm. The inside of the cone was painted black and eight stripes of fluorescent tape, each 20 mm wide, had been fixed radially to the inner surface. The stripes joined at the apex of the cone, where a black circle of 20 mm diameter was fixed. Prior to each session, the fluorescent stripes were charged by 10 s illumination with a 60W light bulb at approximately 80 cm distance. Trials started 30 s after illumination had terminated. In darkness, the luminance of the black background was below 0.01 cd/m^2. The luminance of the fluorescent stripes decayed according to the power function $L = 1.31t^{-0.61}$, with a determination coefficient $r^2 = 0.96$. The corresponding contrasts calculate as 0.89 for the beginning of the recording and 0.67 for the end as demonstrated in Figure 2.2.

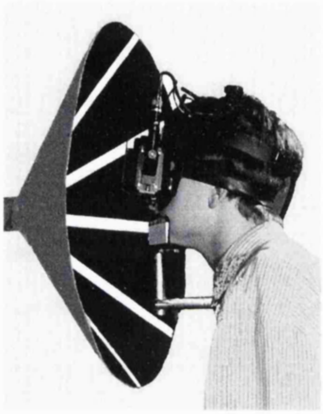


***Figure 2.1** Upright subject wearing the video-oculography spectacles and sitting in front of the optokinetic stimulus*

The cone was driven by an electrical motor, which was fixed at the back of the apex. Angular speed was regulated and kept constant by a standard power supply. Subjects were sitting upright with their head on a chin rest and the axis of rotation of the stimulus cone was rotated into alignment with the subjects' line of sight. The apex of the cone was maintained at a distance of 28 cm from the viewer's nasion.

Eye Movement Recording

Continuous monocular recording of the subjects' left eyes was obtained by means of an infrared camera and infrared light emitting diodes mounted in a headframe as shown in Figure 2.1. The eye was illuminated and filmed via a dichroic mirror, so that the recording equipment was invisible for the subject. At an eye-to-eye distance of 69 mm, the aperture of the recording device allowed non-restricted vision of approximately 90° width and 70° height. Camera signals were recorded at the PAL/CCIR standard of 50 fields/s. Three dimensional eye movement analysis was carried out offline, using the SensoMotorics Instruments, Teltow, Germany, system re-sampling at

25 frames/s and with a spatial resolution of approximately 0.1° for torsional eye movements.

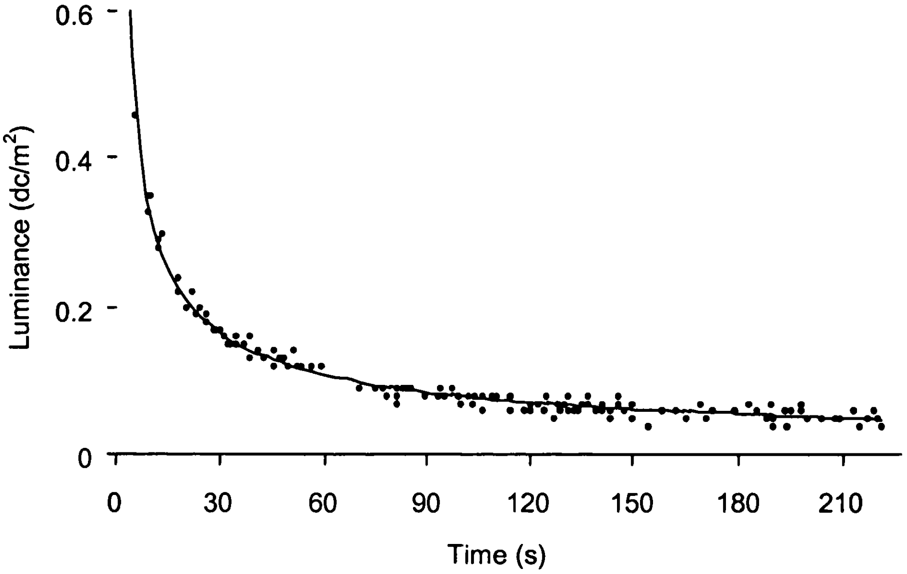


Figure 2.2 Luminance decay of the fluorescent stimulus elements after termination of 10 s illumination at 60 W. The power function $L=1.31t^{-0.61}$ *fits the data with* $r^2=0.96$

Procedure

After illumination of the stimulus, testing began with 30 s baseline, which allowed the stimulus luminance to settle, followed by 5 min clockwise optokinetic stimulation at a velocity of 60°/s during which time eye movements were recorded. Subjects viewed the stimulus with both eyes and were instructed to fixate the spot in the centre of the cone and to avoid eye blinks during recording. They signalled the perception of rollvection, which was defined as the perception of self-rotation instead of self-tilt, by depressing a pushbutton.

Data Analysis

Torsional eye position recordings were displayed on a personal computer and subjected to further offline analysis. Over all oculomotor recordings acquired, every single torsional nystagmus slow phase was identified visually and fitted with a linear regression line, the slope of which equals the mean eye velocity during the corresponding slow phase. For each subject the obtained regression slopes were pooled with respect to whether their slow phases were performed during perception of object motion or during CV. Accordingly, two average slow phase velocities were computed, one for the sensation of stimulus motion, one for the sensation of vection.

Mean torsional eye position data were computed automatically by averaging the eye position values with respect to the perceptual state in which they were recorded. Again, for each subject one average was obtained for vection, one for object motion perception.

2.1.3 Results

Psychophysical Data

Following optokinetic stimulation onset, all subjects reported perceiving circularvection with an average onset latency of 15.4s (SEM 5.3s). Two subjects perceived one epoch of circularvection and the remainder reported between 3 and 12 epochs. Of note, the two subjects reporting only one period of self-motion perception were the female participants but no significant correlation between gender and number of vection periods reported was obtained ($r=0.66$; $p>0.05$; t-test). Mean number of vection periods perceived was 4.9 (SEM 1.3). Average time spent perceiving self-motion was 134.0 s (SEM 28.6 s), or 44.7% of total trial duration, with the remaining average 166.0 s per trial spent perceiving object-motion.

Oculomotor Responses

The rotating cone evoked a typical pattern of torsional optokinetic nystagmus with slow phases in the direction of cone rotation and fast phases in the opposite direction. As shown in Figure 2.3, mean slow phase velocity was 2.29°/s (SEM 0.33°/s) during the perception of object-motion and rose to 3.71°/s (SEM 0.58°/s) when subjects reported circularvection. This difference, an average 1.42°/s (SEM 0.34°), which constitutes a relative increase in slow phase velocity by 62%, was highly significant in a paired t-test ($p<0.01$; two-tailed) with all of the subjects showing an increase in slow phase velocity when perceiving circularvection.

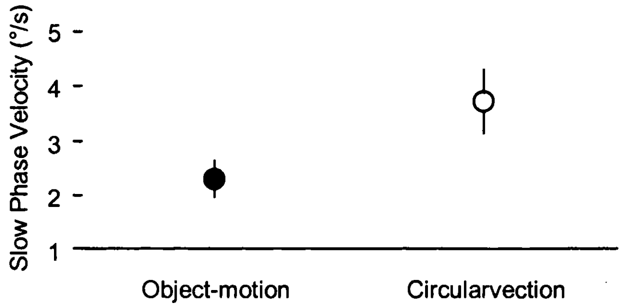


Figure 2.3 Change (mean ±SEM) in torsional optokinetic nystagmus slow phase velocity between the perception of object-motion and circularvection in upright observers

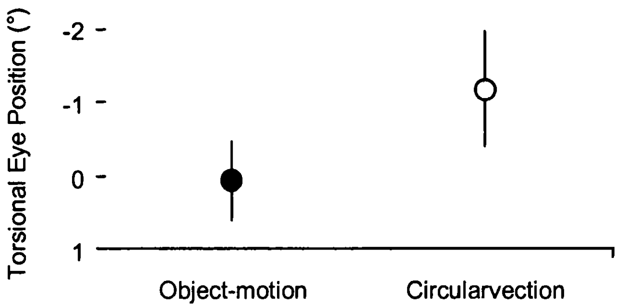


Figure 2.4 Means and standard errors of mean torsional eye position during the perception of object-motion and circularvection during upright viewing

Mean torsional eye position was 0.07° (SEM 0.54°) during the perception of object-motion and shifted anticlockwise to a mean position of –1.18° (SEM 0.79°) during the perception of self-motion as can be seen in Figure 2.4. On average the difference in eye position was –1.26° (SEM 0.61°). However, only six subjects demonstrated an anticipatory positional shift during perceived circularvection and a paired t-test demonstrated the difference of eye position during the two perceptual states to be only marginally statistically significant (p=0.08; two-tailed).

2.1.4 Discussion

In summary, the results of the present experiment demonstrate the existence of a systematic relationship between certain objective oculomotor parameters and subjective reports about the perceptual interpretation of a moving visual full-field stimulus as originating from stimulus-motion or from self-motion relative to a stationary stimulus. Although generally low in gain (Kertesz and Jones, 1969), torsional optokinetic nystagmus slow phase velocity showed a consistent and significant increase when subjects perceived circularvection, compared to when they felt stationary. Furthermore, throughout the trial subjects' torsional eye position was on average oriented towards the oncoming visual field and was not "pulled" in the direction of visual stimulus rotation. Comparing torsional eye position during the differential perceptual states, there appeared to be a tendency for the torsional beating field to deviate further in the direction opposite to stimulus motion when subjects perceived circularvection with average eye position closer to primary torsional gaze during the perception of object-motion. This effect was, however, not statistically significant in the present experiment and shall therefore not receive a detailed interpretation at this stage.

The finding of increased optokinetic nystagmus slow phase velocity during the perception of self-motion stands in contrast to the findings of a study measuring eye movements during torsional optokinetic stimulation using an afterimage method (Finke and Held, 1978). The authors reported not having found any relationship between torsional eye movements and the perceptual state induced in an observer. Although their stimulus was rotated at a speed of 40°/s, two thirds of the velocity used in the present experiment, the most obvious reason for the different findings are the methods that have been used to measure torsional eye movements. The spatial as well as the temporal resolution of videooculography is far superior to those of the afterimage method (Howard and Evans, 1963) and it can easily be conceived that the minute and dynamic changes in torsional slow phase velocity reported here are impossible to detect with the afterimage method. Another reason for the negative finding of Finke and Held (1978) might, however, have been introduced by the afterimage method itself since it requires the continuous presentation of a stationary reference line in the visual field of the observers that itself might inhibit the eye to deviate from the torsional primary position. 14 years before the study of Finke and Held (1978), Howard and Templeton (1964) have claimed it to be essential for the study of visually induced ocular torsion not to introduce any stimuli in an observer's visual field that are not to be tested specifically for their ability to induce ocular torsion. The authors go further and write "(...) this requirement rules out any method of measuring eye torsion in which the subject has to align (...) after-images (...) or other visible objects)" (ibid., p. 433).

A greater challenge for the results of the present experiment are posed by Cheung and Howard (1991) who studied torsional nystagmus slow phase velocity during sustained as well as during sinusoidally oscillating optokinetic stimulation and did not find any relation between torsional nystagmus and the sensation of vection or whole-body tilt. Firstly, however, their stimulus differed from the one used in the present experiment in that it consisted of a larger proportion of white elements (75%) and had a higher contrast between black and white elements (98%). Furthermore, subjects were seated at more than twice the distance from the stimulus and could see the stationary laboratory environment in their peripheral visual field. A number of studies have found the ability of a stimulus to induce the perception of self-motion to be influenced by several factors like its angular velocity, temporal and spatial frequencies (Brandt et al., 1973; Howard and Heckmann, 1989; de Graaf et al., 1990). More likely to be responsible for their negative finding, however, is the fact that they used scleral search coils to record torsional eye movements. The application of the search coils that are mounted on contact lenses causes considerable discomfort in the subject and requires local anaesthesia of the sclera. Furthermore, it cannot be fully excluded that a small degree of slippage occurs between the sclera and the contact lens which, although minute, might prevent the detection of such minimal changes in slow phase velocity as are reported here.

2.2 Experiment 2: Supine Observers

2.2.1 Introduction

The previous experiment demonstrated that slow phases of torsional optokinetic nystagmus are executed at a markedly higher velocity when subjects perceive circularvection than when observers feel themselves to be stationary. In the previous experiment, observers were sitting upright and the optokinetic stimulus was rotated around an earth-horizontal axis. As has been detailed before, optokinetic stimulation around an off-vertical axis does not only induce the perception of circularvection but also the simultaneous perception of a static whole-body tilt in the direction of perceived self-motion due to the presence of graviceptive conflict (Dichgans et al., 1972; Young et al., 1975). It remains to be determined whether the observed changes in torsional eye movements that occur when observers shift from one perceptual state to another will still be present and, if so, whether they are of similar quality and magnitude, when the perception of self-motion is induced without the simultaneous presence of a graviceptive conflict and perceived tilt. It is therefore the purpose of the subsequent experiment to record torsional eye movements of observers who are lying on their back and watch the optokinetic stimulus revolving around their then earth-vertical naso-occipital axis.

2.2.2 Materials and Methods

Subjects

Three women and five men, from 22 to 50 years of age (mean 32.8 years), without history of relevant neurological or sensory disease, consented to participate in the experiment. All had normal vision or were mildly myopic, and had no difficulty in fixating the stimulus without the need of corrective lenses. Informed consent had been obtained from all subjects prior to the start of the experiment.

Apparatus

The stimulus (see Figure 2.1) was identical to the one that has been used in the previous experiment and, again, was illuminated by a 60W bulb for 10 s prior to the start of a trial. Subjects were lying supine with their head in a mould and the axis of rotation of the stimulus cone was rotated into alignment with the subjects' line of sight. The apex of the cone was maintained at a distance of 28 cm from the viewer's nasion.

Eye Movement Recording

The same videooculography device and recording procedure as in the previous experiment was used.

Procedure

As before, trials and eye movement recording started following the termination of stimulus illumination. Trials consisted of 30 s baseline and 5 min clockwise optokinetic stimulation at 60°/s. Subjects viewed the stimulus binocularly, had been asked to fixate the centre of the cone as well as to reduce eye blinks and signalled the perception of circularvection using a pushbutton.

Data Analysis

After digitisation, raw recordings were analysed in the same way as for the previous experiment. For each subject and perceptual state, average torsional nystagmus slow phase velocity and average torsional eye position were computed.

2.2.3 Results

Psychophysical Data

Following optokinetic stimulation onset, all subjects reported perceiving circularvection with an average onset latency of 20.8 s (SEM 5.8 s). Subjects reported perceiving between 4 and 14 epochs of circularvection. Mean number of vection periods perceived was 8.8 (SEM 1.3). Average time spent perceiving self-motion was 130.9 s (SEM 20.1 s), or 43.6% of total trial duration (300 s), with the remaining 169.1 s spent perceiving object-motion..

Oculomotor Responses

Torsional nystagmus was performed by all subjects throughout the duration of optokinetic stimulation and all subjects demonstrated an increase in slow phase velocity during circularvection. During the perception of object-motion, mean slow phase velocity was 2.74°/s (SEM 0.54°/s) and rose to 4.30°/s (SEM 0.74°/s) during circularvection which constitutes a mean difference of 1.56°/s (SEM 0.57°/s). This relative increase in slow phase velocity by 57% was significant in a paired t-test ($p<0.05$; two-tailed). See Figure 2.5.

During perceived object-motion, mean torsional eye position was –0.25° (SEM 0.87°), whereas during self-motion perception it deviated anticlockwise to a mean position of –1.19° (SEM 1.11°) as can be seen in Figure 2.6. However, only six subjects responded with a shift of torsional eye position in the direction of perceived heading and a paired t-test demonstrated the difference (mean –0.94°, SEM 0.41°) of eye position during the two perceptual states to be only marginally statistically significant (p=0.05; two-tailed).

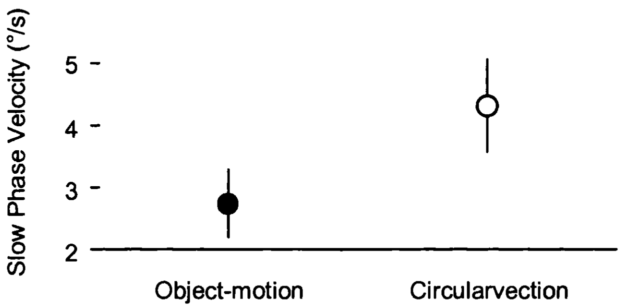


Figure 2.5 *Means and standard errors of torsional optokinetic nystagmus slow phase velocity during the perception of object-motion and circularvection in supine subjects*

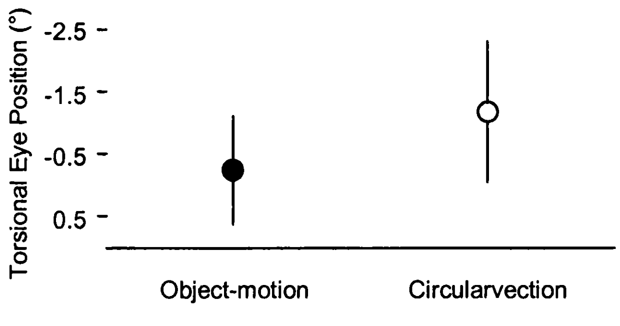


Figure 2.6 *Means and standard errors of mean torsional eye position during the perception of object-motion and circularvection in subjects lying supine*

Comparison with Experiment 1

Since the samples of Experiments 1 and 2 were not identical, statistical comparisons between the oculomotor parameters obtained during upright and supine viewing of the optokinetic stimulus have been performed using two-samples t-tests. Neither the comparison of slow phase velocities acquired during the perception of object motion nor of those obtained during circularvection were significant (all $p>0.05$). Similarly, torsional eye position did not differ significantly between experiments in either perceptual state (all $p>0.05$). Furthermore, statistical comparison of the differences in slow phase velocity and mean eye position between perceptual states across experiments did not reveal any significance (all $p>0.05$).

2.2.4 Discussion

In summary, this experiment shows that torsional optokinetic nystagmus also undergoes systematic, perceptual state-related changes when observers are lying supine with optokinetic stimulation occurring around an axis that is aligned with the gravitational vector. The changes observed in this experiment seem equivalent to the ones seen in the previous study. During circularvection, torsional nystagmus slow phase velocity rises by a similar relative amount than it does in upright subjects and in both circumstances a tendency for a shift in mean torsional eye position in the direction of perceived self-motion by about 1° can be observed.

None of the oculomotor parameters obtained differed statistically between this and the previous experiment that was identical apart from observers sitting upright whilst viewing the optokinetic stimulus. The results therefore replicate the findings of the first experiment and demonstrate that, irrespective of the body position, torsional nystagmus slow phase velocity is enhanced when observers perceive the optokinetic stimulation to be caused by sustained contra-directional self-motion with respect to a stationary visual stimulus.

The two experiments conducted have demonstrated a systematic facilitation of torsional optokinetic nystagmus during the perception of circularvection in the presence as well as the absence of the simultaneous perception of whole-body tilt. This design could not identify the effects of observers' body position. Because of sampling differences within-subjects comparison of the two experiments was not possible and no conclusions about interactions between perceptual states and graviceptive conflict could be drawn. The next experiment addressed these questions by deploying a repeated-measures design.

2.3 Experiment 3: Upright and Supine Observers

2.3.1 Introduction

The perceptual effects of optokinetic stimulation in roll under varying body positions are similar in that in both conditions the illusory perception of continuous self-motion can be elicited. The difference, however, is that during upright viewing, subjects also perceive a sustained illusion of body tilt in a direction opposite to visual environment rotation. The experiments conducted so far demonstrate a relation between torsional optokinetic nystagmus and the spontaneously alternating perceptual interpretations of one and the same moving visual stimulus. Irrespective of the body position assumed by observers and the tilt illusion induced, a similar enhancement of torsional nystagmus slow phase velocity can be observed when observers perceive the relative motion to originate from sustained self-rotation with respect to a stationary visual surround. Similar to the perceptual switches elicited by viewing a Necker cube, optokinetic motion in roll induces a bistable percept with observers switching spontaneously between the perception of object-motion and that of circularvection, although the former switches occur suddenly whereas the perception of vection often develops gradually from the perception of object-motion (see e.g. Wertheim, 1994). Since several of these perceptual transitions occur during the course of a trial, the oculomotor changes observed are not confounded with a temporal order and cannot merely be explained by a slow build-up of optokinetic nystagmus slow-phase velocity over time (Yee et al., 1979; Mossman et al., 1992).

There are, however, a number of questions that have not been addressed by the previous experiments. Both studies have used an optokinetic stimulus rotating at a speed of 60°/s and it would be of interest to examine the oculomotor behaviour under a wider range of velocities. Furthermore, in order to assess a potential systematic role of the variation of body positions on torsional optokinetic nystagmus itself as well as on the observed percept-related changes, it is necessary to vary body position in a within subjects design. This will also increase the statistical power and might therefore elucidate the effect of perceptual state on mean torsional eye position.

2.3.2 Materials and Methods

Subjects

Two women and four men, from 23 to 50 years of age (mean 33.5 years), without history of relevant neurological or sensory disease, consented to participate in the experiment. All had normal vision or were mildly myopic, and had no difficulty in fixating the stimulus without the need of corrective lenses. Informed consent had been obtained from all subjects prior to the start of the experiment.

Apparatus

The same stimulus as in the previous two experiments was used (Figure 2.1). As before, the fluorescent stripes were charged by 10 s illumination with a 60W light bulb prior to each trial. Trials started 30 s after illumination had terminated.

Subjects were either sitting upright with their head on a chin rest or lying supine with their head resting in a mould. In either condition, the axis of rotation of the stimulus was rotated into alignment with the subjects' line of sight with the fixation target kept at a distance of 28 cm from the viewer's nasion.

Eye Movement Recording

The same videooculography device and recording procedure as in the previous experiments was used.

Procedure

Subjects were tested on two consecutive days, with 3 trials per day. Trials consisted of 30 s baseline and of 3 min clockwise optokinetic stimulation at a stimulus velocity of 30°/s, 45°/s and 60°/s, respectively. Eye movements were recorded for the duration of a trial. The sequence of velocities was varied according to a Latin square and reversed on the following day. Trials were interspersed with a rest period of 5 min. Half of the subjects were tested sitting upright on the first day and lying supine on the following day. The other half were tested in the opposite order.

Subjects viewed the stimulus with both eyes and were instructed to keep looking at the fixation target and to try to suppress eye blinks during recording. They signalled the perception of rollvection by depressing a pushbutton. During the 5 min rest, they were asked to keep their eyes closed and during this time the fluorescent stripes were recharged.

Data Analysis

For each subject, mean slow phase velocities were computed the same way as in the analysis of the previous two experiments at all combinations of body positions, stimulus velocities and perceptual states. Since this experiment utilised a range of optokinetic stimulus velocities, average slow phase velocities were normalised with respect to the stimulus velocity and their gain was calculated as torsional oculomotor slow phase velocity over angular stimulus velocity. Similarly, individual mean torsional eye position was obtained for the same combinations of conditions.

To test whether subjects maintained fixation of the central target, standard deviations of horizontal and vertical eye position were computed for each subject and session.

2.3.3 Results

Psychophysical Data

Table 2.1 *Means and standard errors (in brackets) of the psychophysical parameters measured at different combinations of optokinetic stimulus velocity and body position*

Body Position	Upright			Supine		
Stim. Vel. (°/s)	30	45	60	30	45	60
Number of Vection Epochs	5.5 (1.5)	6.0 (1.5)	6.3 (1.6)	5.3 (1.7)	5.8 (1.2)	6.2 (1.4)
Onset Latency (s)	26.1 (5.7)	24.7 (15.2)	30.2 (21.4)	51.3 (27.0)	19.2 (5.4)	38.2 (19.2)
Average Duration of Vection (s)	15.5 (2.3)	18.8 (9.1)	13.9 (5.9)	17.0 (3.1)	10.2 (3.1)	13.6 (2.7)

Subjects reported perceiving self-motion, albeit intermittently, at all stimulus velocities and in both body positions. The average number of vection onsets per trial and subject was 5.9, with an average duration of 14.8 s. On average, the onset latency of the first perception of rollvection per trial was 31.6 s. These values showed a high interindividual variability and did not differ significantly between body positions or stimulus velocities in two-way repeated measures ANOVAs (all $F<1$). A priori one would have expected the vection onset latency to be shortened when lying supine, because the effect of gravity pull is then abolished. Since per subject and condition only one latency value was obtained, statistical power might have been too small to detect such an effect and would require further investigation using several trials per subject and condition. A detailed listing of the psychophysical parameters measured in the experimental conditions is given in Table 2.1.

Table 2.2 shows the psychophysical variables grouped by the number of trial during which they were obtained. One-way repeated measures ANOVAs with time as within-subjects factor detected no significant effect of time on onset latency of the first epoch of circularvection reported ($F_{5,25}=1.8$; $p>0.15$) nor on average duration of vection epochs ($F_{5,25}<1$). There was, however, a significant effect of time on the average number of vection sensations per trial ($F_{5,25}=4.5$; $p<0.01$). Post-hoc planned comparisons revealed a significant quadratic ($F_{1,5}=10.8$; $p<0.05$) and cubic contrasts ($F_{1,5}=10.7$; $p<0.05$) As Table 2.2 demonstrates, this effect is likely to be caused by the larger number of vection sensations in trials 1 and 4, the first trials of each day of testing.

Table 2.2 *Time course of means and standard errors (in brackets) of the psychophysical parameters obtained*

Trial Number	1	2	3	4	5	6
Number of Vection Epochs	7.8 (0.9)	5.0 (1.6)	4.7 (1.4)	6.5 (1.4)	5.8 (1.4)	5.3 (1.5)
Onset Latency (s)	13.1 (3.5)	62.6 (28.3)	32.4 (12.9)	15.8 (5.8)	32.8 (21.0)	32.9 (15.0)
Average Duration of Vection (s)	10.6 (1.8)	12.3 (3.3)	13.0 (3.8)	18.4 (7.3)	18.2 (6.7)	16.3 (9.9)

Oculomotor Responses

Torsional Optokinetic Nystagmus

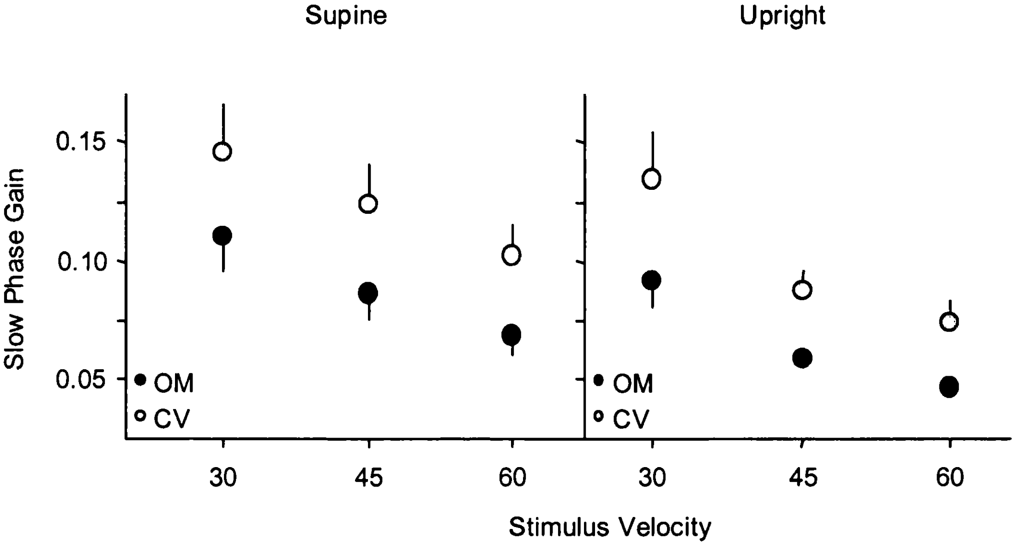


Figure 2.7 *Changes in torsional optokinetic nystagmus gain between perception of object-motion (OM) and circularvection (CV) at various stimulus velocities. Note the gain-enhancing effect of supine body position*

In all trials, subjects exhibited torsional optokinetic nystagmus throughout stimulation. Means and standard errors of torsional nystagmus slow phase gain under the different combinations of body positions, stimulus velocities and perceptual states are displayed in Figure 2.7 and are listed in Table 2.3. During circularvection, gains increased by a factor of 1.46 at a stimulus speed of 30°/s, 1.47 at 45°/s and 1.61 at 60°/s when subjects were sitting upright whilst viewing the stimulus. In sessions with subjects lying supine, the according gain enhancement factors during vection were 1.33, 1.45 and 1.49. The main effect of vection on gain was significant in a three-way repeated measures ANOVA ($F_{1,5}$=33.0; $p<0.01$). Figure 2.8 demonstrates the gain increase during vection in an example of raw recordings.

At increasing stimulus velocities, torsional nystagmus slow phase velocity also increased at both body positions and perceptual states, respectively. However, as slow phase velocities rose slower than the corresponding stimulus velocities, the actual gain decreased significantly with faster stimulus revolutions ($F_{2,10}=24.5$; $p<0.01$; see Table 2.3).

Table 2.3 *Means and standard errors (in brackets) of torsional optokinetic nystagmus gain obtained at both object-motion perception (OM) and circularvection (CV), during the six experimental conditions*

Body Position		Supine		Upright	
Perceptual State		OM	CV	OM	CV
Stimulus Velocity	30°/s	0.110 (0.014)	0.146 (0.020)	0.092 (0.012)	0.134 (0.020)
	45°/s	0.086 (0.010)	0.124 (0.017)	0.059 (0.004)	0.087 (0.009)
	60°/s	0.069 (0.008)	0.102 (0.013)	0.046 (0.003)	0.074 (0.009)

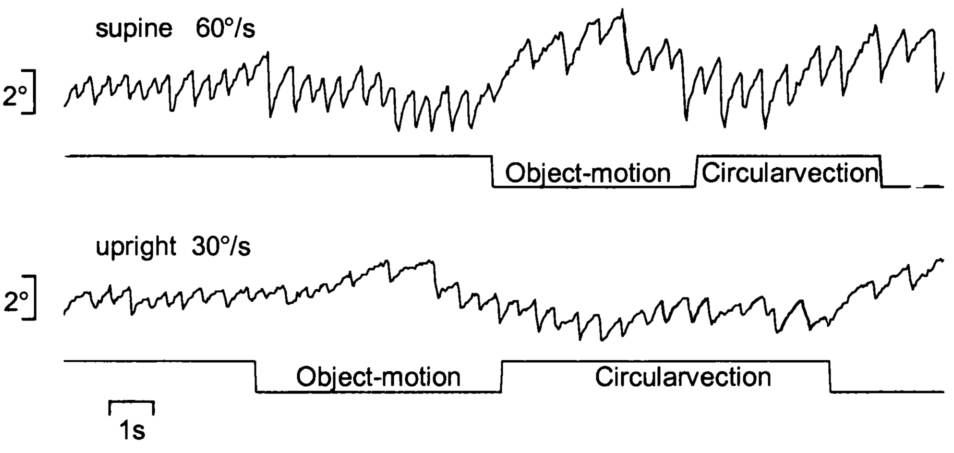


Figure 2.8 *Raw recordings of torsional optokinetic nystagmus demonstrating the changes in slow phase velocity as well as the shift in average eye position across the different states of motion perception. The top trace was recorded at a stimulus velocity of 60°/s with the observer lying supine. The bottom trace shows torsional eye movements in an upright-sitting subject watching a stimulus revolving at 30 °/s*

The supine body position resulted in a significant enhancement of torsional nystagmus gain, compared to when subjects were watching the stimulus while sitting upright ($F_{1,5}=11.6$; $p<0.05$). The absolute mean increase of gain was 0.024 between upright and supine, which is a relative enhancement of 29%.

Grouped by time of recording, torsional nystagmus slow phase velocities did not show any relation with the sequence of sessions in a one-way repeated measures ANOVA ($F_{5,25}=1.1$; $p>0.38$).

Eye Position

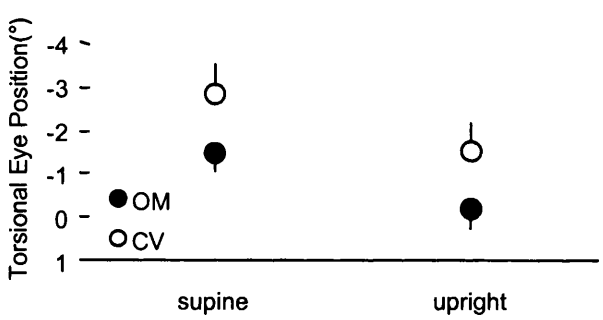


***Figure 2.9** Means and standard errors of torsional eye position during the perception of object-motion (OM) versus circularvection (CV) in supine and upright body positions*

During object motion perception, mean torsional eye position deviated counter-clockwise, i.e. in the direction of the fast phase. On average, this deviation was -0.19° at the upright body position and –1.49° when lying supine. During vection, eye position shifted further in the direction of the fast phase at either body position. The average positional shift was –1.35° when viewing upright and –1.38° when supine. A two-way repeated measures ANOVA revealed a significant main effect of body position ($F_{1,17}=8.0$; $p<0.05$), and a highly significant effect of vection ($F_{1,17}=33.7$; $p<0.01$). Figure 2.9 shows the effects of body position and perceptual states on average torsional eye position. The raw recordings in Figure 2.8 also give an example of torsional eye position shift during vection.

No significant effect of time on mean torsional eye position was obtained in a one-way repeated measures ANOVA ($F_{5,25}=1.0$; $p>0.43$).

Subjects managed to maintain fixation of the target throughout the stimulation. The mean standard deviation was 0.86° for horizontal, and 1.12° for vertical eye position.

2.3.4 Discussion

This study confirms the previous observations that visually induced perception of rotary self-motion around the naso-occipital axis coincides with a systematic increase in the slow phase gain of torsional optokinetic nystagmus. Enhanced torsional slow phase velocity during rollvection was present irrespective of whether subjects were upright or supine and average eye position deviated in the direction of the nystagmus fast phase during self-motion sensation. Furthermore, all slow phase velocities at either perceptual state tended to be faster when subjects were lying supine. Over the course of the experimental sessions, a mild perceptual adaptation effect could be observed with the average number of rollvection sensations reported during each optokinetic stimulation decreasing over time. The oculomotor variables, however, did not show any detectable temporal dynamics. It is tempting to draw parallels between the nystagmus seen with and without rollvection and "look" and "stare" nystagmus observed for horizontal optokinetic stimulation (Hood and Leech, 1974), but their characteristics do not correspond. In "stare" nystagmus the fast phases are more anticipatory, beating away from the torsional primary position towards the newly appearing visual environment. In addition, "stare" nystagmus has a lower slow phase velocity than "look" nystagmus, in which slow phases track the visual flow with the fast phases returning the eyes to their primary position. Fast phases are also anticipatory for torsional nystagmus, but they are more so during rollvection where slow phases are faster. The results raise two questions: Why is the nystagmus slow phase velocity enhanced when supine, and why does slow phase velocity enhance with nystagmus fast phase anticipation during vection?

In answer to the first question; the upright observer receiving visual roll stimulation in his frontal plane has to integrate two competing demands on gaze strategy. First, in order to maintain an upright retinal image, the torsional eye position needs to be adjusted to earth-vertical, as sensed by the otoliths. Second, at a rotating visual environment, optokinetic reflex mechanisms counteract this impulse by inducing torsional nystagmus with the slow phase in the direction of stimulus rotation. For the supine observer, however, otolithic inputs onto the oculomotor system cannot contribute to the torsional positioning of the eyes to earth-vertical, as the axis of eye rotation is aligned with the direction of gravity. Hence, they exert less suppression or restraint on the torsional oculomotor system and, consequently, slow phase gain is higher. This effect also becomes evident in the average torsional eye position under upright and supine body positions. When lying supine, overall torsional eye position deviates considerably towards the nystagmus fast phase during either state of motion perception. Neurophysiological evidence is in accord with this explanation based on disinhibition. Single unit recordings in monkeys have shown that the multidirectionally oriented hair cells of the utricle have a reduced overall depolarisation rate when the otolith membrane is deflected backwards, as is the case at a supine body position (Löwenstein, 1974).

The enhancement of slow phase velocity with increased saccadic anticipation during vection may be explained by the relegation of signals in sensory channels other than the visual motion input. If we assume that the rotating visual stimulus accesses the mechanisms of vestibular space perception through vestibular nuclei neurones innervated by primary afferents from the vertical canals then, presumably, vestibular and somatosensory inputs fail to provide a parallel confirmatory signal of roll motion as head and body remain stationary. In order to perceive self-motion in the roll plane, rather than object-motion, we have to assume that there is some suppression, or neglect, of these signals. Thereby, their restraint on the optokinetic-vestibular input to the torsional oculomotor system might be attenuated and the resulting eye movement is a fully developed response to spatial reorientation with anticipatory saccades and disinhibition of nystagmus slow phases. This explanation is in accord with studies reporting inhibitory interactions between various sensory systems serving spatial orientation (Berthoz et al., 1975; Probst et al., 1985; Wenzel et al., 1996; Probst et al., 1996a).

Several animal experiments have shown that optokinetic stimulation increases the firing rate of vestibular nuclei type I units in various species and it has been suggested that enhanced activity in the vestibular nuclei is the neural basis of circularvection (Dichgans et al., 1973; Henn et al., 1974; Allum et al., 1976; Waespe and Henn, 1977; Waespe and Henn, 1979). This is in agreement with our hypothesis, as an increase in vestibular nuclei neurones firing rate might well be modulated by non-vestibular structures converging on the vestibular nuclei. Straube and Brandt (1987) suggested the hypothesis that circularvection occurs under excitation of the vestibular nuclei innervated by a descending projection from motion-sensitive areas of the primary visual cortex. Also, the vestibular nuclei are a highly integrative structure, being innervated by primary vestibular, optic, somatosensory and proprioceptive afferents, with a strong and direct connection to subcortical oculomotor areas.

Our experimental design does not allow the inference of a causal relationship between the observed changes in eye movements and the perception of vection. Although the vestibular nuclei possess afferent connections with oculomotor nuclei (Carleton and Carpenter, 1983; Carpenter and Cowie, 1985), it seems plausible to assume that the enhancement of torsional nystagmus slow phase velocity is a result of vection rather than the cause of it. This explanation is supported by the findings of Brandt et al. (1973), who concluded that eye movements were not a necessary condition to elicit horizontal circularvection in an observer. Subjects are able to perceive visually induced self-motion when gaze is being kept stable by presentation of a fixation target and, furthermore, circularvection is even elicited when the direction of horizontal optokinetic nystagmus is being reversed by pursuing a small superimposed central pattern moving in the opposite direction to the surrounding large-field stimulus.

3 Oculomotor Correlates: Horizontal Optokinetic Nystagmus

3.1 Experiment 1: Upright Observers

3.1.1 Introduction

The experiments of the previous chapters have investigated circularvection in the frontal plane induced by an optokinetic stimulus revolving around the line of sight and found that subjects' torsional optokinetic nystagmus was enhanced when they entered into self-motion perception.

There are mechanical and physiological differences between torsional and horizontal eye movements: In contrast to ocular torsion, horizontal eye movements are largely under voluntary control, can cover a much wider amplitude and originate from different underlying neuroanatomical structures (Carpenter, 1988; Leigh and Zee, 1991). The purpose of the present experiment is therefore to investigate the interrelationships between oculomotor dynamics, object-motion perception and circularvection during optokinetic stimulation in the horizontal plane.

3.1.2 Materials and Methods

Subjects

Three women and five men, from 22 to 31 years of age (mean 26.3 years), without history of relevant neurological or sensory disease, agreed to participate in the experiment. All had normal vision or were mildly myopic, and had no difficulty in fixating the stimulus without the need of corrective lenses. Informed consent had been obtained from all subjects prior to the start of the experiment.

Apparatus

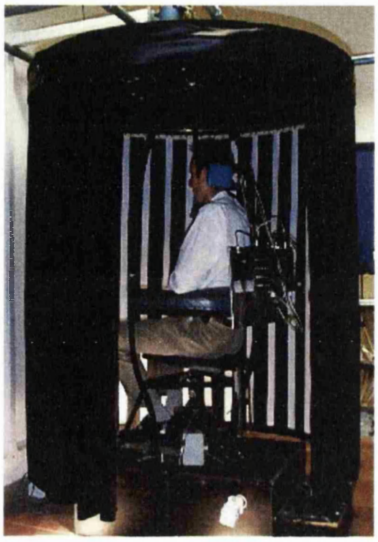


Figure 3.1 *Optokinetic drum*

The apparatus was a servo-controlled optokinetic drum, 190 cm high with a diameter of 150 cm, which rotated about its vertical axis. The inner surface was covered in alternating black and white vertical stripes, 9 cm and 4 cm wide respectively. Indirect illumination of the stripes rendered the corresponding luminances 0.12 cd/m^2 and 6.08 cd/m^2. The subjects' head was held in position by a chin rest so that the distance between the nasion and the stripes was 65-70 cm.

Eye Movement Recording

Continuous recording of the subjects' right eyes was obtained by 2-dimensional infrared videooculography (SensoMotorics Instruments, Teltow, Germany). The same head frame as in the previous experiment was used to illuminate and record the eye movements. Digitisation of the signal was carried out offline, re-sampling at 50 Hz with a spatial resolution of 0.2° for horizontal eye movements.

Procedure

After eye movement calibration, subjects were exposed to 12 trials of optokinetic stimulation. The sequence of drum rotation velocities (30°/s, 45°/s, 60°/s and 70°/s) was counterbalanced across subjects according to a Latin square. The direction of motion was alternated between trials. Each trial lasted for 30 s with an inter-trial interval of 90 s. Between trials, subjects were kept in darkness and eye movement recording was paused. Subjects were instructed to "gaze passively at the stripes", which they viewed binocularly, and to try to avoid blinking. They signalled their perceptual states by flicking a hand-held switch between two positions.

Data Analysis

For the analysis of the oculomotor recordings a computer program was developed that identified every nystagmus slow phase automatically and subsequently fitted a linear regression line through the according data points, the slope of which equals the mean eye velocity during the corresponding slow phase. Because the onset of circularvection is known to vary considerably between subjects and often commences as soon as 7-12 s after stimulation (Kennedy et al., 1996), periods of only 5 s pre- and post-onset of circularvection were chosen to be analysed in order to ensure that equal amounts of data would be obtained during each perceptual state for all trials and subjects. Furthermore, this approach is more sensitive to the perceptual transition whereas the epoch-based analysis of the previous experiments focused predominantly on the oculomotor behaviour related to the perceptual states in their entity. For each subject and stimulation condition, the obtained regression slopes were therefore pooled with respect to whether they were performed during the 5 s period that preceded or followed the transition from object- to self-motion perception. Accordingly, two average slow phase velocities were computed, one for the sensation of stimulus motion, one for the sensation of circularvection. Subsequently, for each average slow phase velocity, gain was calculated as slow phase velocity over angular stimulus velocity.

Mean eye position was computed by averaging all sampled eye position values during the according periods as above. Again, per condition and subject, one average was obtained for object-motion perception, one for circularvection.

3.1.3 Results

Psychophysical Data

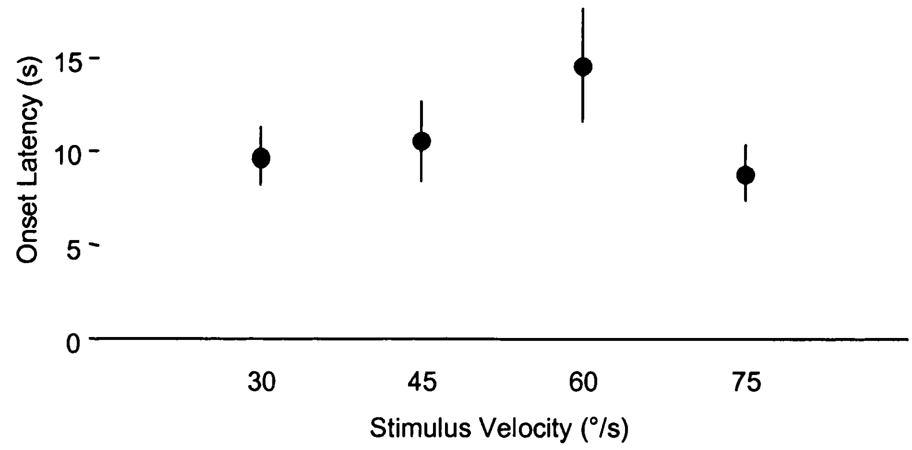


***Figure 3.2** Mean and standard errors of latency between the onset of optokinetic stimulation and the first report of perceived self-motion at all stimulus velocities tested*

All subjects reported perceiving circularvection once per trial without dropping back into the perception of object-motion during the 30 seconds of stimulation. Average circularvection onset latencies were 9.7 s (SEM 1.5 s) at a stimulus velocity of 30°/s, 10.5 s (SEM 2.1 s) at 45°/s, 14.7 s (SEM 3.1s) at 60°/s and 8.9 s (SEM 1.5 s) at 75°/s. One-way repeated-measures analysis of variance demonstrated a significant main effect of stimulus velocity on mean vection onset latency ($F_{3,21}=4.6$; $p<0.05$). Post-hoc comparisons were made by computing first-, second- and third-order within-subjects contrasts which showed a significant quadratic relationship in the data ($F_{1,7}=6.3$; $p<0.05$). No significant linear ($F_{1,7}<1$) and a marginally significant cubic ($F_{1,7}=4.7$; $p=0.07$) relationship between stimulus velocity and vection onset latency was detected. Therefore, no obvious trend is apparent in the data and the main effect of stimulus velocity is most likely to be caused by the somewhat outlying high onset latency at a velocity of 60°/s. Figure 3.2 shows mean circularvection onset latencies as a function of optokinetic drum velocities.

Oculomotor Responses

Horizontal Optokinetic Nystagmus

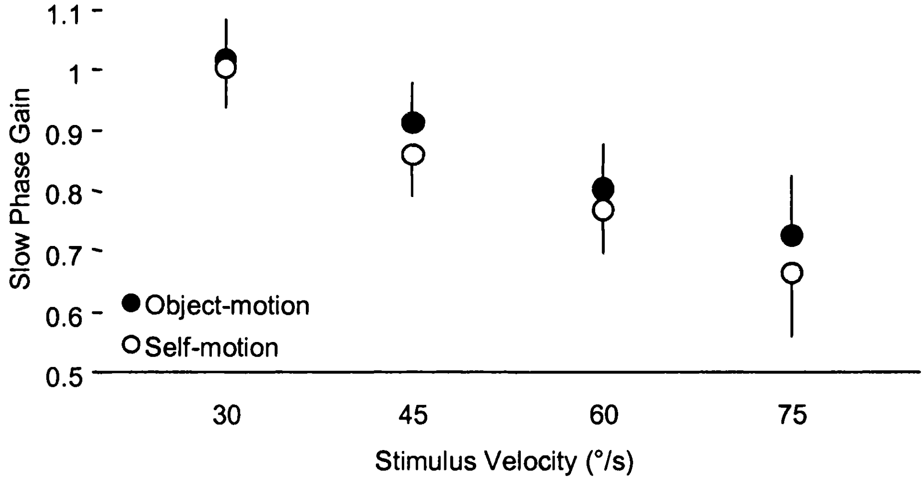


***Figure 3.3** Means and standard errors of horizontal optokinetic nystagmus slow phase gain during both perceptual states and at the different stimulus velocities tested*

Onset of optokinetic stimulation evoked an immediate nystagmic oculomotor response that was sustained throughout stimulation. As can be seen in Figure 3.3, stimulus velocity had a highly significant main effect on horizontal nystagmus slow phase gain, decreasing from 1.02 at a velocity of 30°/s to 0.73 at 75°/s during object-motion perception ($F_{3,21}=14.9$; $p<0.01$). During circularvection, slow phase gain was reduced by an average of 0.04 which is small but was sufficiently consistent across subjects and velocities to give rise to a significant main effect of perceptual state ($F_{1,7}=7.7$; $p<0.05$). No interaction between velocity and perceptual state could be detected ($F_{3,21}=1.1$; $p>0.35$). Table 3.1 gives a detailed listing of slow phase gain values obtained at different stimulus velocities and perceptual states.

Table 3.1 *Means and standard errors (in brackets) of horizontal optokinetic nystagmus slow phase gain during the different optokinetic drum velocities*

Stimulus Velocity		30°/s	45°/s	60°/s	75°/s
Perceptual State	Object-motion	1.02 (0.06)	0.91 (0.07)	0.80 (0.07)	0.73 (0.10)
	Circularvection	1.01 (0.07)	0.86 (0.07)	0.77 (0.08)	0.67 (0.11)

Eye Position

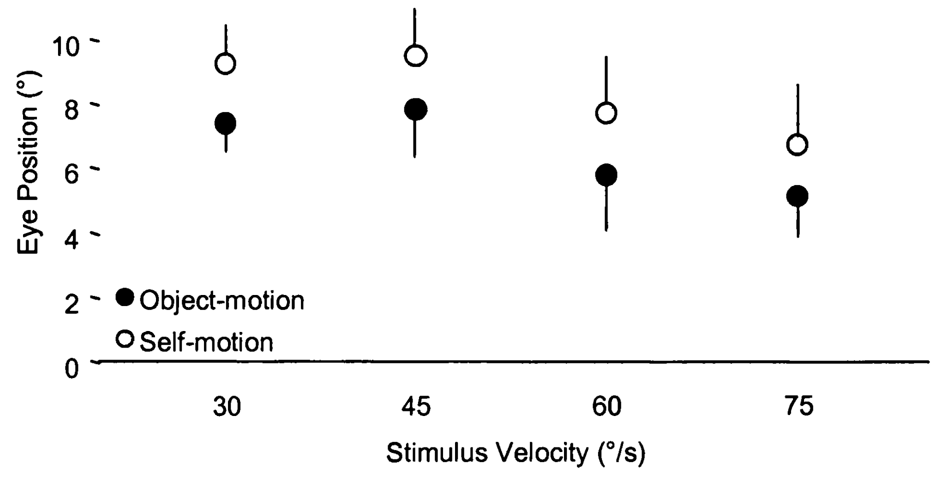


Figure 3.4 *Means and standard errors of horizontal eye position during the perception of object-motion versus self-motion at a range of optokinetic drum velocities. Eye position values are normalised according to the direction of visual motion stimulation with positive values denoting a deviation from primary gaze in the direction opposite to stimulus motion*

With respect to primary gaze, visual motion stimulation induced a deviation of mean eye position in the direction opposite to stimulus motion during all velocities as shown in Figure 3.4. Over all velocities tested, mean eye position shifted by 6.6° in the direction contrary to stimulus motion during the perception of object-motion. Comparison of mean eye position between perceptual states revealed an additional significant deviation in the same direction during circularvection ($F_{1,7}=9.8$; $p<0.05$). Averaged over all velocities, this deviation was a further 1.8° (27%) in the anticipatory direction. No main effect of stimulation velocity on eye position could be detected ($F_{3,21}=1.8$; $p>0.18$), nor an interaction between velocity and perceptual state ($F_{3,21}<1$). Individual eye position values are listed in Table 3.2.

Table 3.2 *Means and standard errors (in brackets) of horizontal eye position during both perceptual states obtained at various stimulation velocities. Values are normalised with respect to the direction of optokinetic drum rotation so that positive values indicate an ocular deviation in the direction contrary to drum rotation*

Stimulus Velocity		30°/s	45°/s	60°/s	75°/s
Perceptual State	Object-motion	7.4 (0.9)	7.9 (1.6)	5.8 (1.8)	5.2 (1.3)
	Circularvection	9.3 (1.1)	9.6 (1.4)	7.8 (1.7)	6.8 (1.8)

3.1.4 Discussion

The results of the present study are consistent with previous reports showing a decrease in optokinetic nystagmus slow phase gain with increasing stimulation velocities (Dodge et al., 1930; Honrubia et al., 1967). Comparison of the two states of motion perception reveals an enhancement of anticipatory deviation of overall eye position with a simultaneous decrease of nystagmus slow phase gain during the perception of circularvection at all stimulus velocities.

(Hood and Leech, 1974) investigated the effect of different perceptual strategies on horizontal optokinetic nystagmus. When subjects were instructed to pursue the stimulus actively, mean horizontal eye position deviated in the direction towards which the stimulus was moving with nystagmus fast phases resetting the eyes towards primary gaze. In contrast, when subjects gazed passively at the stripes, nystagmus slow phases were reduced in velocity and fast phases were anticipatory with the slow phases returning the eyes towards primary gaze. In our experiment, all responses were characteristic of passive viewing with greater anticipation during circularvection.

An anticipatory shifting of gaze, and thereby attention, towards the direction from which new visual elements are appearing enables early detection of relevant changes in the visual environment. When visual motion is perceived to be originating from actual self-motion, however, an orienting response towards the direction of heading would be of even greater relevance, especially when there is no need to pursue the visual scene. An attentional shift of such kind may be reflected by our finding of enhanced passive nystagmus characteristics during circularvection. The gaze shift towards the fast phase would correspond to an increase in anticipation and the decrease in slow phase velocity would result from a reduced emphasis on active pursuit. It should be noted that the latter reduction in horizontal optokinetic nystagmus slow phase gain accounts for a relative change of an average 4.8%. This effect only constitutes a small expense for ocular tracking accuracy since during a pursuit period of 300 ms, retinal slippage would increase by an average 0.12° of visual angle at a stimulation velocity of 30°/s and by 1.35° at 75°/s. Therefore the increased angular amount of retinal slip during each slow phase is smaller than an adult fovea and, hence, presumably of little consequence for visual motion perception. Although this decrease in slow phase gain is small it has additional significance because it is in the opposite direction to Alexander's law from which one would expect an increase in slow phase velocity with larger amplitude decentring saccades (Carpenter, 1988).

It appears that the anticipatory characteristic of both horizontal and, as has been shown in Experiment 3 of the previous chapter, torsional optokinetic nystagmus is enhanced when the subject enters circularvection. However, torsional slow phase gain also enhances during circularvection whereas that of horizontal optokinetic nystagmus decreases. This discrepancy may be resolved when the different natures of torsional and horizontal eye movements are taken into account. The torsional optokinetic reflex in humans is largely vestigial and its slow phase is up to more than thirty times smaller than that of horizontal optokinetic nystagmus (Collewijn et al., 1985; Gresty and Bronstein, 1992b). The main purpose of torsional eye movements is a static one, namely to maintain an upright retinal image during motion in the roll plane and ocular counterrolling only compensates for about 50-70% of head tilt in roll (Collewijn et al., 1985; Vieville and Masse, 1987; Gresty and Bronstein, 1992b). Also, torsional eye movements do not shift the orientation of the fovea with respect to the visual environment. Horizontal optokinetic eye movements, however, largely reduce retinal slip and anticipate the direction of heading. Torsional nystagmus may be enhanced during circularvection because the threat of the body tilting makes maintenance of orientation imperative.

To summarise, this experiment found that the characteristics of optokinetic responses to lateral visual field motion become more anticipatory when subjects switch from perceiving object-motion to self-motion with the eyes deviating more towards the oncoming visual field during circularvection. The optokinetic behaviour during object-motion perception might have a monitoring function whereas, during circularvection, the response is tuned to exploration of, or orientation to, the emerging environment. In line with the results of the previous experiments, this finding is another demonstration of a physiological correlate which corresponds to a spontaneous perceptual shift in response to otherwise constant and unchanged visual motion stimulation.

3.2 Experiment 2: Upright and Supine Observers

3.2.1 Introduction

The previous experiment investigated the relationship between horizontal optokinetic nystagmus and circularvection in an optokinetic drum and found systematic oculomotor changes when observers began to perceive circularvection. Compared to object-motion perception, mean horizontal eye position was demonstrated to perform an anticipatory shift in the direction of the oncoming visual stimulus and nystagmus slow phases were reduced in gain. A limitation of this study was, however, that once observers reported perceiving circularvection they did not shift back to the perception of object-motion, thereby possibly creating a confound between the changes in eye movements observed and the time that had passed since the onset of stimulation. Here, a stimulus of reduced contrast will be employed that is sufficiently ambiguous to yield several spontaneous alternations between the two perceptual states with approximately equal durations.

As has been outlined before, optokinetic stimulation around an axis that is not aligned with the direction of gravity does not only induce the perception of continuous self-motion but also the simultaneous perception of static whole-body tilt in the direction of circularvection due to the presence of a graviceptive conflict (Dichgans et al., 1972). Hence, a further aim of the subsequent experiment was to determine whether the introduction of a graviceptive conflict would have a systematic influence on the eye movement patterns observed during pure horizontal circularvection. Therefore, subjects were exposed to optokinetic stimulation around their naso-occipital axis whilst sitting upright, thereby inducing a graviceptive conflict, as well as lying supine, abolishing the conflict.

3.2.2 Materials and Methods

Subjects

One woman and seven men, from 21 to 32 years of age (mean 26.5 years), consented to participate in the experiment. Subjects had no history of neurological or sensory disease. They had normal vision or were mildly myopic, and had no difficulty in fixating the stimulus without the need of corrective lenses.

Apparatus

The optokinetic stimulus was a pattern of alternating vertical dark and bright stripes projected onto the concave surface of a hemisphere that was mounted in front of the subjects' head at a distance of 30 cm from the nasion. The hemisphere had a diameter of 60 cm, was centred with respect to the subjects' lines of sight and fully subtended their visual fields. The projection mechanism was mounted out of sight in front of the subjects' chins and consisted of a small globe, with regular incisions along the meridian, that was illuminated from inside and could be rotated around its poles by means of a servo-controlled motor. The projected dark and bright stripes were each 10° wide and, when projected onto the white-painted hemisphere in an otherwise dark room, had luminances of 0.41 cd/m^2 and 1.64 cd/m^2, respectively.

Eye Movement Recording

Horizontal eye movements were recorded from the subjects' left eyes using the same equipment settings for recording and digitisation as in the previous experiment.

Procedure

Subjects were tested repeatedly in two sessions on separate days with eight trials per day. Trials consisted of 60 s of optokinetic stimulation, during which eye movements were recorded, interspersed by 90 s of rest in darkness. During each trial, optokinetic stimulation was delivered at a constant velocity of 30°/s, 45°/s, 60°/s or 75°/s with the sequence of velocities and stimulation directions counterbalanced across subjects according to a Latin square. Throughout each session, subjects were either sitting upright or lying supine in a counterbalanced order across subjects. Subjects were instructed to gaze passively at the stripes and to avoid eye blinks during recording. They rested their head on a chin support in the upright condition or in a mould when lying supine and indicated transitions between the perception of object- and of self-motion using a hand-held dial.

Data analysis

Digitised horizontal eye position recordings were analysed offline. Slow phase gain was computed as the slope of a regression line fitted through an individual slow phase divided by the visual stimulus velocity. Further development of the automatic analysis software mentioned before now permitted the application of a linearity criterion. Therefore, regression fits with a determination coefficient of below 0.96 were discarded to ensure sufficient linearity of the identified slow phases. For each session and subject, the obtained gain values were pooled with respect to whether their slow phases were performed during the 5 s before or after the perceptual transition from object-motion to circularvection. Accordingly, two slow phase gain averages were computed, one for the periods during which stimulus-motion was perceived, one for the perception of self-motion.

Similarly, for each trial and subject mean horizontal eye position was computed by averaging eye position values sampled during the 5s before and after each transition from object-motion perception to circularvection.

To further elucidate the nature of the optokinetic nystagmus changes found in the previous experiment, two further slow phase parameters were now analysed. Mean slow phase amplitude was obtained by subtracting the angular end position of each slow phase from the corresponding start position and averaging the obtained values for each subject, condition and perceptual state during the same time periods. Mean slow phase duration was determined in an equivalent manner using the time elapsed between the beginning and end of each nystagmus slow phase.

3.2.3 Results

Psychophysical Data

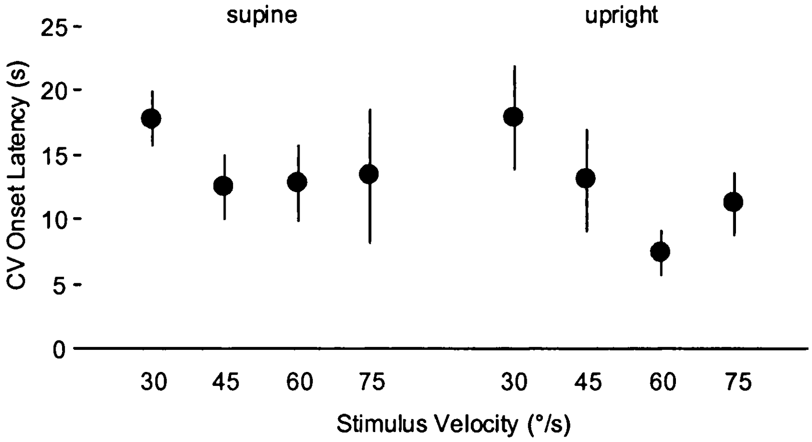


__Figure 3.5__ Means and standard errors of circularvection onset latencies at the different stimulus velocities and body positions tested

Subjects signalled the perception of circularvection at all stimulus velocities and in either body position. When supine, all subjects reported perceiving whole-body tilt around their longitudinal axis in the same direction as self-motion. Two-way repeated measures analysis of variance revealed a main effect of stimulation velocity on the latency between the onset of optokinetic stimulation and the first perception of self-motion. Averaged over body positions, mean onset latency of circularvection declined from 17.9 s at a velocity of 30°/s to 12.3 s at 75°/s ($F_{3,21}=3.33$, $p<0.05$). Post-hoc comparisons using within-subjects contrasts revealed a marginally significant linear ($F_{1,7}=4.3$; $p=0.08$) and quadratic ($F_{1,7}=3.9$; $p=0.09$) relationship between optokinetic stimulus velocity and circularvection. A third-order contrast was not statistically significant ($F_{1,7}<1$). Body position had no effect on circularvection onset ($F_{1,7}<1$), nor could an interaction with stimulus velocity be detected ($F_{3,21}<1$). Figure 3.5 shows the relation between body position, stimulus velocity and circularvection onset latency.

On average, subjects perceived 2.3 periods of self-motion sensation per trial when sitting upright as well as when lying supine. No effect of body position ($F_{1,7}<1$) or stimulus velocity ($F_{3,21}=2.45$; $p>0.05$) was shown by a two-way repeated measures ANOVA, nor was there an interaction ($F_{3,21}<1$).

Table 3.3 *Means and standard errors (in brackets) of the psychophysical parameters measured at different combinations of optokinetic stimulus velocity and body position*

Body Position	Supine				Upright			
Stimulus Vel. (°/s)	30	45	60	75	30	45	60	75
Number of CV Epochs	2.1 (0.2)	2.3 (0.3)	2.3 (0.2)	2.4 (0.3)	2.1 (0.2)	2.1 (0.3)	2.7 (0.2)	2.5 (0.1)
CV Onset Latency (s)	17.8 (2.0)	12.5 (2.5)	12.8 (3.0)	13.4 (5.2)	17.9 (4.0)	13.1 (4.0)	7.4 (1.7)	11.2 (2.4)
Average Duration of CV (s)	30.6 (0.0)	28.3 (0.1)	31.1 (0.1)	27.9 (0.1)	26.9 (0.0)	29.2 (0.1)	31.9 (0.0)	29.6 (0.0)

During the 60 s of optokinetic stimulation per trial, subjects spent an average 29 s perceiving circularvection when sitting upright and 30 s when lying supine. Paired t-tests for each stimulation condition demonstrated that the stimulus parameters chosen were suited to ensure that there was no prevalence of one perceptual state over the other (all $p>0.5$). No effect of body position, of stimulus velocity, nor an interaction between these could be detected in a two-way repeated measures ANOVA (all F<1). Table 3.3 contains a list of all psychophysical parameters measured during the different experimental conditions.

Oculomotor Responses

Slow Phase Gain

As the raw recording in Figure 3.6 demonstrates, subjects exhibited optokinetic nystagmus with the slow phases in the direction of stimulus motion throughout stimulation.

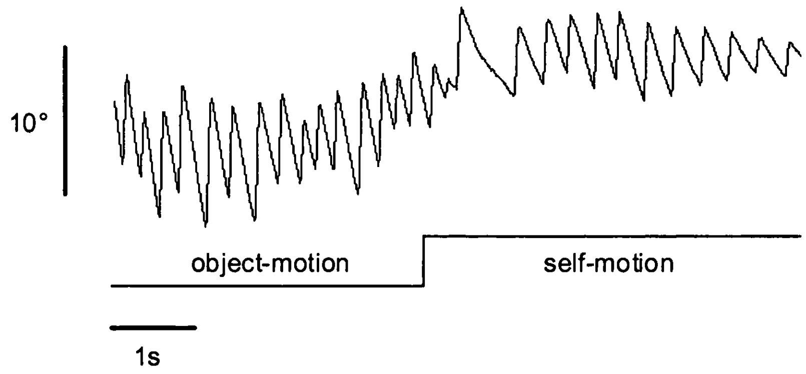


Figure 3.6 *Raw recording of horizontal optokinetic nystagmus obtained in an upright observer during leftwards optokinetic stimulation at a velocity of 60°/s. Note the anticipatory shift of average eye position as well as the reduction of slow phase velocity after the onset of circularvection*

Three-way repeated measures ANOVA demonstrated the body position subjects were in to have a significant main effect on horizontal nystagmus slow phase gain. Averaged over velocities and perceptual states, slow phase gain was 0.55 when subjects were sitting upright and was reduced to 0.45 with subjects lying supine ($F_{1,7}=12.25$; $p<0.01$). With stimulation velocities increasing from 30°/s to 75°/s, slow phase gain declined from 0.62 to 0.47 in the upright condition and from 0.50 to 0.40 whilst lying supine, resulting in a significant main effect of stimulus velocity ($F_{3,21}=34.81$;$p<0.01$). The perceptual state reported by the observers also had a significant main effect on slow phase gain. When sitting upright, slow phase gain decreased from 0.56 during the perception of object-motion to 0.53 during circularvection and from 0.49 to 0.43 during supine viewing ($F_{1,7}=13.62$; $p<0.01$). None of the interactions reached significance (all $p>0.05$). A summary of the slow phase gains obtained with the different combinations of body positions, stimulus velocities and perceptual states is shown in Table 3.4 and Figure 3.7.

Table 3.4 *Means and standard errors (in brackets) of horizontal optokinetic nystagmus slow phase gain at the different body positions, stimulus velocities and perceptual states*

Body Pos.		Upright		Supine	
Perc. State		OM	CV	OM	CV
Stimulus Velocity	30°/s	0.64 (0.06)	0.61 (0.06)	0.52 (0.05)	0.48 (0.05)
	45°/s	0.59 (0.06)	0.57 (0.06)	0.51 (0.08)	0.48 (0.07)
	60°/s	0.54 (0.05)	0.49 (0.05)	0.46 (0.08)	0.40 (0.07)
	75°/s	0.49 (0.06)	0.46 (0.06)	0.44 (0.07)	0.36 (0.06)

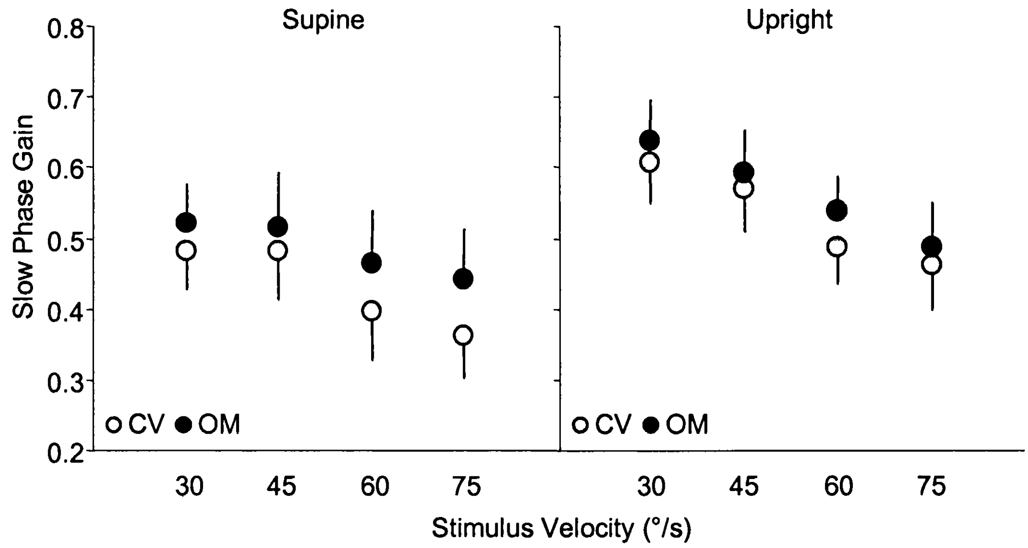


Figure 3.7 Means and standard errors of horizontal optokinetic nystagmus slow phase gain during perception of object-motion (OM) and circularvection (CV) at the different combinations of body positions and optokinetic stimulus velocities

Slow Phase Amplitude

Nystagmus slow phases subtended an increasingly larger angle with rising stimulation velocities. On average, slow phase amplitudes were 5.6° during visual motion at 30°/s and went up to 8.7° at 75°/s. This main effect of stimulus velocity was significant in a three-way repeated measures ANOVA ($F_{3,21}=11.67$; $p<0.01$). As can be seen in Figure 3.8, there appears to be a tendency for amplitudes to be reduced during the perception of self-motion which, however, failed to reach significance. Values decreased from 8.0° during the perception of object-motion to 6.7° during circularvection ($F_{1,7}=4.5$; $p=0.07$). Observers' body position did not exert a significant effect on slow phase amplitudes ($F_{1,7}<1$) nor were any of the interactions significant (all $p>0.05$). Table 3.5 contains a list of average slow phase amplitudes obtained during all experimental and perceptual conditions.

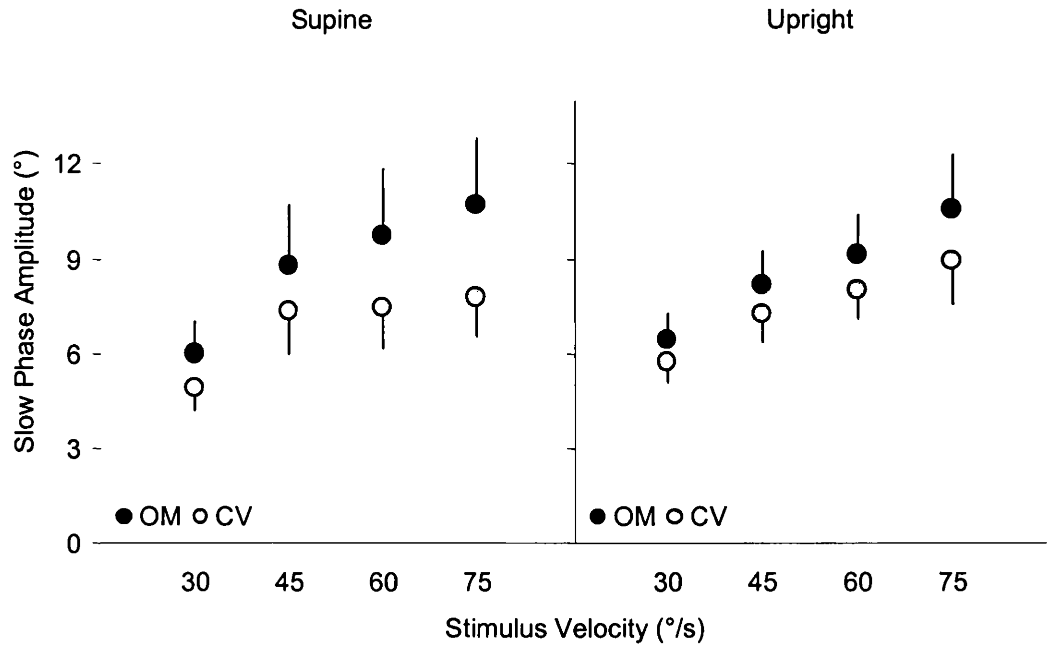


Figure 3.8 *Means and standard errors of average nystagmus slow phase amplitudes during the experimental conditions and differential perceptual interpretations of the visual motion stimulus as originating from object-motion (OM) or circularvection (CV)*

Table 3.5 *Means and standard errors (in brackets) of average amplitudes (°) of nystagmus slow phases during both body positions, perceptual states and the four different optokinetic stimulus velocities tested*

Body Position		Upright		Supine	
Perceptual State		OM	CV	OM	CV
Stimulus Velocity	30°/s	6.4 (0.8)	5.7 (0.6)	6.0 (1.0)	4.9 (0.7)
	45°/s	8.1 (1.1)	7.3 (0.9)	8.8 (1.9)	7.3 (1.3)
	60°/s	9.1 (1.2)	8.0 (0.9)	9.8 (2.1)	7.5 (1.3)
	75°/s	10.5 (1.8)	8.9 (1.3)	10.7 (2.1)	7.8 (1.3)

Slow Phase Duration

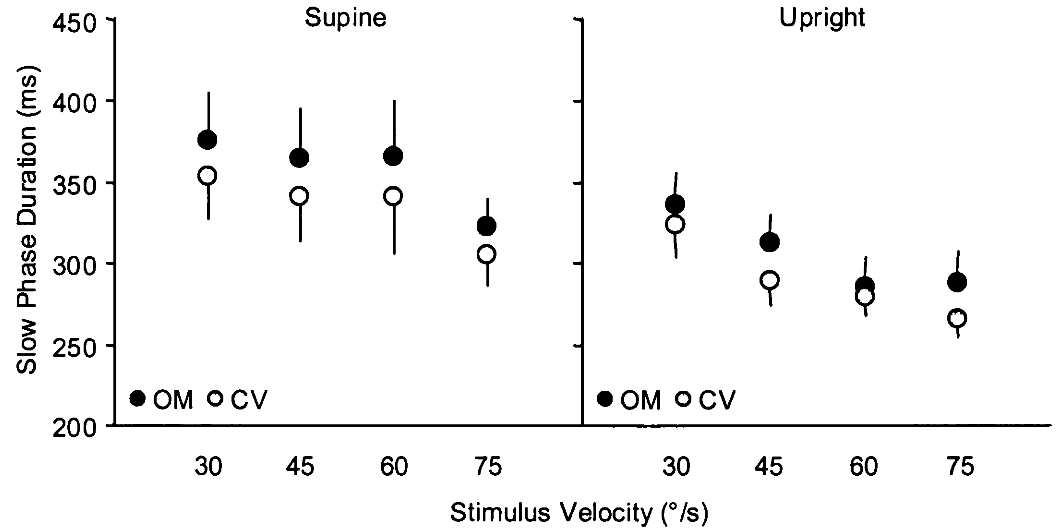


Figure 3.9 *Means and standard error of average optokinetic nystagmus slow phase duration at both perceptual states of object-motion (OM) and circularvection (CV), observer body positions and stimulus velocities*

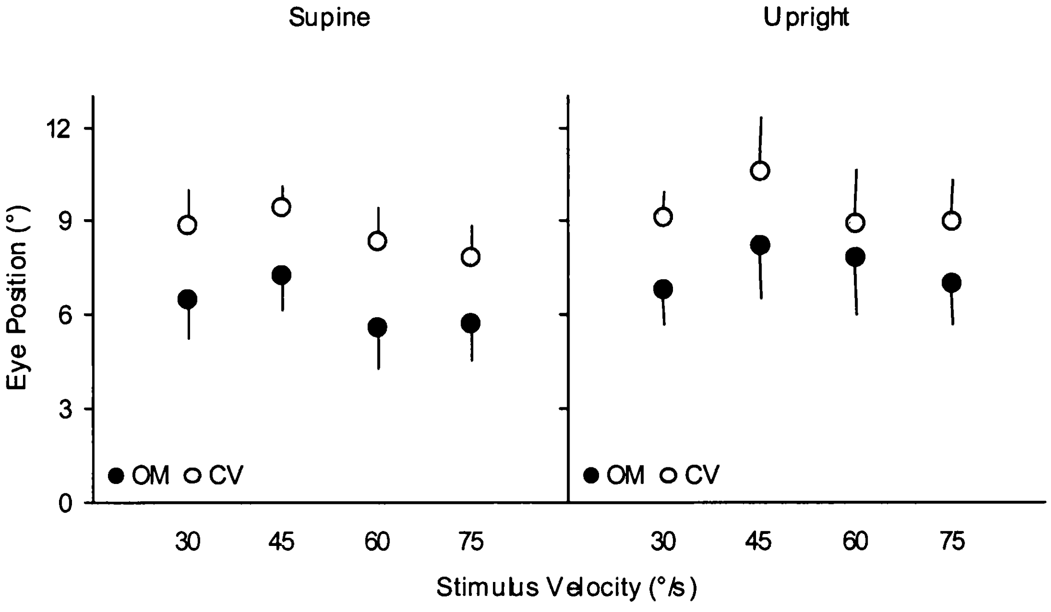
Figure 3.9 and Table 3.6 show the behaviour of mean slow phase duration in the experiment. There was a significant effect of stimulus velocity in a three-way repeated measures ANOVA with duration decreasing from an average 345 ms at 30°/s to 291ms at 75°/s ($F_{3,21}=9.63$; $p<0.01$). Viewing the stimulus in an upright position resulted in an average slow phase duration of 292 ms which increased significantly to an average 338 ms during supine posture ($F_{1,7}=11.07$; $p<0.05$). Slow phase duration was not influenced by the perceptual state observers were reporting ($F_{1,7}=1.5$; $p>0.05$). All interactions remained non-significant (all $F<1$).

Table 3.6 *Means and standard errors (in brackets) of the average duration (ms) of nystagmus slow phases performed during all combinations of experimental conditions and perceptual interpretations of the optokinetic stimulus*

Body Position		Upright		Supine	
Perceptual State		OM	CV	OM	CV
Stimulus Velocity	30°/s	336 (20)	324 (20)	376 (30)	354 (27)
	45°/s	313 (18)	289 (15)	364 (31)	341 (27)
	60°/s	285 (19)	279 (12)	366 (35)	341 (34)
	75°/s	288 (19)	265 (10)	322 (18)	306 (19)

Eye Position

Figure 3.10 *Deviations from primary gaze (means and standard errors) of average horizontal eye position during the perception of object-motion (OM) versus circularvection (CV) at both body positions and the applied optokinetic stimulus velocities. Eye position values are normalised according to the direction of stimulus rotation with positive values indicating a deviation from primary gaze into the direction opposite to stimulus motion, i.e. in the same direction as perceived self-motion*



During visual motion stimulation in all experimental conditions and perceptual states, mean horizontal eye position shifted from primary gaze into the direction of the newly appearing stimulus elements, i.e. in the opposite direction of stimulus motion, as demonstrated in Figure 3.10. A three-way repeated measures ANOVA showed stimulus velocity to have a significant main effect on horizontal eye position ($F_{3,21}=5.16$; $p<0.01$) with a slight overall decrease of average deviation from 7.8° at a velocity of 30°/s to 7.4° at 75°/s. During the perception of self-motion, horizontal ocular deviation from primary gaze was consistently greater than during object-motion perception in all combinations of body positions and stimulus velocities, yielding a significant main effect of perceptual state: With respect to the perception of object motion, the mean anticipatory shift after the transition to circularvection was 1.9°, or 26.0%, in the upright observer and 2.4°, or 38.0%, when lying supine ($F_{1,7}=9.58$; $p<0.05$). This pattern was obtained irrespective of body position ($F_{1,7}<1$) with no detectable interactions (all $p>0.05$). Details of eye position values are given in Table 3.7.

Table 3.7 *Means and standard errors (in brackets) of average horizontal eye position (°) during the perception of object-motion (OM) and self-motion (CV) at the different experimental conditions. The values are normalised with respect to the direction of optokinetic stimulation with positive values denoting a deviation contradirectional to stimulus motion*

Body Position		Upright		Supine	
Perceptual State		OM	CV	OM	CV
Stimulus Velocity	30°/s	6.8 (1.1)	9.1 (0.8)	6.5 (1.3)	8.9 (1.2)
	45°/s	8.2 (1.6)	10.6 (1.7)	7.2 (1.1)	9.4 (0.7)
	60°/s	7.8 (1.7)	8.9 (1.7)	5.6 (1.3)	8.3 (1.1)
	75°/s	7.0 (1.3)	9.0 (1.3)	5.7 (1.7)	7.8 (1.0)

3.2.4 Discussion

The results confirm the observation of the previous experiment that the perception of self-rotation in yaw is accompanied by an apparently anticipatory shift of horizontal optokinetic nystagmus with average eye position consistently deviating in the direction into which subjects perceive themselves to be moving. The main finding is that this behaviour was present irrespective of whether the perceived self-motion was, or was not, combined with the concurrent perception of tilt due to the presence of a graviceptive conflict. At either condition, slow phase gain was slightly, but consistently, reduced when subjects perceived circularvection compared to object-motion. Of note, gain was generally higher when subjects were sitting upright and did not perceive a graviceptive conflict during self-motion and, as shown before, gain declined with increasing stimulation velocities (Dodge et al., 1930; Honrubia et al., 1967). Also, there was a trend for anticipatory eye deviation to be reduced at higher visual motion velocities.

Neither slow phase amplitude nor slow phase duration were significantly modulated by the perceptual state reported by observers. This seems puzzling since slow phase velocity, or gain, does change across percepts and is mathematically equivalent to dividing amplitude by duration. A likely explanation for this finding is that the changes in slow phase velocity are a product of simultaneous adjustments of slow phase amplitude as well as duration that, in isolation, are too small and variable to be statistically detected with the present number of observations and therefore require further investigation. It should also be noted that both slow phase amplitude and slow phase duration were significantly affected by a change in optokinetic stimulus velocity and showed some degree of dissociation. While slow phase amplitude rose with increasing stimulation velocity, slow phase duration decreased simultaneously with a reduction of slow phase gain.

During horizontal optokinetic stimulation there is some evidence for an inverse relationship between slow phase amplitude and anticipatory mean eye position. Ocular anticipation decreased at higher stimulation velocities but mean slow phase amplitude increased. However, shifting from the perception of object-motion to circularvection coincides with an increase in anticipation and slow phase amplitudes become reduced in size although the latter effect only reached marginal statistical significance and thus requires further investigation.

The behavioural relevance of shifting eye position further towards the perceived direction of heading at the onset of circularvection may lie in a modified strategy of spatial attention causing subjects to switch from monitoring the visual environment during object-motion perception to actively explore and anticipate the oncoming visual targets during self-motion perception. Likewise, for the vestibulo-ocular reflex, it has been demonstrated that the beating field of horizontal nystagmus shifts further in the direction of the fast phase when subjects use a more anticipatory strategy of spatial orientation (Siegler et al., 1998).

The concurrent weak reduction of slow phase gain appears to stand in contrast to Alexander's law, postulating an enhanced velocity of slow phases directed towards primary gaze at increasingly eccentric eye positions (Carpenter, 1988; Leigh and Zee, 1991). This effect as well as the tendency for reduced slow phase amplitudes might, however, be considered a consequence of the increased horizontal ocular deviation since the needs for accurate pursuit of a moving visual scene at the same time as efficient anticipation constitute opposing demands on the oculomotor system. The former aims to orient the eyes dynamically in the direction of visual motion whereas the latter demands a static positioning of the eyes in the opposite, anticipatory, direction. This conflict may result in a trade-off, increasing mean anticipatory ocular deviation at the expense of a small reduction of slow phase gain and amplitude.

This explanation can also account for the reduction of gaze eccentricity at increasing stimulus velocities. Although slow phase gain decays with faster optokinetic stimulation, slow phase velocities actually increase in speed, only at a lower rate than the increment in stimulus velocity. Thus, at increasing stimulus velocities, the rise in slow phase velocity as well as amplitude might necessitate the described trade-off between ocular pursuit and anticipation and may therefore result in anticipatory horizontal eye position, on average, deviating less far from primary gaze.

Optokinetic stimulation in the supine position resulted in an overall reduction of slow phase gain compared to when observers were sitting upright. The previous chapter investigated the effect of optokinetic stimulation around the sagittal axis and, on contrast, found torsional optokinetic nystagmus slow phase gain to be enhanced when observers were lying supine. This apparent contradiction is resolved when considering the orientation of the rotational axis and the consequent presence or absence of a graviceptive conflict during visual motion stimulation. Both, during horizontal optokinetic stimulation in the upright observer and during torsional optokinetic stimulation when lying supine, the axis of rotation is aligned with the direction of gravity. The induced optokinetic nystagmus does therefore not reorient the eyes with respect to gravity, and perceived upright, and slow phase gains are high. During earth-horizontal optokinetic stimulation, however, a graviceptive conflict exists and slow phase gains are reduced. It appears that in this situation otolithic inputs exert an inhibitory influence on optokinetic nystagmus tending to reduce an ocular reorientation with respect to the perceived direction of gravity as has been described for torsional nystagmus where such a strategy ensures the maintenance of an upright retinal image of the environment.

It is of interest to note that no systematic effect of the observers' body position on the degree of mean horizontal ocular deviation from primary gaze was found in the present study. One might expect that the added perception of whole-body tilt when subjects are lying supine should also give rise to an increase of ocular anticipation because the percept might be of a more startling nature. On the contrary, it may be conceived that the perception of a graviceptive conflict would attenuate the plausibility of the perception of sustained self-rotation around an earth-horizontal axis, since continuous signals about subjective stationarity with respect to gravity are conveyed simultaneously. In consequence, the hypothetical demand for increased anticipation due to the perception of tilt might have been counteracted by this reduced plausibility of perceived self-rotation.

Several neurophysiological studies demonstrated that optokinetic stimulation is well suited to modulate the activity of neurones in the vestibular cortex, thalamus and vestibular nuclei and it has been suggested that vestibular nuclei neurones may participate in the modulation of the perceptual states of object-motion and circularvection (Henn et al., 1974; Büttner and Henn, 1976; Waespe and Henn, 1977; Büttner and Henn, 1981; Grüsser et al., 1990; Henn et al., 1974). Since the vestibular nuclei are closely coupled with subcortical and vestibulocerebellar ocular motor areas that are known to belong to the neural substrate of vestibulo-ocular and optokinetic reflexes it may be conceived that the observed oculomotor changes originate, at least in part, in structures as early as these. More recent evidence from PET (Brandt et al., 1998) demonstrates a differential, and presumably synergistic, involvement of human parieto-insular vestibular and visual cortices in the perception of visual motion as arising from object- or self-motion. Additionally, damage to the right parietal, frontal and temporal lobes as well as to right-hemispheric subcortical and thalamic nuclei has been demonstrated to induce a marked impairment in anticipatory eye movements following the illusory perception of head-rotation further substantiating the notion of a distributed network participating in the generation of anticipatory gaze orientation (Ivanenko et al., 2000).

Taken together, employing a stimulus that caused subjects to report alternations between perceptual states, this study confirms that the onset of visually induced self-motion perception is accompanied by a characteristic oculomotor reorientation that is not affected by the presence, or absence of, a graviceptive conflict leading to the additional perception of whole-body tilt at the same time as that of self-motion. The anticipatory shift of horizontal optokinetic nystagmus at the onset of circularvection appears to be a general adaptive response whose behavioural relevance may lie in directing the observer's attention to, and promoting active exploration of, the visual environment in the direction of perceived heading.

4 Neural Correlates

4.1 *Experiment 1: Functional Magnetic Resonance Imaging*

4.1.1 Introduction

Moving visual stimuli have been the subject of numerous brain imaging studies but only few have utilised large-field visual motion stimulation capable of eliciting the perception of circularvection in human observers. In studies by Brandt et al. (1998) and Previc et al. (2000), imaging by positron mission tomography (PET) was conducted with subjects lying supine viewing a torsional optokinetic stimulus to induce the perception of rollvection. In order to induce the two differential perceptual states of object-motion sensation and circularvection, both used an approach that required two different types of visual motion stimuli. The perception of circularvection was elicited by a visual stimulus rotating uniformly and continuously around the x-axis. The feeling of object-motion, on the other hand, was elicited by an equal number of individual elements in the visual field, each of which was rotated incoherently in the roll plane, the rationale being that only coherent visual motion can stem from actual self-motion through a stationary environment. Undeniably, this approach yields a clear distinction between the perceptual states elicited in different trials but it also creates a confound between the type of stimulation used and the perceptual state elicited in the observer. Consequently, any differential activation patterns obtained cannot solely be ascribed to a specific perceptual experience. Any differences observed might equally well be caused by certain brain regions responding preferentially to the visual stimulus employed at that time.

In order to identify brain systems processing self-motion, the subsequent experiment employed a paradigm using continuous torsional optokinetic stimulation that yielded both perceptual states in spontaneous alternation. Using functional magnetic resonance imaging (fMRI), brain activity was recorded in volunteers who, exposed to this stimulus, fluctuated between perceiving object-motion and circularvection. Thus, the distinction of object-and self-motion was addressed at the level of perceptual awareness rather than at that of specialised visual feature processing. Any brain activity change correlating with either of the percepts cannot be accounted for by the stimulus properties per se.

4.1.2 Materials and Methods

Subjects

One woman and seven men, from 22 to 48 years of age, without history of relevant neurological or sensory disease, agreed to participate in the experiment. All had normal vision or were mildly myopic, and had no difficulty in fixating the stimulus without the need of corrective lenses. Informed consent had been obtained from all subjects prior to the start of the experiment.

Functional Imaging

Data were acquired on a 2 T magnetic resonance imager (Siemens Vision, Erlangen, head coil), obtaining a structural (T1 weighted) scan and then series of blood-oxygenation-sensitive (T2* weighted) echoplanar image volumes every 4.1 s (image repetition time/echo time 80.7/40 ms; 48 contiguous transverse slices, voxel size 3x3x3 mm^3).

Stimulus

The optokinetic stimulus consisted of a sectored disk, subtending approximately 45° of visual angle, that was covered with an alternating pattern of 12 black and 12 luminescent stripes, each of 30° width, at equal intervals. The stimulus was mounted above the head coil (approximately

12 cm viewing distance to centre) and mechanically controlled by a geared connection to a propylene rod that was driven by a motor in the console room.

Procedure

Subjects lay supine in the MRI scanner and held a response box and a panic button in their right and left hand, respectively. A total of three scanning series per subject were acquired. Each series consisted of 118 image volumes and lasted for approximately 8 min. Prior to each trial subjects started looking at the rotational centre of the stimulus in an otherwise dimmed scanner room. For the first 18 image volumes the disk remained stationary and then started rotating about its centre at a constant speed of 45°/s. Both clockwise and counter-clockwise rotation of the disc was used in different trials. Since no significant brain activity differences were found between these conditions, the data were subsequently pooled for analysis. Previous behavioural measurements using videooculography had established that subjects could maintain fixation over the length of time chosen for the runs.

Using the response-box, subjects performed key presses with the right index finger to indicate the onset of visual motion stimulation and of epochs during which they perceived object-motion. Middle finger key presses indicated the onset of rollvection perception. Thus, a sequence of alternating key presses was recorded, defining the subjects' bistable perceptual experience after the onset of stimulation. Subjects were familiarised with the stimulus and the perceptual states it evokes as well as with the task prior to the experimental runs during functional imaging.

Data Analysis

The dataset acquired for this study comprised approximately 127,000 functional images. Data processing and analysis were performed using statistical parametric mapping (Wellcome Department of Cognitive

Neurology, Institute of Neurology, London). After discarding the initial 8 volumes, all image volumes were corrected for motion artefact (realigned to the first volume), coregistered with the subject's corresponding anatomical (T1-weighted) images, non-linearly normalised into standard stereotactic space (template provided courtesy of the Montreal Neurological Institute), and smoothed using a 9 mm full width at half maximum Gaussian kernel. Low-frequency fluctuations were removed using a temporal high-pass filter with a cut-off at 70 s. Two types of responses were analysed, sustained (perceptual state) and transient (perceptual switch). These were modelled as box-car functions (sustained) and delta functions (transient) that were convolved with a synthetic haemodynamic response function (Boynton et al., 1996).

Statistical comparisons were performed by contrasting parameter estimates for the modelled sustained responses during visual-motion stimulation (across both perceptual states) with the stationary baseline and, as an embedded comparison within ongoing constant visual-motion stimulation, by contrasting those responses obtained during perceived object-motion with the ones obtained during perceived self-motion and vice versa. For event-related responses, the evoked transient haemodynamic responses were analysed both as changes against baseline activity and against each other (Kleinschmidt et al., 1998). The three event-types that subjects reported by key presses were the onset of visual-motion, of perceived self-motion and of perceived object-motion.

These procedures resulted in a statistical parametric value for every voxel showing sustained or transient activity differences related to the stimulus and to either of the perceptual states. Statistical inferences were corrected for multiple non-independent comparisons by using Gaussian random field theory (Worsley et al., 1996). Unless stated otherwise, a significance threshold of $p<0.05$, corrected for multiple comparisons, was applied.

4.1.3 Results

Psychophysical Data

All subjects experienced circularvection intermittently, the first epoch after a mean onset latency of 9 s (SEM 0.7 s) after onset of disk rotation and ensuing epochs of perceived self- and object-motion with a mean duration of 16 s and 19 s, respectively.

Regions responsive to optokinetic stimulation

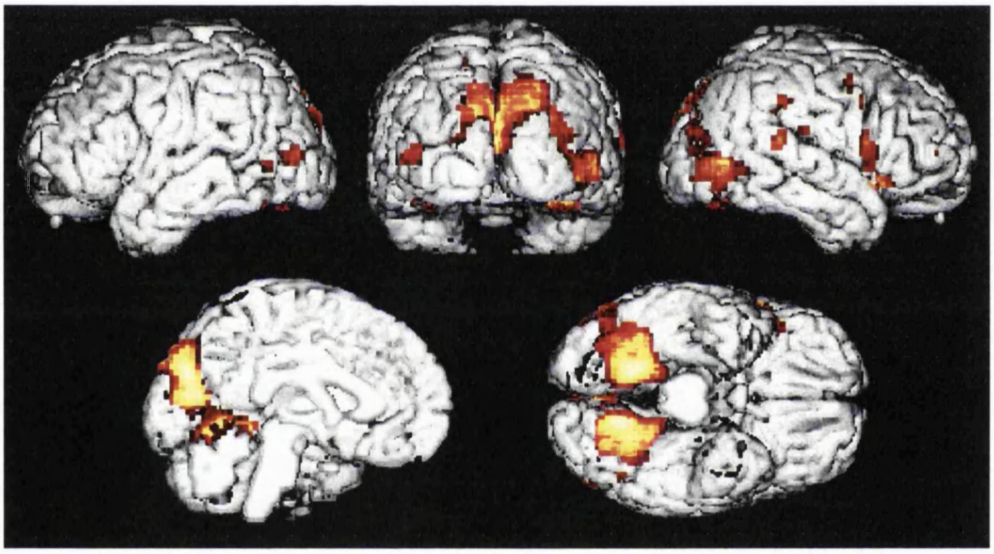


Figure 4.1 *Brain areas responsive to optokinetic stimulation. Statistical parametric maps showing areas with greater activity during visual motion stimulation (stimulus rotating) than during baseline (stimulus stationary). To illustrate the overall cortical response pattern, the results are displayed by colour coding and rendered onto an anatomical template image (visualised at* $p<0.05$*, corrected)*

In a first step, those brain areas sensitive to the optokinetic stimulus were determined by contrasting brain activity between the whole period of stimulus motion and the preceding stationary phase. Multiple brain regions were activated in correspondence with previous neuroimaging studies mapping the responses to visual-motion (Watson et al., 1993; Zeki et al., 1993; Dupont et al., 1994; De Jong et al., 1994; Tootell et al., 1995; Cheng et al., 1995;

McCarthy et al., 1995; McKeefry et al., 1997; Brandt et al., 1998; Previc et al., 2000; Greenlee, 2000). As the cortical response topography in Figure 4.1 demonstrates, optokinetic stimulation resulted in extensive activation of early visual areas with a band of activation extending into both dorsal and ventral visual cortex and a bilateral activation of the MT+ complex.

Sustained responses to the perception of object- or self-motion

In a second step, activity levels during the two perceptual states were determined in a set of candidate areas that previous animal electrophysiology, human lesion and the neuroimaging studies suggested as important for the processing of optical flow (Straube and Brandt, 1987; Vaina, 1998; Heide et al., 1999). These regions include dorso-medial cortex ("DM", comprising cuneus and parieto-occipital cortex, see Richer et al., 1991 and Lee et al., 2000, for human electrostimulation studies), the anterior portion of the human visual-motion complex ("V5/MT complex") at the occipito-temporal junction (hypothetical "V5a/MST", see Duffy and Wurtz, 1991; Orban, 1997; Tanaka, 1998), an area of superior temporal cortex ("ST", see Bruce et al., 1981; Anderson and Siegel, 1999) and posterior (intra-) parietal cortex (see Siegel and Read, 1997). All these brain regions responded to optokinetic stimulation compared to the stationary baseline (see Figure 4.1) but there was no differential activation in relation to the alternative perceptual states (Figure 4.2). For these comparisons, where areas of interest were targeted on the basis of prior knowledge, a more sensitive threshold ($p<0.001$, uncorrected) was used that took account of the greatly reduced number of multiple comparisons involved. In a third step, the data were tested for an influence of perceptual state on regional activity levels. This was done by mapping activity differences between images reflecting the perception of object-motion and those reflecting the perception of self-motion and vice versa. When contrasting perceived object- with self-motion (Figure 4.3), activity in a subset of the motion-sensitive brain areas shown in Figure 4.1 was found to correlate with alternating perceptual dominance. Relative activation was found during perceived object-motion and relative deactivation during perceived self-motion. The "earliest" cortical activity change occurred in primary (calcarine) visual cortex ("V1") and extended over an intermediate level in the superior occipital gyrus ("V3/V3A") into ventral occipital cortex (fusiform gyrus, "V4") and onto the convexity (occipito-temporal junction, posterior "V5/MT"). These activity differences were significant at thresholds corrected for multiple comparisons.

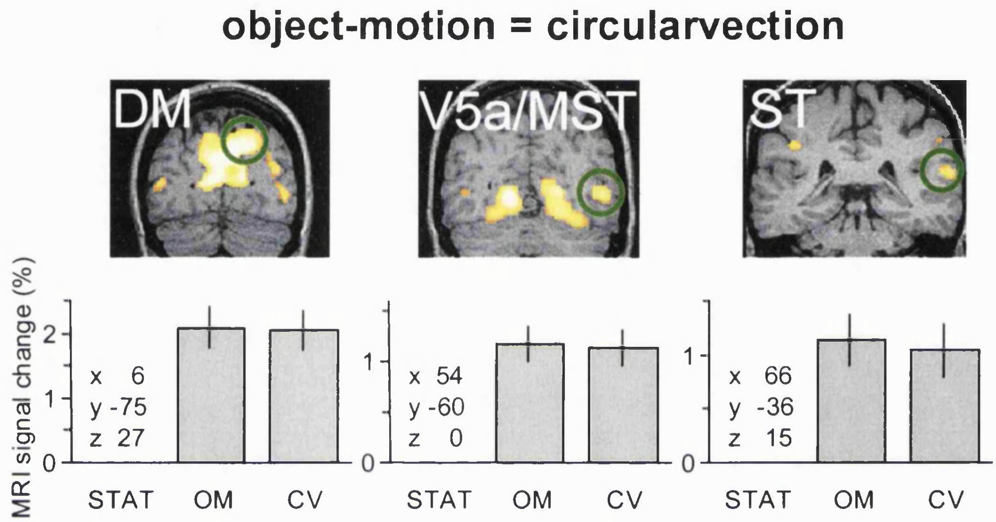


Figure 4.2 *Motion-sensitive brain areas equally responsive during perceived object-motion (OM) and circularvection (CV). Top panels: Statistical parametric maps of areas responsive to optokinetic stimulation compared to baseline (STAT). The results are derived from the same comparison as in Figure 4.1, colour-coded and superimposed onto sections from an individual structural dataset (visualised at p<0.001, uncorrected). The location of the significance maxima contained in circles is given in stereotactic coordinates and in terms of corresponding brain areas: dorsomedial cortex (DM), superior temporal area (ST), accessory V5 (V5a) / middle superior temporal cortex (MST). Bottom panels plot mean and standard error of response strength in these foci during each perceptual state relative to baseline.*

A significant activity change also occurred in an area not activated by the visual-motion stimulus namely, the posterior parieto-insular cortex, a region proposed to be a human homologue of the vestibular cortex (Guldin and Grüsser, 1998). Comparison with activity levels elicited by the stationary stimulus demonstrates that the activity change is a deactivation during perceived self-motion. Hence, while activity levels were not significantly different between the stationary and rotating stimuli as long as the latter was perceived as object-motion, there was a significant activity decrease when the stimulus evoked the perception of self-motion.

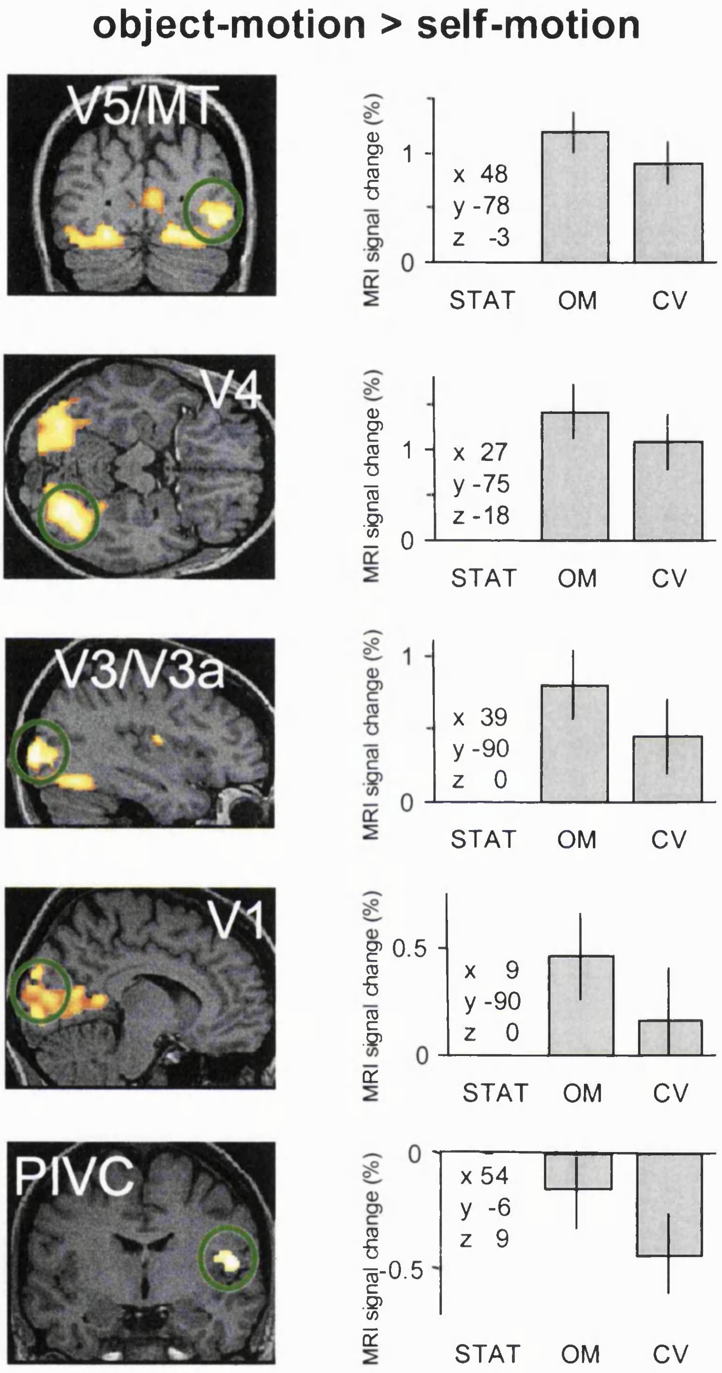
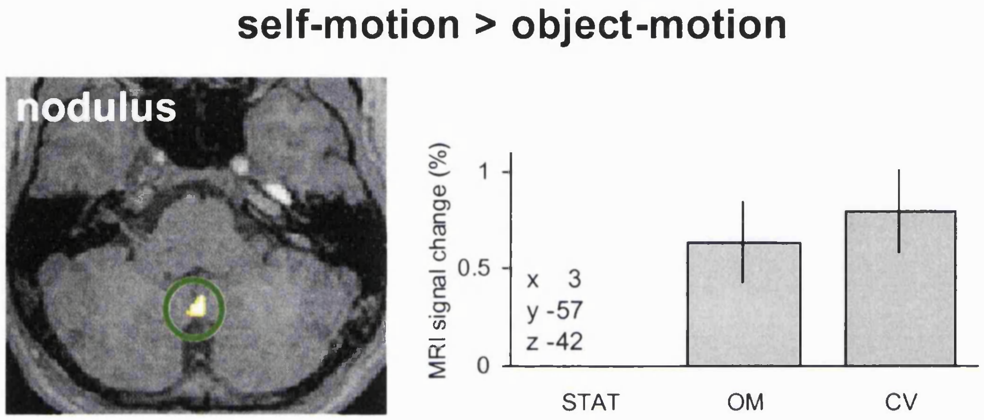


Figure 4.3 *Brain areas more active during the perception of object-motion (OM) than during circularvection (CV) visualised at $p<0.001$, uncorrected, and superimposed onto individual structural sections. Green circles highlight response foci (V1-V5: visual areas 1-5, PIVC: parietoinsular vestibular cortex). The corresponding activity levels are plotted in the right-hand panels for each perceptual state relative to the stationary baseline. All differences were significant at $p<0.05$*

While a large subset of motion-sensitive areas showed greater activity during perceived object-motion, there was only one structure with enhanced activity during vection relative to perceived object-motion (Figure 4.4), the cerebellar vermis in the area of the nodulus (possibly extending into the adjacent uvula). The nodulus is a subcortical structure responsive to the optokinetic visual-motion stimulus compared to the stationary control. Other subcortical motion-sensitive responses occurred in the flocculus and thalamus but these showed no differential responsiveness as a function of perceptual state.



self-motion > object-motion

Figure 4.4 *The response focus for greater activity during the perception of circularvection than of object-motion. The statistical parametric map in the left panel shows the cerebellar nodulus, the right-hand panel shows the corresponding parameter estimates during both perceptual states relative to the stationary baseline*

Transient responses during perceptual switches

A separate set of event-related analyses was performed to identify those brain regions that showed transient activity changes during the transitions between the perception of object-motion and that of circularvection. The duration of the perceptual states was sufficiently long to address percept- and perceptual switch-related activity separately. Hence, only in the event-related analyses was there activation in the primary and supplementary motor areas on the left-hemispheric convexity and medial wall correlating with the right finger movements produced by subjects to signal each perceptual transition. Additionally, the event-related responses found fell into three classes: those common to both directions of perceptual reversal (from perceived object-motion to self-motion and vice versa) and those specific to either of the two directions. In line with previous observations (Kleinschmidt et al., 1998; Lumer et al., 1998), transient signal changes at each perceptual switch, irrespective of its direction, occurred in predominantly right-hemispheric inferior and intra-parietal cortex and premotor, inferior frontal and prefrontal cortex and bilaterally in the mid-fusiform gyrus. Additionally, however, similar signal changes were observed in the anterior portion of the right-sided motion complex ("V5a/MST", Figure 4.5A). These responses show that the continuously elevated activity during visual-motion is modulated by transient activations that occur at each perceptual reversal and are of very similar magnitude at the onset of both perceived object-motion and self-motion. The same behaviour was found in other regions ("DM" and "ST") that displayed sustained activations of identical level in either perceptual state.

Further transient activations were observed that occurred only at the onset of perceived object-motion (Figure 4.5B). This functional behaviour was found in all early visual-motion sensitive regions with greater sustained activity during perceived object-motion than during vection, and is thus interpretable as the phasic counterpart of the tonic response components identified in state-related analyses. Similarly, a transient activation at the onset of perceived self-motion was only found in the cerebellar nodulus (Figure 4.5C).

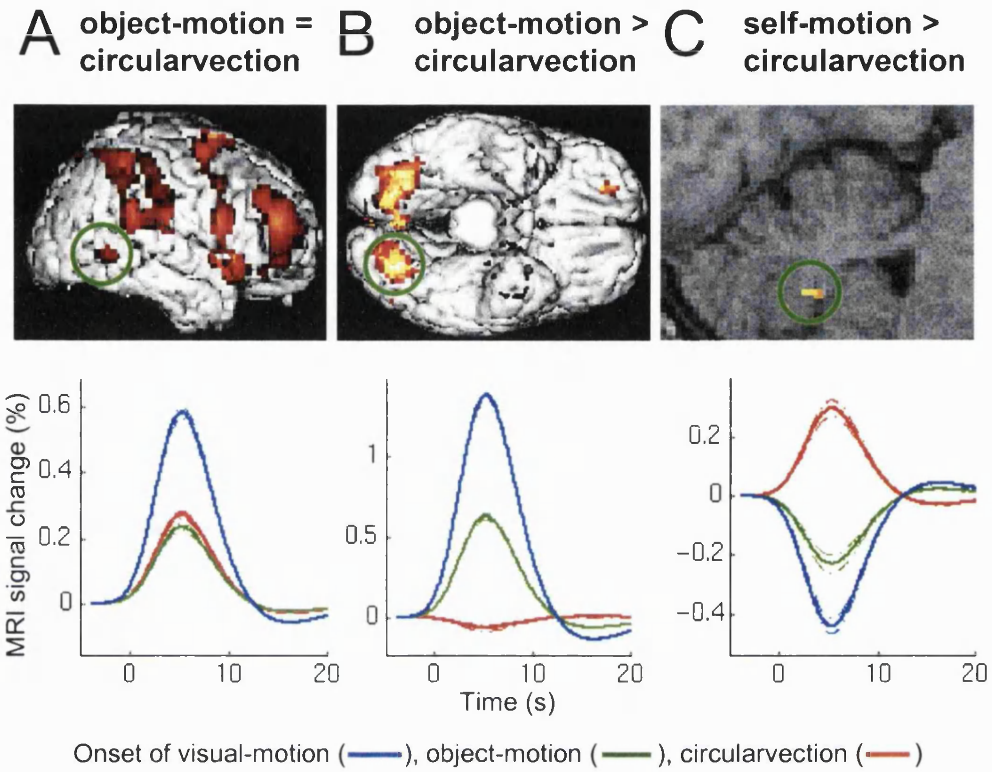


Figure 4.5 Transient activations during perceptual reversals. ***A.*** *The regions responsive to both the perceived onset of circularvection and of object-motion are shown by rendering them onto a surface reconstruction of the right hemisphere (thresholded at $p<0.001$). Note that there is predominantly fronto-parietal activation whereas effects in visual areas are restricted to the anterior pole of the temporo-occipital motion complex. The modelled responses (solid line) and their standard deviation (hatched) in that area are plotted below.* ***B.*** *The responses occurring at the onset of perceived object-motion. The result of the comparison of greater responses during the onset of perceived object-motion than circularvection (at $p<0.001$) are displayed on a rendering of the ventral brain surface (cerebellum removed) with the underlying responses (maximum difference encircled) and standard deviations shown below.* ***C.*** *The result of the comparison of greater responses during the onset of circularvection than object-motion perception (at $p<0.001$) is displayed on a median-sagittal section of the structural MRI scans of one of the participants. The modelled underlying responses are displayed below*

4.1.4 Discussion

Previous neuroimaging studies on the visual processing of self-motion have pursued the experimental avenue that self-motion inevitably generates complex but widely coherent visual-motion, so-called optical flow fields (Gibson, 1954). In these studies (De Jong et al., 1994; Cheng et al., 1995;

McKeefry et al., 1997; Brandt et al., 1998; Previc et al., 2000; Greenlee, 2000), flow responses were compared to responses to visual stimuli that cannot originate from self-motion. Several brain areas thus appear as candidate regions contributing to the perception of self-motion but no previous neuroimaging study has correlated brain activity changes with the perception of self-motion while controlling for processing of the underlying visual-motion stimulus. This study shows that, during sustained optokinetic stimulation, the temporo- and parieto-occipital areas did not change their activity as a function of perceptual state but displayed transient activations when perception switched. Furthermore, all earlier motion-sensitive visual areas and the parieto-insular vestibular cortex deactivated during perceived self-motion.

Irrespective of the perceptual states induced, optokinetic stimulation itself evoked activation in a widespread set of brain areas. Both the spatial distribution and the overall right hemispheric predominance (Figure 4.1) are to be expected for this type of stimulus (Brandt et al., 1998; Dieterich et al., 1998). Moreover, these areas include the candidate areas for the visual processing of self-motion but examination of the activity levels in these areas did not reveal any change as a function of the perceptual state. This behaviour was found in a dorsomedial region (putatively corresponding to activity in visual area V6/PO, (Rosa, 1997; Galletti et al., 1999) and in a superior temporal focus (presumably corresponding to the anterior superior temporal polysensory area described in non-human primates, (Bruce et al., 1981; Cusick, 1997; Anderson and Siegel, 1999). It was also found in the anterior portion (presumed homologue of V5a/MST; Rockland et al., 1997) of the lateral occipito-temporal motion complex which has been repeatedly localised in humans with a variety of visual motion paradigms.

Electrophysiological recordings in non-human primates (Duffy and Wurtz, 1991; Orban, 1997; Tanaka, 1998) have shown neurones preferentially responsive to flow stimuli in a satellite of the motion complex, the dorsal medial superior temporal area (MSTd). They receive congruent vestibular input during real self-motion (Duffy, 1998; Bremmer et al., 1999). These neuronal response properties suggest that this area is ideally suited to contribute to the reconstruction of self-motion (Andersen et al., 2000) although other areas that have been less well characterised by single unit recordings may also play an important role.

Until recently, there has been no unequivocal demonstration of a human homologue of V5a/MST. From an evolutionary perspective, one would expect it to be situated at the anterior pole of the human motion complex (Rockland et al., 1997). As functional response properties are partially shared with neurones in adjacent area V5/MT, functional imaging studies might often represent related activations as one larger focus because of lack of spatial resolution or sensitivity to dissociate sub-components of the motion complex. For this reason even individually determined retinotopic maps usually refer to this area as "MT+" or "MT/MST". The activation foci in response to the optokinetic stimulus used here included the lateral occipito-temporal human motion complex. In the left hemisphere, this focus split into a separate anterior and posterior portion as in McKeefry et al. (1997) and in the right hemisphere, which responded more strongly, there was one large confluent activated area (Figure 4.1). Its anterior portion showed identical activity levels during the two perceptual states, the posterior portion showed greater activity during perceived object-motion than during vection, the two left-hemispheric foci behaving likewise. Assuming that the separation between these foci is not merely the consequence of a spread of activity resulting from the spatial normalisation of individual brains, the results might provide evidence for a functional subdivision of the human motion complex with the posterior portion potentially reflecting the functional behaviour of area V5/MT and the anterior that of area V5a/MST(d). This area, however, is unlikely to be the only one relevant for self-motion perception since, for instance, medial parieto-occipital cortex displayed the same functional behaviour during alternations of perceived self-motion and object-motion.

Identical activity levels during the two perceptual states might, however, not necessarily speak against a functional role for these areas in the perception of vection. The visual stimulation pattern arising from self-motion is only one of many cases of complex visual motion for which processing capacities exist in the human brain and it has been proposed that any visual area implicated in self-motion processing will also possess the capability to process other functional contexts (Probst et al., 1984; Geesaman and Andersen, 1996; Zemel and Sejnowski, 1998). Therefore, the areas where activity remained constantly elevated during both perceptual states are unlikely to be insensitive to these perceptual contexts. Instead, it can be conceived that they are sensitive to the optic flow caused by self-motion but that they may also process other types of coherent visual-motion. It should, however, also be borne in mind that the finding of elevated activity levels at the same time as an absence of a perceptual state-related difference could also be caused by a potential saturation of the BOLD response in these areas during the optokinetic stimulation employed.

These observations point to the importance of temporo-occipital and parieto-occipital structures for visually induced self-motion perception. Yet, an analysis of the sustained response properties alone could only provide indirect evidence in support of this interpretation since an area sensitive to the perceptual consequence of a visual stimulus should display transient signal changes when switches between perceptual transitions occur, as has been reported by Kleinschmidt et al. (1998), although subjects reported truly sudden inversions of the perceived perspective of a Necker cube there whereas in the present study subjects report the more gradual transitions between object-motion perception and vection. This, however, cannot be deduced from analysis of the sustained responses if the degree of activity evoked by each of the perceptual states is equivalent. The sustained response levels found in the presumptive human homologue of MSTd indicate that it is responsive to our stimulus but that its response level is identical across the two perceptual states. A behaviour of this kind could correspond to one continuous sustained response unaffected by perceptual changes but it could also be that every perceptual change is accompanied by a transient response and that the activity level between such switches remains constant. The findings presented show that the latter is the case (Figure 4.5). Several brain areas responsive to optokinetic stimulation underwent transient activations each time the subjects reported a change in perceptual state and the strength of these activations was identical for both directions of perceptual transitions, as were the sustained activity levels for both perceptual states.

The comparison of sustained activity levels between the two perceptual states revealed elevated activity levels during perceived object-motion in a range of areas extending from primary visual cortex to ventral occipital cortex and lateral occipitotemporal cortex. The latter focus corresponds to the posterior portion of the motion complex, the former was centred on the fusiform gyrus. These two functional ramifications of the visual system are differentially engaged by the processing of colour and form (V4) and of motion (V5/MT), respectively (Van Essen and Gallant, 1994). The results show that, when optokinetic stimulation induces the perception of object-motion, there is conjoint activation from primary visual cortex to areas dedicated the processing of form and to those processing motion. This activation might correspond to a figure-ground segregation derived from integratively constructing “form-from-motion” (Lamme et al., 1993; Van Essen and Gallant, 1994).

During vection, early motion-sensitive areas undergo widespread deactivation. The visual stimulus used elicits torsional optokinetic nystagmus (Brecher, 1934; Finke and Held, 1978; Cheung and Howard, 1991) consisting of alternating saccadic fast phases and slow smooth pursuit movements. Chapter 2 reported that torsional optokinetic nystagmus receives a facilitation during the perception of circularvection and it could be argued that the activity changes observed in visual cortex might therefore be due to the difference in the retinal stimulus caused by a changed oculomotor strategy. It has to be noted, however, that the changes in slow phase gain were small and, at a stimulus velocity of 45°/s, only reduced retinal slip by about 2°/s, which is unlikely to be to be of sufficient magnitude to account for the activity differences observed.

Yet, it has been reported that saccades reduce activity in early visual cortex (Paus et al., 1995; Wenzel et al., 1996). This suppression, however, mainly acts through the magnocellular system (Burr et al., 1994), whereas parvo-innervated areas are, if at all, more active during saccades. Therefore, saccade-related suppression cannot explain the activity pattern observed. In addition, dorsal stream areas have been found to increase activation during smooth pursuit eye movements (Freitag et al., 1998). Therefore, if the results presented here were merely due to the enhancement of torsional nystagmus slow phase gain during vection, areas of the dorsal stream should have been activated and not deactivated.

Parieto-insular vestibular cortex has been suggested to be the principal site of cortical vestibular processing (Bottini et al., 1994; Guldin and Grüsser, 1998) and has been found to deactivate during torsional optokinetic stimulation (Brandt et al., 1998). In line with the suggestion by Brandt et al. (1998), this deactivation at the same time as visual cortical deactivation may serve a common purpose similar to that of saccadic suppression (Burr et al., 1994). During real self-motion at constant velocity, coincidental and unrelated accelerations, for instance in the vertical plane while driving on an uneven road, might occur that displace the head and therefore stimulate vestibular receptors and destabilise retinal images. In order to maintain the sustained and undisturbed perception of self-motion, it might be advantageous for an observer to deactivate vestibular and early visual cortices and to suppress the processing of such stimuli. However, those higher-order areas processing the continuous optic flow, are presumably not affected by this mechanism. Even though they do not show an increased activation during vection, they are then relatively overactive in comparison to the deactivated vestibular and visual areas (Figure 4.2).

Another vestibular structure identified in this experiment is located in the vestibulocerebellum. The nodulus was the only brain area that showed an increase of activity during the perception of vection, compared to that of object-motion (Figure 4.4). Furthermore, event-related analysis revealed the nodulus to transiently activate during perceptual transitions into circularvection and to transiently deactivate around the onset of object-motion perception (Figure 4.5C). The nodulus receives most of its afferents from the vestibular nuclei (Akaogi et al., 1994a; Akaogi et al., 1994b; Büttner-Ennever, 1999; Horn et al., 1999), many of which are sensitive to visual motion. It is involved in visual-vestibular interaction (Precht et al., 1976) and is necessary for torsional optokinetic nystagmus (Angelaki and Hess, 1994). Therefore, the increase in nodulus activation observed is likely to reflect the facilitation of torsional optokinetic nystagmus when observers perceive circularvection.

The activation patterns observed in the present experiment are in agreement with Wertheims (1994) model on the generation of self-motion and object-motion perception during visual motion stimulation. A central element of this theory is the presence of a reference signal which acts as an estimator of retinal surface velocity in space. This consists of a combination of information on the eye velocity in space, created by an oculomotor efference copy and a vestibular signal, and on motion of the visual environment. An absence of this reference signal during visual motion stimulation implies the interpretation of visual motion as originating from object-motion. At increasing magnitude of the reference signal, optokinetic stimulation is increasingly interpreted as resulting from self-motion. Optokinetic stimulation itself gradually charges the reference signal, thereby explaining the build-up of vection during sustained visual motion stimulation. The results of this experiment demonstrate that during a stationary optokinetic stimulus as well as during optokinetic stimulation when perceived as object-motion, parieto-insular vestibular cortex showed no significant activity change but it deactivated when vection was perceived. This corresponds to the reference signal in Wertheims model, which is absent during stationary optokinetic stimulation as well as during perceived object-motion. During perception of self-motion and object-stationarity, however, a reference signal is present and it cancels the retinal motion signal. The deactivation of PIVC might therefore be related to the generation of a reference signal or to its induced suppression of the retinal motion signal. This can also account for the deactivation of all earlier motion sensitive areas observed during the perception of self-motion.

4.2 Experiment 2: Visually Evoked Potentials

4.2.1 Introduction

In addition to functional brain imaging techniques like fMRI and PET, electrophysiological scalp recordings are an alternative, and complementary, method of indirectly measuring neural activity. Offering a much higher temporal resolution, they have, however, a very limited capability of spatially resolving the underlying neural tissue. Nevertheless, they are still widely used in neuroscience and are diagnostic tools routinely used in neurological practice (Brigell and Celesia, 1999). Whereas continuous electroencephalographic recordings (EEG) do not permit a detailed analysis of specific perceptual, behavioural or cognitive events occurring during their acquisition, evoked (EP) or event-related potentials (ERP) do so. Usually, a large number of short epochs of recordings, whose onset and offset are time-locked to the event of interest, are sampled and subsequently averaged. This approach reduces the relative contribution of ongoing spontaneous neural activity that is uncorrelated with the occurrence of the event. Eventually, a signal is obtained that is relatively uninfluenced by spontaneous neural activity and reflects the activity related to the event. The magnitude of this signal is usually considerably smaller than the ongoing spontaneous activity and would therefore remain undetected in continuous EEG recordings (Regan and Spekreijse, 1986; Halgren, 1990; Aminoff and Goodin, 1994).

A number of studies investigating vestibular function and visual-vestibular interaction by means of evoked potentials have been conducted in the past using optokinetic stimulation (Hood, 1983; Mergner et al., 1989), vestibular stimulation on earth (Hood, 1983; Hood and Kayan, 1985; Mergner et al., 1989; Probst and Wist, 1990; Probst et al., 1995; Probst et al., 1997) and during parabolic flight (Probst et al., 1996b).

The experiment presented here is specifically aimed at probing the differential activation pattern observed in primary visual cortex using fMRI in the previous experiment. The paradigm used differs from the various studies mentioned above since neither vestibular, nor visual-motion stimulation, nor subjective perceptual reports were used as an event relative to which the recordings were averaged. Instead, a conventional checkerboard-reversal pattern, presented in the central visual field, was used to elicit a visually evoked potential (VEP). Simultaneously, a large-field torsional optokinetic stimulus was presented peripherally, capable of inducing the perception of rollvection in observers fixating the continuously reversing checkerboard. Two evoked potentials were calculated subsequently, one elicited by those checkerboard reversals that took place while subjects reported the perception of object-motion, one corresponding to the reversals that were presented during periods of perceived circularvection.

4.2.2 Materials and Methods

Subjects

Five women and three men, from 24 to 29 years of age (mean 26.0 years), without history of relevant neurological or sensory disease, consented to participate in the experiment. All had normal or corrected-to-normal vision. Informed consent had been obtained from all subjects prior to the start of the experiment.

Apparatus

The optokinetic stimulus consisted of an alternating pattern of black and white radial sectors, spaced at equal intervals, that was back-projected onto a screen subtending 110° of visual angle horizontally and 110° vertically, refreshing at a rate of 60Hz. The stimulus rotated around an earth-horizontal axis that was aligned with the subjects' line of sight. The white and black stimulus elements had luminances of 0.11 cd/m^2 and 0.08 cd/m^2, respectively and therefore a comparatively low contrast of 0.16. The checkerboard-reversal stimulus was presented on an LCD monitor, 287 mm wide and 215 mm high, that was positioned immediately in front of the optokinetic stimulus and centred with respect to subjects' line of sight. The checkerboard pattern consisted of 32 vertical columns and 24 horizontal rows of alternating black and white squares that inverted continuously every 750 ms and subtended approximately 45' of visual angle. At its centre was a medium grey circular fixation target whose diameter was a quarter of the side length of a square.

Electrophysiological Recording

Following skin preparation, 8mm silver/silverchloride electrodes were fixed on the scalp according to the 10-20-system (Jasper, 1958) at positions O_Z (occipital midline), O_1 (occipital left), O_2 (occipital right) and F_Z (frontal midline) using adhesive conductive electrode paste. Additional electrodes were attached to each earlobe and connected together as inactive reference. Impedances between pairs of electrodes were below 5 kΩ. Differential recordings were obtained between the electrode pairs O_1-F_Z, O_Z-F_Z, O_2-F_Z and F_Z-earlobes at an amplification of 50 µV/V, a high-cut frequency of 30 kHz and a time constant of 500 ms. As a control of fixation and eye blinks, cyclopean horizontal and right monocular vertical DC-electrooculogram was recorded. Sweeps were sampled at a rate of 1 kHz for a duration of 300 ms commencing 50 ms prior to pattern reversal.

Procedure

Subjects were seated at a distance of 68 cm from the fixation target with their head supported by a chinrest. Subjects were instructed to look at the fixation target and to reduce eye blinks and other sources of artefacts. Sessions began with the recording of 200 pattern-reversal sweeps whilst the optokinetic stimulus was stationary. After a break, 600 sweeps were recorded with the optokinetic stimulus revolving clockwise at a velocity of 45°/s. For the duration of this trial, subjects signalled the perception of object-motion or rollvection by switching a hand-held dial between two pre-defined settings.

Data Analysis

All recordings were analysed and processed off-line after data acquisition had terminated. In a first step, sweeps containing artefacts, mainly caused by eye blinks, were excluded following visual inspection of the raw data. Subsequently, the five sweeps preceding as well as following each transition between perceptual states were excluded in order to avoid contamination of the signal by components related to movement and to decision-making processes. Following this, evoked potentials were computed by averaging the remaining sweeps with respect to the type of trial and/or the perceptual state during which they were recorded. Hence, a total of four evoked potentials were obtained per subject and recording site: 1) An average consisting of sweeps that were recorded while the optokinetic stimulus was stationary; 2) one consisting of sweeps sampled during optokinetic stimulation, irrespective of the perceptual state reported by the subjects; 3) one composed by those sweeps of the latter trace that were recorded while subjects reported the perception of object-motion; 4) one containing sweeps during which circularvection was reported. Following three-point smoothing, baseline was calculated as the average signal obtained during the 50 ms preceding pattern reversal. The first negative inflection (N70) and the first positive (P100) inflection of the signals were determined automatically. Latencies relative to pattern-reversal and amplitudes relative to baseline were computed for each subject, trial and perceptual state.

4.2.3 Results

Psychophysical Data

Following optokinetic stimulation onset, all subjects reported perceiving rollvection with an average onset latency of 11.0 s (SEM 4.8 s). During the

450 s optokinetic stimulation, subjects perceived circularvection for, on average, 215.6 s (SEM 16.3 s).

Evoked Potentials

***Table 4.1** Means and standard errors (rounded) of the onset latencies (ms) of the N70 and P100 components of the checkerboard reversal VEP during the perception of object-motion (OM) versus circularvection (CV) and during a stationary peripheral visual field (ST) versus rotating optokinetic stimulation (OKS)*

Electrode Site	O_1		O_Z		O_2		F_Z	
Percept. State	OM	CV	OM	CV	OM	CV	OM	CV
N70	63 (2)	59 (4)	66 (3)	66 (3)	62 (3)	59 (4)	59 (6)	60 (5)
P100	96 (2)	96 (3)	95 (2)	95 (2)	96 (2)	96 (2)	95 (3)	93 (6)
Periph. Field	ST	OKS	ST	OKS	ST	OKS	ST	OKS
N70	57 (4)	63 (2)	68 (2)	66 (2)	61 (3)	59 (4)	51 (5)	55 (6)
P100	98 (3)	96 (2)	95 (2)	95 (2)	98 (3)	96 (2)	96 (2)	96 (3)

After rejections of sweeps containing artefacts and of those that were acquired adjacent to perceptual transitions, individual averages formed consisted of 152 to 355 single sweeps. A detailed list containing mean onset latencies of the visually evoked potential N70 and P100 components during stationary versus moving optokinetic stimulus and during the perception of object-motion versus circularvection for the different electrode positions is presented in Table 4.1. The corresponding baseline-to-peak amplitudes are listed in Table 4.2. It should also be noted that in the 2-way repeated measures ANOVAs presented subsequently no interaction reached significance unless stated otherwise.

Table 4.2 *Means and standard errors (rounded) of the baseline-to-peak amplitudes (µV) of the N70 and P100 components of the checkerboard reversal VEP during the perception of object-motion (OM) versus circularvection (CV) and during a stationary peripheral visual field (ST) versus rotating optokinetic stimulation (OKS)*

Electrode Site	O_1		O_Z		O_2		F_Z	
Percept. State	OM	CV	OM	CV	OM	CV	OM	CV
N70	3.4 (1.0)	2.5 (1.0)	5.3 (1.3)	4.6 (1.2)	2.6 (0.8)	2.0 (0.8)	-1.6 (0.5)	-1.2 (0.6)
P100	9.1 (1.3)	9.5 (1.3)	12.2 (1.7)	12.4 (1.8)	11.7 (1.4)	11.7 (1.5)	-3.3 (0.7)	-3.4 (0.8)
Periph. Field	ST	OKS	ST	OKS	ST	OKS	ST	OKS
N70	3.4 (1.1)	3.0 (0.9)	5.4 (1.5)	4.9 (1.3)	2.4 (0.9)	2.2 (0.8)	-1.1 (0.5)	-1.3 (0.5)
P100	9.9 (1.5)	9.2 (1.3)	12.6 (1.8)	12.2 (1.7)	12.3 (1.7)	11.7 (1.4)	-4.2 (0.8)	-3.2 (0.7)

N70 - Stationarity versus Optokinetic Stimulation

Latency. The latency between pattern reversal and the peak of the first negative inflection of the visually evoked potential was not significantly affected by rotation of the optokinetic stimulus as demonstrated by a 2-way repeated measures ANOVA ($F_{1,7}<1$). Averaged across occipital electrode positions, mean peak latencies were 62.0 ms during stationary trials and 61.8 ms during optokinetic stimulation. There was a significant main effect of electrode position ($F_{2,14}=4.1$; $p<0.05$) on onset latency with a latency of 58.4 ms at O_1, 67.1 ms at O_Z and 60.2 ms at O_2. This main effect is explained by the increased latency at the midline electrode position with a significant post-hoc quadratic contrast ($F_{1,7}=10.3$; $p<0.05$).

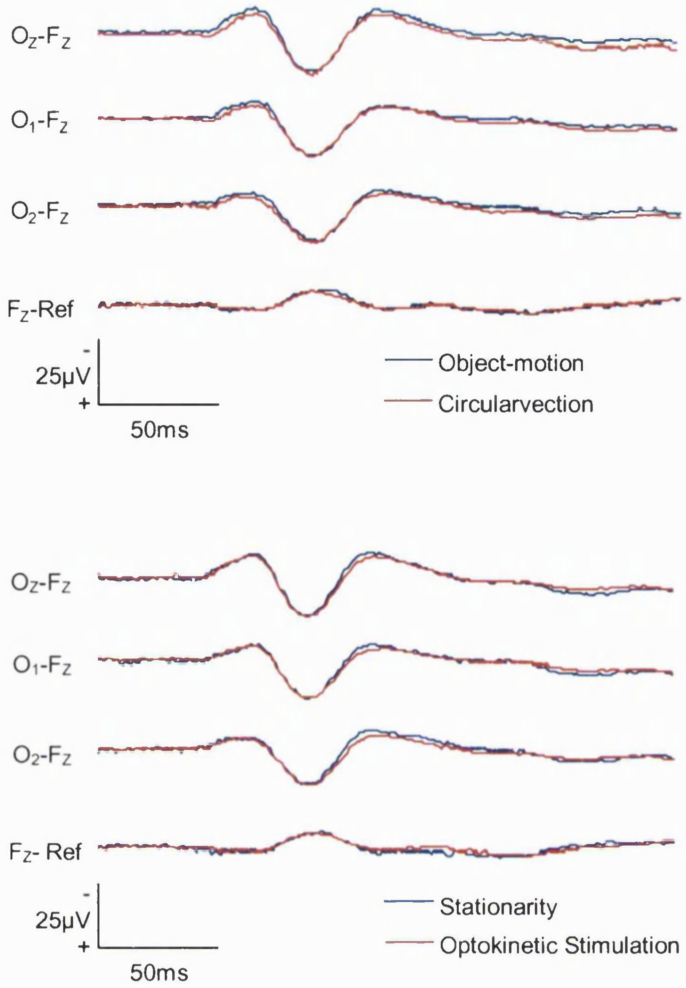


Figure 4.6 *Sample of visually evoked potentials in a single subject at the different comparisons performed. Note the difference in amplitude of the first negative (upward) inflection between the traces obtained during perception of object-motion and circularvection (top traces). Also note the absence of a difference when comparing the potentials recorded during a stationary visual surround with optokinetic stimulation (bottom traces)*

Amplitude. A similar, non-significant, result was obtained for the corresponding baseline-to-peak amplitudes with values of –3.8 µV during stationarity and –3.4 µV at a rotating background ($F_{1,7}<1$). A significant main effect of electrode position (O_1: -3.2 µV; O_Z: –5.2 µV; O_2: -2.3 µV; $F_{2,14}=5.7$; $p<0.05$) was found and demonstrated to be due to a significant quadratic contrast ($F_{1,7}=7.1$; $p<0.05$).

P100 - Stationarity versus Optokinetic Stimulation

Latency. Mean peak onset latencies for the first positive inflection were, averaged across sites, 97.2 ms without and 95.8 ms with optokinetic stimulation ($F_{1,7}=1.1$; n.s.). Electrode position also had no significant effect on onset latencies (O_1: 96.8 ms; O_Z: 95.3 ms; O_2: 97.3 ms; $F_{2,14}=1.6$; n.s.).

Amplitude. Motion of the visual surround had no significant effect on baseline-to-peak amplitudes which were, on average, 11.6 μV without and 11.0 μV with optokinetic stimulation ($F_{1,7}<1$). There was, however, a significant effect of electrode position on P100 amplitudes, which were 9.6 μV at O_1, 12.4 μV at O_Z and 12.0 μV at O_2 ($F_{2,14}=6.3$; $p<0.05$).

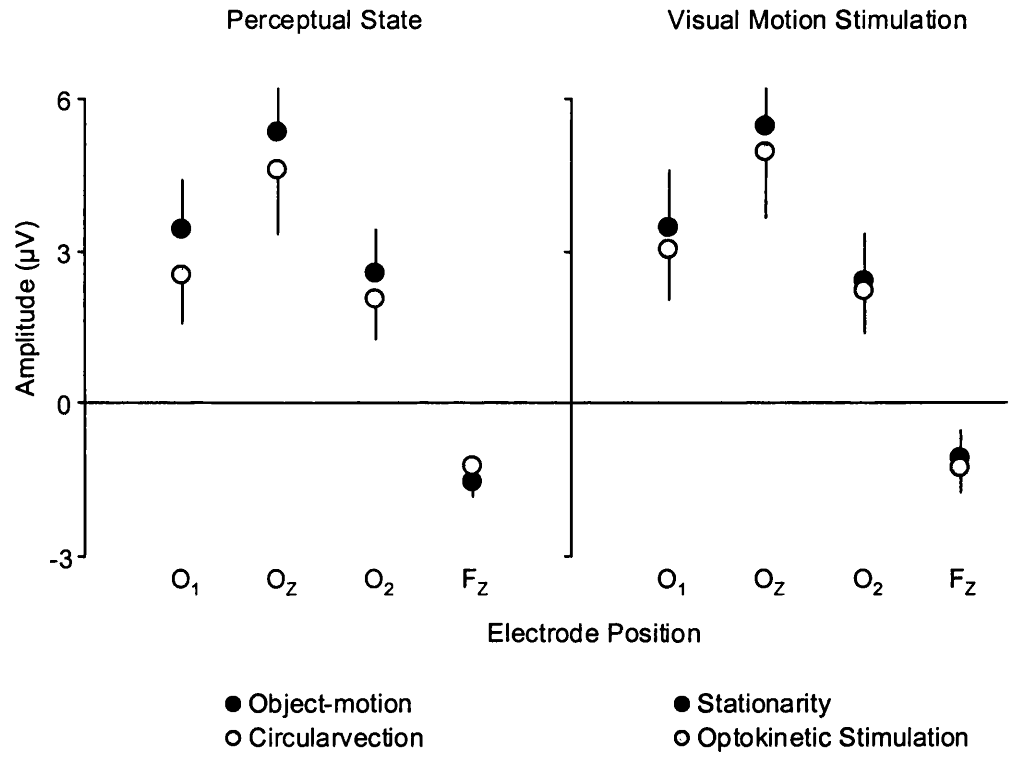


***Figure 4.7** Means and standard errors of the amplitudes of the N70 components of the visually evoked potential during stationary versus rotating optokinetic stimulation and during the perception of object-motion versus circularvection*

N70 – Perception of Object-motion versus Circularvection

Latency. The perceptual state subjects experienced while their brain activity was recorded had a significant effect on the N70 peak latency. During reported object-motion, mean latency was 63.3 ms and during circularvection it was 62.8 ms ($F_{1,7}=6.0$; $p<0.05$). Note that although statistically significant, the magnitude of this effect lies below the temporal resolution permitted by the sampling rate and is therefore not likely to be of physiological relevance. Average over perceptual states, mean latencies obtained at the different electrode positions were 63.1 ms at O_1, 65.9 ms at O_Z and 60.0 ms at O_2. There was also a significant main effect of recording site ($F_{2,14}=3.84$; $p<0.05$) with a significant quadratic post-hoc contrast ($F_{1,7}=12.1$; $p<0.05$).

Amplitude. During perception of object-motion, baseline-to-peak amplitude of the P100 component was –3.8 µV whereas during circularvection the inflection was –3.0 µV and therefore significantly lower as demonstrated by ANOVA ($F_{1,7}=7.6$; $p<0.05$). A main effect of recording site also was significant ($F_{2,14}=5.0$; $p<0.05$) with corresponding values being –3.0 µV (O_1), -5.0 µV (O_Z) and –2.3 µV (O_2).

P100 – Perception of Object-motion versus Circularvection

Latency. No effect of perceptual state (OM: 95.7 ms; CV: 95.4 ms; $F_{1,7}<1$) nor of electrode position (O_1: 95.5 ms; O_2: 95.1 ms ;O_3: 96.0 ms ; $F_{2,14}<1$) on peak latency of the first positive inflection was detected.

Amplitude. During perception of object-motion, average P100 amplitude was 11.0 µV and 11.2 µV during vection with no main effect of perceptual state detected by ANOVA ($F_{1,7}<1$). Electrode position had a highly significant effect with amplitudes being 9.3 µV at O_1, 12.3 µV at O_Z and 11.7 µV at O_2 ($F_{2,14}=7.2$; $p<0.01$).

Contribution of the Prefrontal Electrode Site

Since all results described so far were obtained as differential recording between an occipital electrode site and another electrode placed medially over the prefrontal cortex, any potential recorded is reflecting an electrical dipole between occipital and frontal regions. In order to determine to what extent the results observed were caused by changes in electrical activity underlying the prefrontal electrode, amplitudes and latencies of the N70 and P100 peaks were analysed for the differential recording between the prefrontal electrode position and the linked earlobe electrodes, serving as inactive reference. Therefore, paired t-tests, comparing stationarity versus optokinetic stimulation and perception of object-motion versus circularvection, were computed for the latencies and amplitudes of the N70 and P100 components separately. No comparison demonstrated a significant effect of optokinetic stimulation or perceptual state on the frontal electrode site (all $p>0.05$).

4.2.4 Discussion

In summary, the main finding of this experiment was that during vection, the first negative inflection of the visually evoked potential was of a significantly lower amplitude than it was during the perception of object-motion. This effect was also reflected in a slightly, but significantly, shortened latency between pattern reversal and peak amplitude of the N70 component during the perception of vection. The presence, or absence, of optokinetic stimulation, however, did not influence any parameter of the N70 component. On the other hand, neither amplitude nor latency of the P100 component were affected systematically by either a change in perceptual state or rotation of the visual environment.

In addition, a general tendency was observed for N70 latency to be increased, and for its amplitude to be raised, at the midline electrode position. P100 latency, on the contrary, was not influenced by electrode position but its amplitude, too, was elevated at electrode position O_Z.

There is now considerable agreement that the neuronal generators of the N70 and P100 components of the pattern-reversal VEP are located in primary visual cortex (Brodmann area 17). In patients with lesions restricted to striate cortex these components are generally absent or abnormal (Aldrich et al., 1987), whereas in patients with lesions in visual association cortex they are preserved (Bodis-Wollner et al., 1977). The two components are likely to be functionally dissociated since patients with a preserved N70 and an abnormal P100 have been reported (Celesia et al., 1980; Celesia et al., 1982). Intracortical recordings in monkey have demonstrated that the N70 component is caused by excitatory postsynaptic potentials of stellate cells in primary visual cortex layer 4C (Schroeder et al., 1991). These cells receive input from primary thalamic afferents, from other striate cortical layers and projections from extrastriate cortex. The following P100 component presumably reflects inhibitory postsynaptic potentials of pyramidal neurones in layers 2 and 3 (Schroeder et al., 1991), possibly mediated by GABAergic transmission (Zemon et al., 1986; Halgren, 1990). At this level of specification it is not possible to distinguish the relative contributions of the magnocellular and parvocellular pathways to the N70 component since geniculofugal fibres of both systems terminate in striate cortex layer 4C – the magnocellular pathway in layer 4Cα and the parvocellular pathway in layer 4Cβ (Lamme et al., 1998).

From a physiological perspective, the finding of reduced net excitation in primary visual cortex during the perception of circularvection fits well with the observation of a decrease in activation in the same area as demonstrated in the previous experiment using fMRI. Hence, this result lends support to the hypothesis that in order to maintain an uncontaminated perception of self-motion the sensorial weight might be shifted away from primary visual processing in order to reduce the influence of distracting visual motion signals that could otherwise lead to oscillopsia, a blurring and destabilisation of the visual percept (Morland et al., 1995; Morland et al., 1998)

Of note, although there was a significant reduction of negativity in the evoked potential during circularvection in comparison to the perception of object-motion, no such effect was found when optokinetic stimulation was compared with a stationary peripheral visual field. This result further substantiates the claim of the previous experiment that the differential activation patterns observed at contrasting perceptual states cannot be explained by the changes in retinal motion which occur when torsional optokinetic nystagmus is facilitated during circularvection as has been found consistently in the experiments presented in Chapter 2. Although rotation of the stimulus induces torsional optokinetic nystagmus and therefore causes a most fundamental change in oculomotor behaviour, the evoked potential remains unaffected, whereas it reliably shows perceptual state-related changes although they are accompanied by a much smaller change of torsional nystagmus. The same observation demonstrates that the occipital cortical changes observed at changing perceptual states are not a consequence of the changed retinal stimulus as a result of enhanced torsional nystagmus slow phase gain. Torsional optokinetic nystagmus is performed at a gain far too low to enable efficient slow-phase pursuit during visual field rotation. Hence, retinal slip changes by a considerably larger amount when the visual environment is rotating, rather than stationary, than it does when slow phase gain enhances between the perception of object-motion and that of circularvection.

The claim that the observed VEP changes are not caused by a change in retinal stimulus do not contradict the fact that the N70 component is generated by excitation of target neurones of the optic radiation. A large body of evidence exists on the influence of feedback projections onto primary visual cortex neurones originating in other striate cortex layers as well as in extrastriate visual and parietal areas (Lamme et al., 1998) mediating, amongst others, attentional phenomena (Ashbridge et al., 1997). Although likely to be involved in the evoked potential changes observed, feedback projections from higher cortical areas are not necessarily the only mechanism involved. Attentional effects have been shown to be mediated by feedforward gating through the thalamus, presumably relayed via the nucleus reticularis thalami (Guillery et al., 1998).

5 Autonomic Nervous System Correlates

5.1 Experiment 1: Real versus Illusory Self-motion

5.1.1 Introduction

Spatial reorientations with respect to gravity trigger homeostatic mechanisms which maintain an appropriate distribution of blood volume throughout the body. Much of this regulation is achieved through reflexive neuronal circuitries involving the continuous measurement of vascular tension through baroreceptors and, after relay in the brain stem and hypothalamus, acting on preganglionic sympathetic and parasympathetic neurones thereby modulating peripheral vasoconstriction and cardiac function.

In man, vestibulo-autonomic mechanisms do not appear to influence cardiovascular control in the same differential manner as seen in laboratory animals. In human subjects, forwards as well as backwards linear acceleration along the naso-occipital axis is followed by an increase in peripheral vessel blood pressure in healthy volunteers and this response is largely reduced in bilateral avestibular subjects (Yates et al., 1999). In cat, however, nose-up rotation of the head produces a large increase in sympathetic nerve activity and blood pressure, whereas nose-down pitch of the head elicits a depressor response (Yates, 1992; Yates, 1996b; Yates and Kerman, 1998).

It has therefore been proposed that the autonomic adjustments seen in man following vestibular stimulation might in part reflect unspecific reactions. Although unlikely to represent a mere startle response since no habituation occurs with increased exposure to the stimuli, the cardiovascular action could be part of a readiness response, rapidly redistributing blood to skeletal muscles involved in postural reflexes and thereby enhancing the organism's ability to efficiently perform compensatory postural readjustments following threatened balance (Yates et al., 1999).

Irrespective of the specific or unspecific nature of vestibulo-autonomic adjustments, the purpose of the present experiment is to characterise human cardiovascular reactions to illusory (vection) versus real whole-body reorientation. For this purpose, subjects sitting upright in a flight simulator were rotated towards their side whilst having their peripheral blood pressure, blood flow and heart rate recorded. Responses obtained during these tilts were compared with measurements taken when the same subjects reported the perception of rollvection, and therefore illusory rotation, induced by torsional optokinetic stimulation.

5.1.2 Materials and Methods

Subjects

Ten men, from 29 to 52 years of age (mean 36.2 years), without history of neurological or cardiovascular disease, consented to participate in the experiment. None had taken any medication during the 24 hours preceding testing and sessions were performed mid-morning or mid-afternoon, separated from meals by at least 2 hours. Informed consent had been obtained from all subjects prior to the start of the experiment.

Apparatus

Subjects were seated with head upright in a flight simulator (SEGA, Tokyo, Japan) that executed discrete tilts from the upright position by rolling subjects about an antero-posterior, earth-horizontal axis aligned through the midline of the trunk approximately at the level of the heart (Figure 5.1). Head, trunk and limbs were supported and restrained with foam padding.

The torsional optokinetic stimulus consisted of the motorised cone used for the experiments in Chapter 2. It was mounted so that the axis of rotation was aligned with the viewer's line of sight and the fixation target was at a distance of 28 cm from the subject's nasion, enabling full-field optokinetic stimulation.

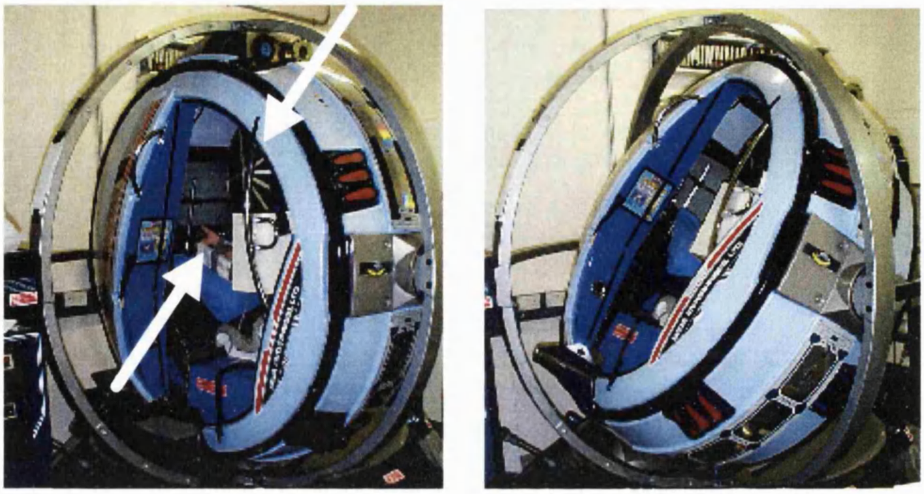


Figure 5.1 *Flight simulator in upright position and tilted 30° rightward. The arrows point at the optokinetic stimulus and at the subject's arm to which the blood pressure monitor is attached. For demonstration purposes the flight simulator door is left open*

Autonomic Recordings

The electrocardiogram (ECG) was recorded using a BP-508 patient monitor (Colin, Komaki, Japan) with a time constant of 0.5 s. This unit was also used to measure continuous tonometric arterial blood pressure from a robotic sensor positioned over the radial artery, about 20mm from the wrist line. The sensor is comprised of an array of servo-controlled detectors that monitor pulsations of the artery. The arterial oscillations are referenced to conventional blood pressure measurements using the Riva-Rocci method by the BP-508 patient monitor every 5 min. To exclude mechanical shocks and artefacts due to wrist movements, the arm was supported by a hand brace and secured in foam-padded trough resting on a pillow on the subject's lap with the sensor in the axis of tilt.

Pulsatile blood flow was measured using photoelectric plethysmography (Model PPS, Grass, Boston, MA, USA) from the index finger of the right hand and high pass filtered with a time constant of 3 s.

Electrocardiogram R-R interval time was computed online as the temporal delay between two adjacent ECG R-waves and was derived in analogue form from the raw signal with a Grass tachograph.

All signals were sampled at a rate of 125 Hz and subsequently averaged according to whether they had been sampled during the 10 s prior to, or following an event. Events were flight simulator tilt and subjective report on the onset of circularvection.

Procedure

After subjects were positioned in the flight simulator and fitted with the recording equipment, cabin illumination was extinguished and its opening was covered. Subjects were instructed to maintain fixation during optokinetic stimulation and to keep their eyes closed during real tilt trials. Subjects indicated the perceived onset of circularvection as well as the onset of flight simulator motion by depressing a pushbutton with their right foot.

Real motion trials consisted of 30° leftwards or rightwards tilts of the flight simulator, achieved within 2 s and maintained for a minimum of 30 s after which a tilt back to upright was performed using the inverted motion profile. Optokinetic stimulation was achieved by rotating the stimulus clockwise or anticlockwise at a constant velocity of 40°/s for a duration of 60 s.

Real tilt and optokinetic stimulation conditions, consisting of 3 trials each, were presented in a balanced order across subjects. Five subjects were exposed to the real tilt condition followed by three trials of optokinetic stimulation, the remainder underwent the inverse sequence. The directions of tilt or optokinetic stimulus rotation were alternated on successive trials. Conditions were interspersed by rest periods of 10 min and intertrial interval was at least 1 min with trial onset kept unpredictable.

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Data Analysis

Data were collected for a minimum of 30 s before delivery of stimuli to ensure sufficiently stable baseline recordings. The perception of circularvection was reported intermittently following stimulation. In order to maintain comparability to trials with real motion, only the first transition between the perception of object-motion and circularvection was analysed. To ensure equal lengths of epochs that do not contain perceptual transitions from circularvection to the feeling of stationarity, the data recorded during the 10 s preceding and following simulator tilt or vection onset were used for further analysis in all trials. Data from these epochs were averaged for each subject and trial and subsequently difference scores between them were computed.

5.1.3 Results

R-R Interval

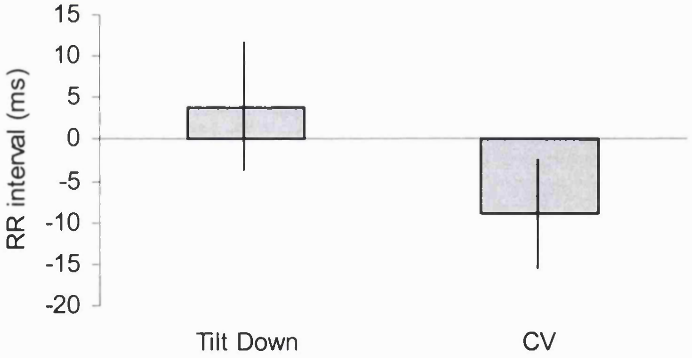

Figure 5.2 *Mean and standard error of change in RR interval during real whole-body reorientation and during the perception of circularvection (CV)*

Following real spatial reorientation R-R interval increased on average by 4 ms (SEM 7.6 ms). During circularvection R-R interval was shortened by 9 ms (SEM 6.4 ms) as demonstrated in Figure 5.2. Neither of these changes was significant, nor did the effects of real versus illusory motion differ significantly using paired t-tests.

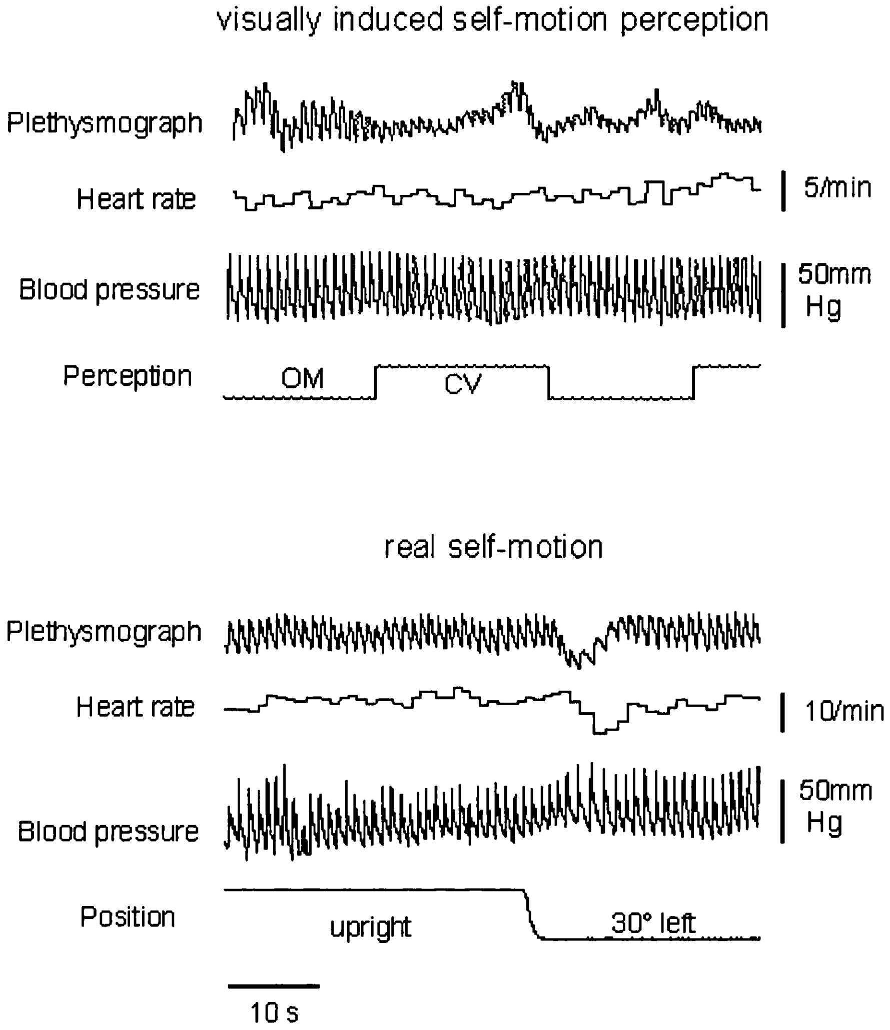

Figure 5.3 Raw records of cardiovascular parameters measured in the experiment. The top panel shows responses to transitions between the perception of object-motion (OM) and circularvection (CV). The bottom panel shows responses to whole-body tilt in roll from upright. Note the pressor response (increased systolic and diastolic blood pressure and reduced peripheral blood flow) following real self-motion

Systolic Arterial Blood Pressure

Figure 5.4 demonstrates that flight simulator tilt caused a highly significant rise in systolic blood pressure by 6.2 mm Hg on average (SEM 1.9 mm Hg; $p<0.01$), as shown by a paired t-test. In contrast, during vection mean systolic blood pressure increased by 1.2 mm Hg (SEM 1.1 mm Hg) which was not significant. The increase in systolic arterial blood pressure following real tilt differed significantly from that following vection (paired t-test; $p<0.05$).

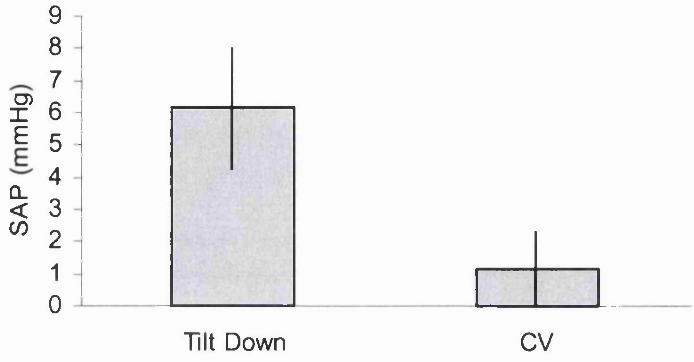

Figure 5.4 *Mean and standard error of change in systolic arterial blood pressure (SAP) during flight simulator tilt and the visually induced perception of self-rotation (CV)*

Diastolic Arterial Blood Pressure

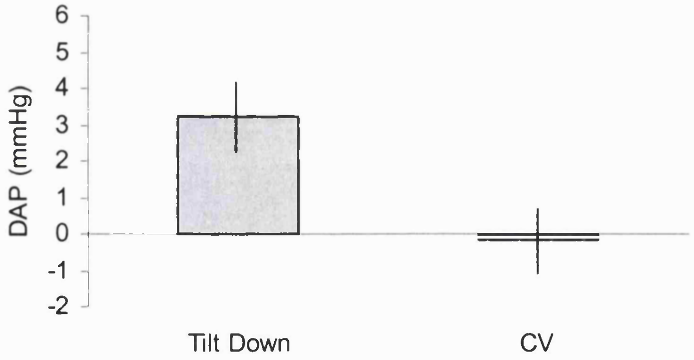

Figure 5.5 *Mean and standard error of change in diastolic arterial blood pressure (DAP) during real lateral tilt and circularvection (CV)*

A similar, but less pronounced, pattern was shown by diastolic blood pressure. In response to real motion, it rose by an average 3.2 mm Hg (SEM 0.9 mm Hg) which was highly significant (paired t-test; $p<0.01$), whereas during circularvection a mean decrease by 0.2 mm Hg (SEM 0.9 mm Hg) was observed that did not reach statistical significance in a paired t-test. The difference between blood pressure changes following real and illusory motion was highly significant in a paired t-test ($p<0.01$) as can be seen in Figure 5.5.

Peripheral Blood Flow

Plethysmographic recordings showed a significant decrease of peripheral blood volume by 76 computer units (SEM 26 cu) after the flight simulator was tilted (paired t-test; $p<0.05$) as demonstrated graphically in Figure 5.6. This decrease differed significantly ($p<0.05$) from a mean increase by 7 cu (SEM 10 cu) following the perception of vection, which itself did not change significantly across perceptual states as shown by paired t-tests.

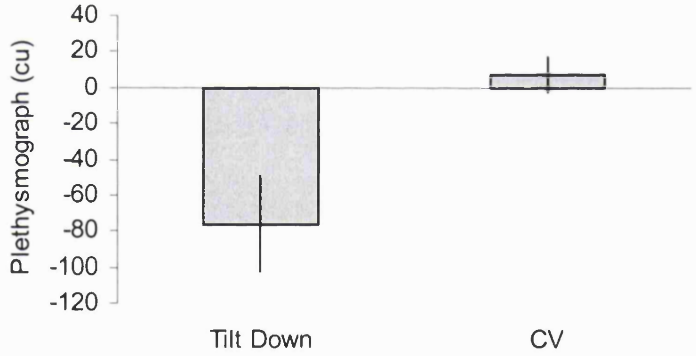

Figure 5.6 *Mean and standard error of change in peripheral blood flow (as measured by plethysmography) following real versus illusory (CV) whole-body rotation in roll*

Individual Responses

Inspection of individual responses following real and illusory rotation revealed a high degree of idiosyncrasy. In nine out of ten subjects systolic and diastolic arterial blood pressure rose subsequent to real motion. Following the onset of circularvection, however, two different types of cardiovascular responses could be observed. Four subjects demonstrated a reduction of systolic and diastolic blood pressure whereas in the remaining six subjects blood pressure rose or remained unchanged (Figures 5.7 and 5.8). Similarly, nine subjects demonstrated a reduction of peripheral blood flow, consistent with a pressor response, following real reorientation. Eight of these showed a consistent increase of peripheral vasodilatation following the perception of circularvection (Figure 5.9). Changes in RR interval were small and highly variable in both conditions as shown in Figure 5.10.

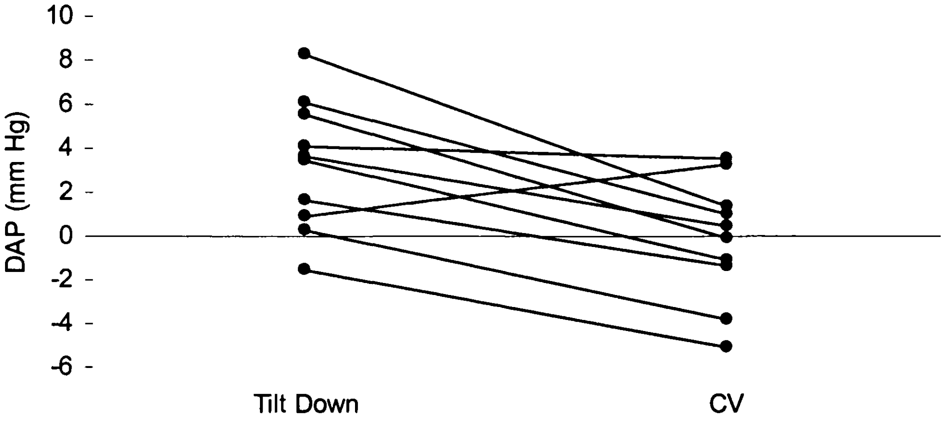

Figure 5.7 Individual changes in diastolic arterial blood pressure (DAP) following real versus illusory (CV) lateral reorientation in roll

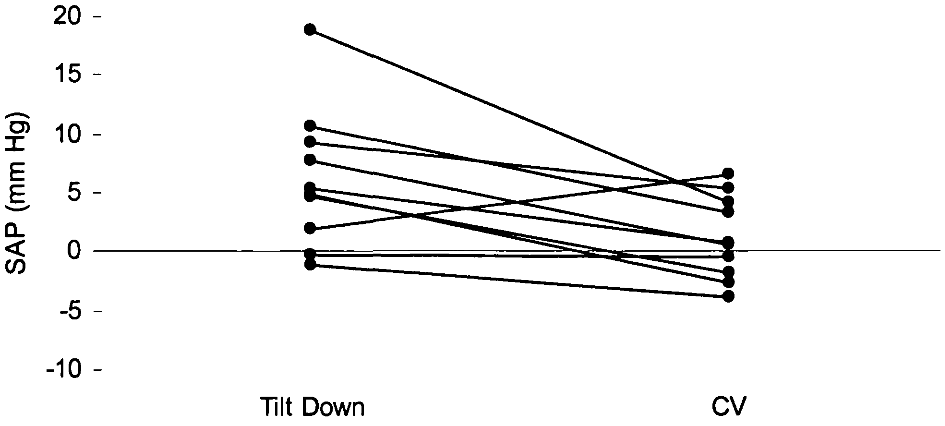

Figure 5.8 Individual changes in systolic arterial blood pressure (SAP) after real versus illusory (CV) motion in roll

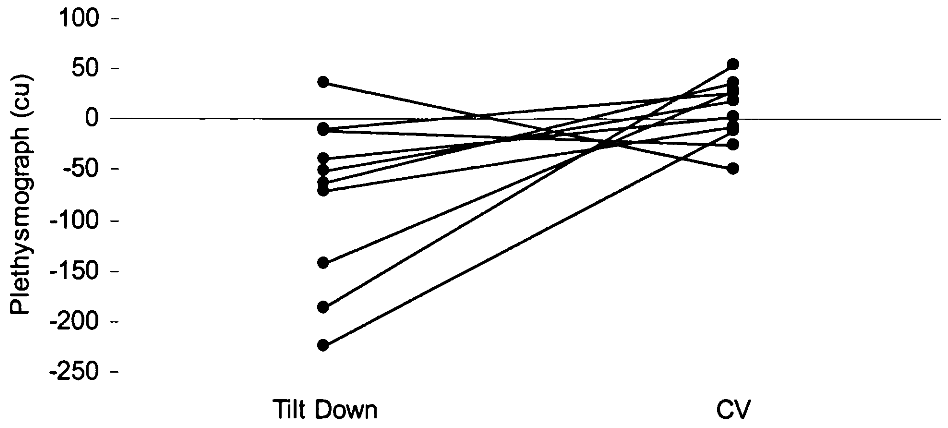

Figure 5.9 Individual changes in peripheral blood flow in response to lateral whole-body tilt and illusory perception of self-motion in roll (CV)

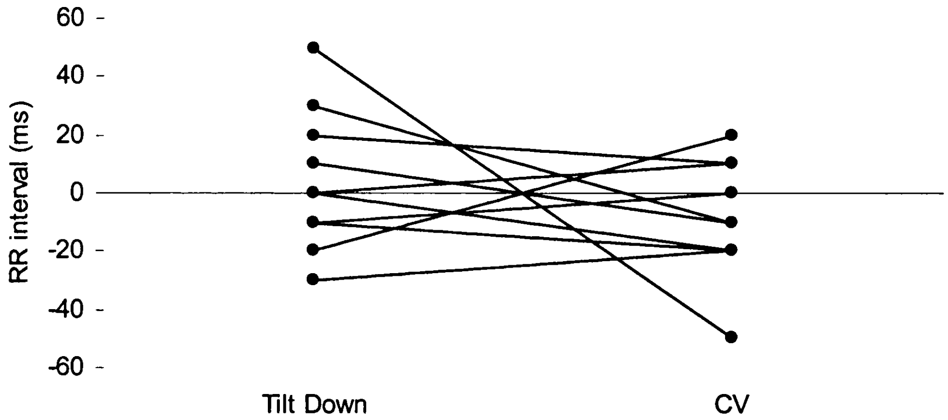

Figure 5.10 Individual changes in RR interval following real whole-body reorientation in roll and illusory perception of rollvection (CV)

5.1.4 Discussion

In summary, the results of the present experiment demonstrate that the autonomic nervous system responds with a uniform increase of peripheral arterial blood pressure following a tilt of the body away from an upright posture. This was accompanied by a decrease in index finger blood flow suggesting a general increase of sympathetic nervous system activity (Johnson et al., 1993; Biaggioni et al., 1998). Visually induced perception of illusory whole-body rotation around the same axis did, in contrast, not coincide with any systematic change in human cardiovascular activity. In all blood flow and blood pressure variables measured, this differential pattern of responses differed significantly during real when compared to illusory perception self-motion. It should be noted that, due to technical constraints, the axes of rotation for rollvection (naso-occipital axis) and real flight simulator motion (sagittal axis on the level of the heart) were parallel but not aligned, although this is unlikely to account for the absence of any detectable cardiovascular adjustments following rollvection.

Several studies investigating cardiovascular responses to vestibular stimulation have previously been carried out in laboratory animals. Vestibular stimulation consisted of caloric stimulation (Spiegel, 1946), rotation of the animal in space (Lindsay et al., 1945; Spiegel, 1946) as well as direct electrical vestibular nerve stimulation (Tang and Gernandt, 1969; Uchino et al., 1970; Ishikawa and Miyazawa, 1980) and was consistently found to lower arterial blood pressure.

The finding of the present experiment that a pressor response is provoked by off-vertical rotation of the body stands in contrast to these observations. Although increases in monkey cardiovascular activity have been reported following centrifugation along the z-axis that are absent in bilateral avestibular animals (Satake et al., 1991), a reduction of sympathetic nervous system activity would have been expected to result from the tilt trials in the present experiment. A depressor response would have been an appropriate reaction since tilting subjects away from a vertical posture effectively reduces the gravity-induced hydrostatic pressure differences in the vascular system and would thus require diminished cardiovascular compensation. This counterintuitive finding stands not alone, however. In a study on human subjects who were lying prone, head-down tilt resulted in a rapid decrease of peripheral blood flow, and therefore in a pressor response, although this would have been an appropriate way to counteract orthostatic hypotension produced by tilt of the head and body in the opposite direction but not to compensate for the hypertension that would have been signalled by the vestibular stimulus used (Essandoh et al., 1988).

Yates et al. (1999) have argued that the generalised pressor response they found in human subjects following linear acceleration irrespective of the direction of the acceleration vector might well be of vestibular origin since it was largely reduced in avestibular subjects. The fact that the response was not absent in avestibular subjects offers the further possibility that the changes observed are due to several different, and perhaps opposing, reactions that occur simultaneously. Responses directly mediated by vestibular stimulation might be counteracted or masked by other, perhaps unspecific, effects that result from the same stimulus as, for instance, a general preparatory and activating responses.

In this light there is no clear and single way of interpreting the observation that the perception of self-motion does not incur any systematic adjustments in cardiovascular activity when induced visually. Assuming that optokinetic stimulation, and vection, activates vestibular nuclei neurones (Henn et al., 1974; Waespe and Henn, 1977; Waespe and Henn, 1979) in a similar manner to congruent vestibular stimulation, vection should induce cardiovascular changes comparable to those elicited by vestibular stimulation. The observation that this is not the case does, however, not necessarily imply that there is no vestibular contribution to the cardiovascular adjustments demanded by the tilt paradigm used. Since it is difficult to estimate the differential perceptual states of object-motion and circularvection in an animal, it could well be that subtle, and therefore unnoticed, differences exist in the response pattern of vestibular nuclei neurones during optokinetic stimulation, circularvection and actual vestibular stimulation that could cause a variation of consequences in autonomic nervous system function. The recording of autonomic responses in animals following optokinetic stimulation as well as vestibular stimulation could further elucidate a possible interrelation between non-labyrinthine activation of vestibular neurones and autonomic consequences.

One has to bear in mind, however, that the present data contained a high degree of interindividual variability especially in autonomic responses to visually induced self-motion perception. There might be multiple reasons for this observation and it is not possible to rule out that these differences are caused by different subjective strategies in reporting the onset of perceived self-motion. Visual inspection of the data may suggest that there are two distinct response patterns following the perception of circularvection with some subjects exerting a pressor response and others showing a depressor response after reported vection onset. One could speculate that those subjects showing a pressor response are perhaps more spatially disoriented and aroused by the perception of circularvection thereby requiring a readiness response of similar quality to the one observed during real spatial reorientations. An alternative speculation can be drawn from the clinical observation that in labyrinthine disease vertigo is often accompanied by vaso-vagal symptoms and depressor responses, occasionally leading to syncope (Radtke et al., 2000). If vection can act as a model for rotational vertigo, the depressor responses obtained in some of the subjects might resemble those experienced during vestibular vertigo (Dix and Hood, 1994). Yet, in order to determine the role of interindividual differences reliably and potentially classify subjects into two types of responders, a substantially larger sample size would be required. Also, further external criteria would need to be measured and subsequently correlated with the autonomic responses observed in order to avoid confounding the statistical comparison of a certain variable between two subgroups when these subgroups were determined according to whether individuals scored high or low in the same variable.

6 Perceptual Correlates

6.1 Experiment 1: Perceived Direction of Gravity

6.1.1 Introduction

The previous experiments have dealt extensively with circularvection, the illusory perception of self-motion when viewing a rotating optokinetic stimulus. Yet, a further property of large-field visual motion stimulation is that under certain circumstances it can bias the perceived direction of verticality. Observers who are presented with a straight line in their visual field and asked to adjust it so that it appears vertical will normally perform very accurately. However, when the line is superimposed onto an optokinetic stimulus rotating in the frontal plane, observers will exhibit a large and consistent tilt of the perceived visual vertical in the direction of visual field rotation (Bronstein et al., 1996). In a similar manner, the somatosensory and proprioceptive modalities are affected by visual field rotation around an earth-horizontal axis (Bisdorff et al., 1996; Bronstein, 1999). A person viewing torsional optokinetic stimulation whilst standing upright will inevitably sway in the direction of visual motion and, if not losing balance, assume a posture that is tilted with respect to gravity (Straube et al., 1987; Van Asten et al., 1988; Previc and Mullen, 1990). Using a paradigm in which subjects were controlling a flight simulator and had to continuously counteract mechanical disturbances in order to maintain an upright orientation, Dichgans et al. (Dichgans et al., 1972) demonstrated that simultaneous visual motion stimulation in roll significantly biased subjects' perception of verticality and induced a systematic deviation towards the direction of visual field rotation.

It could be speculated that, once a moving visual scene is interpreted as originating from self-motion with respect to a stationary visual environment, the tilt illusion is to some extent resulting from an attempt by the brain to resolve a "graviceptive" conflict (Dichgans et al., 1972; Dichgans et al., 1974; Young et al., 1975). This conflict is thought to arise from the need to accommodate the visually induced perception of continuous self-motion in the frontal plane although at the same time the "graviceptors", consisting of the somatosensory-proprioceptive systems and the otoliths, signal an unchanged orientation of the observer with respect to gravity. Resolution of this conflict might be accomplished by a compromise consisting of a partial weighting of graviceptive and visual motion inputs (Cheung et al., 1989).

It remains an open question how the visually induced illusion of whole-body tilt relates to the two differential and mutually exclusive perceptual interpretations of optokinetic stimulation as object-motion or circularvection. It could be hypothesised that the visual-motion induced bias of perceived verticality should be reduced during those periods in which subjects perceive object-motion and increased when circularvection is perceived because a veridical perception of verticality might be more strongly affected by a simultaneous perception of continuous self-rotation around an earth-horizontal axis. Using torsional optokinetic stimulation that was sufficiently ambiguous to cause subjects to spontaneously alternate between the perception of object-motion and circularvection, the present experiment aims to test this hypothesis by asking subjects to continuously report their perceptual state. Simultaneously, observers were repeatedly oscillated around their naso-occipital axis at amplitudes of unpredictable magnitude and signalled as soon as they perceived themselves to be upright. In order to reduce the role of the somatosensory and vestibular systems in providing information about the direction of gravity, lateral oscillations were performed with high-frequency noise superimposed on the underlying motion profile during half of the trials as in the experiments of Dichgans et al. (1972), where subjects were oscillated using a combination of 16 sine waves of several frequencies and of Aoki et al. (1999) using a single low-amplitude oscillation at 1 Hz.

6.1.2 Materials and Methods

Subjects

Four women and six men, from 23 to 42 years of age (mean 29.2 years), without history of relevant neurological or sensory disease, took part in the experiment. All had normal or corrected-to-normal vision. Informed consent had been obtained from all subjects prior to the start of the experiment.

Apparatus

Subjects were seated in a flight simulator (SEGA, Tokyo, Japan) with their head resting on a chin support. Torso and limbs were restrained and padded using rubber foam. The flight simulator was oscillated in roll using two motion profiles as shown in Figure 6.1. The first profile, referred to as "smooth", was composed by adding two sinewaves with frequencies of 0.05 Hz and 0.02 Hz and amplitudes of ±25° and ±5°, respectively. This was done in order to reduce the predictability of the tilts performed by the flight simulator and to avoid passing through upright at equal time intervals after maximal tilt. The second profile, termed "vibration", consisted of the same motion profile with superimposed high-frequency oscillations. It was constructed by adding two further sinewaves with respective frequencies of 2.5 Hz and 1 Hz and amplitudes of ±1.5° and ±0.5° to the waveforms of the smooth motion profile. Each session started with the flight simulator in the upright position and oscillations lasted for 300 s.

The optokinetic stimulus used consisted of the same projection device described in Experiment 3.2. The hemisphere, 60 cm in diameter, was fixed in the flight simulator cabin and centred with respect to the subject's line of sight at a distance of approximately 30 cm from the nasion. A pattern of irregularly spaced circular spots of light was projected onto the concave surface of the hemisphere and fully covered the subject's visual field. The projection mechanism was mounted out of sight in front of the subjects' chins and consisted of a small globe, with circular incisions on its surface, that was illuminated from inside and could be rotated in roll by means of a servo-controlled motor. The projected circles measured between 5° and 10° of visual angle in diameter wide each and had luminances of 1.64 cd/m^2 with a background luminance of 0.41 cd/m^2. During testing, the flight simulator door was closed and the cabin was kept in darkness.

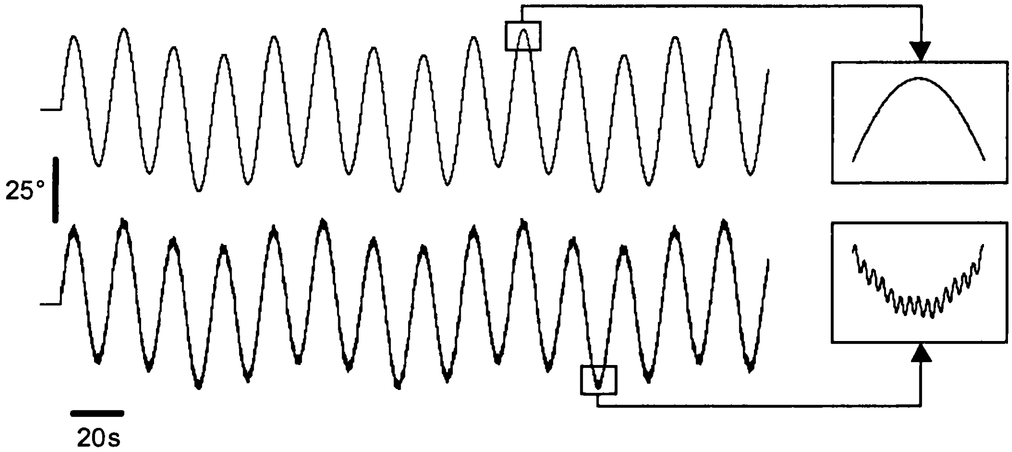

***Figure 6.1** Example of the flight simulator motion profiles used for oscillations in roll. The top trace and insertion show a sequence of "smooth" oscillations, the lower trace and insertion show the added low-amplitude high-frequency oscillations*

Procedure

All subjects underwent four test sessions in total. Sessions lasted for 300 s and consisted of continuous flight simulator oscillation in roll. Two sessions were smooth oscillations, the other half consisted of the vibration motion profile, the sequence of which was randomised. Sessions were subdivided in three blocks of 100 s duration during which the optokinetic stimulus was illuminated but stationary, rotating clockwise at a velocity of 20°/s or rotating anticlockwise at the same velocity. The sequence of blocks was randomised within a session.

Subjects held a response box in their hands and were instructed to press a button with their left thumb to indicate as soon as they felt the flight simulator passing through the upright position. With the right hand, subjects switched a dial between two positions to continuously indicate whether they perceived object-motion or circularvection. Despite being in continuous oscillatory roll-motion, subjects reported no difficulties determining the perception of visually induced self-motion and were comfortable performing the dual task within a short practice session.

Data Analysis

In all four sessions, the flight simulator approached verticality 120 times in total. Therefore, half of the ratings of perceived verticality were obtained whilst the flight simulator was moving clockwise and an equal amount during anticlockwise motion. For smooth and vibration sessions, verticality ratings were pooled for all combinations of direction of simulator motion, optokinetic stimulation condition and perceptual state. From these, averages (constant error) and standard deviations (variable error) were computed. Subsequently, for each combination of motion profile, optokinetic stimulation condition and perceptual state, constant and variable errors were formed by averaging values obtained from anticlockwise and clockwise tilts. This was necessitated since subjects switched between perceptual states spontaneously and unpredictably so that it was not guaranteed to obtain equal numbers of verticality judgements for anticlockwise and clockwise tilts in both perceptual states. Lastly, within subjects and conditions, judgements obtained during clockwise and anticlockwise optokinetic stimulation were pooled and, in the case of constant error, normalised with respect to the direction of stimulus rotation.

6.1.3 Results

Psychophysical Data

Following optokinetic stimulation onset, all subjects reported perceiving circularvection with an average onset latency of 8.9 s (SEM 1.4 s) during smooth simulator motion and 12.9 s (SEM 2.6 s) during vibration. During

100 s of optokinetic stimulation, an average of 4.9 epochs of circularvection (SEM 0.7) were reported during smooth motion profiles and 4.5 epochs (SEM 0.7) when in vibration. On average, subjects spent 53.3 s (SEM 5.2 s) of each block of optokinetic stimulation perceiving self-motion when the flight simulator was oscillating smoothly and 52.3 s (SEM 6.0 s) during vibration. Paired t-tests revealed no significant differences between smooth and vibrating motion profiles in any of the psychophysical parameters.

Constant Error

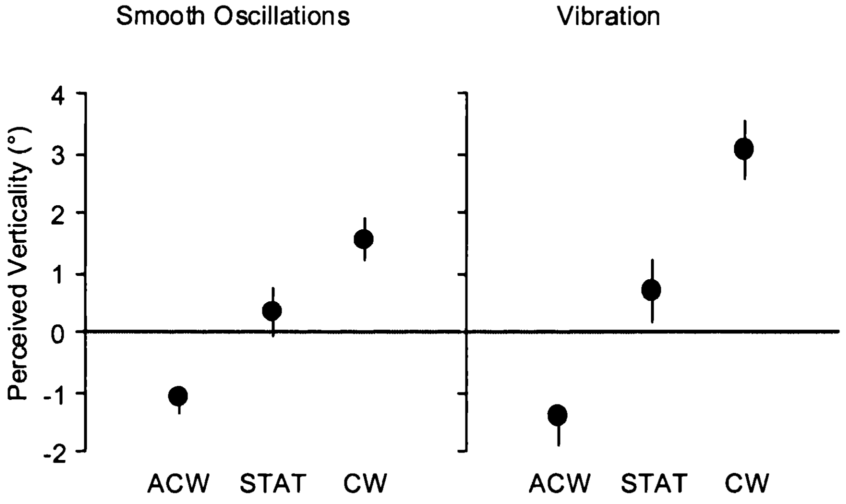

***Figure 6.2** Means and standard errors of constant error of perceived postural verticality during anticlockwise (ACW), stationary (STAT) and clockwise (CW) optokinetic stimulation. Note the enhancement of visual-motion induced bias during vibration of the flight simulator*

During smooth oscillations of the flight simulator, the mean judgement of verticality was 0.3° (SEM 0.4°) while the visual field was stationary and rose to 1.7° (SEM 0.4°) in the direction of visual motion during optokinetic stimulation at a velocity of 20°/s. When vibrated, subjects indicated perceiving verticality on average at 0.7° (SEM 0.5°) with a static visual environment. During optokinetic stimulation, this rating was biased to 2.9° (SEM 0.7°) in the direction of stimulus rotation. The statistical comparison of the effects of optokinetic stimulation and flight simulator motion profile resulted in a significant interaction between these factors in a two-way repeated measures ANOVA ($F_{1,9}=2,0$; $p<0.05$). Paired t-tests demonstrated that optokinetic stimulation significantly biased observers' judgements of verticality in the direction of visual field rotation during smooth motion ($p<0.001$) and during vibration ($p<0.001$). Vibration of the flight simulator had no effect on the verticality ratings obtained at a stationary visual environment ($p=0.48$) but significantly increased the systematic error subjects made during optokinetic stimulation ($p<0.05$).

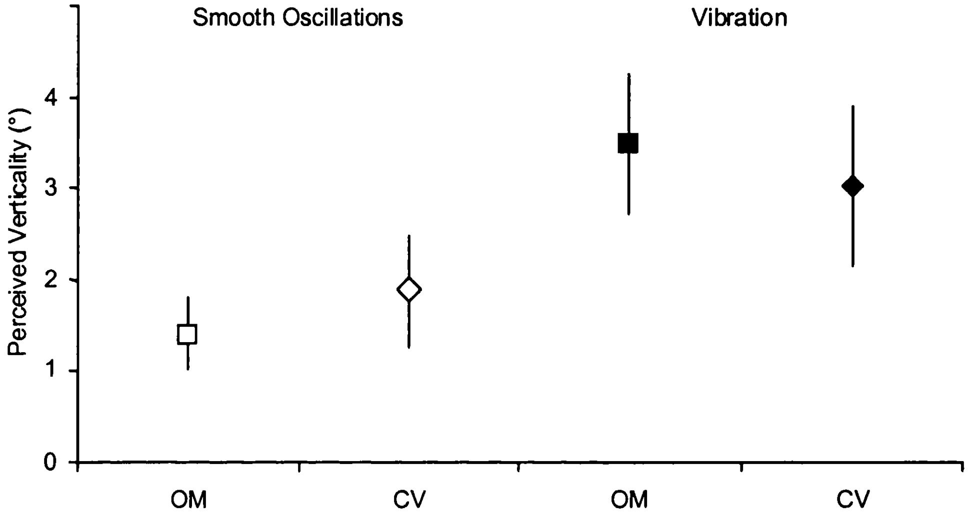

__Figure 6.3__ Means and standard errors of verticality judgements (constant error) during optokinetic stimulation in smooth and vibrating stimulator oscillations grouped by the perceptual state (OM: object-motion, CV: circularvection) during which ratings were obtained. Note that values are normalised for the direction of optokinetic stimulation with positive values denoting bias in the direction of stimulus rotation

Figure 6.3 demonstrates the verticality judgements obtained at smooth simulator motion and vibration grouped by the perceptual state subjects were experiencing during optokinetic stimulation. Two-way repeated measures ANOVA demonstrated again that vibration of the flight simulator significantly biased verticality ratings towards the direction of optokinetic stimulation ($F_{1,9}=8.1$; $p<0.05$). No differential effect of the perceptual state subjects reported was detected ($F_{1,9}<1$) nor was the interaction significant ($F_{1,9}=2.2$; $p=0.14$).

Variable Error

During smooth flight simulator motion, subjects' mean variable error in judging verticality rose from 2.9° (SEM 0.1°) without optokinetic stimulation to 4.8° (SEM 0.4°) when the visual field was in rotation. The corresponding values obtained during vibration sessions are 3.9° (SEM 0.3°) with a stationary visual field and 5.1° (SEM 0.4°) during optokinetic stimulation. This rise in variable error during optokinetic stimulation was highly significant in a two-way repeated measures ANOVA ($F_{1,9}=52.0$; $p<0.001$). Superposition of vibration onto the smooth motion profile also lead to an increase of variable error, however this effect only reached marginal significance ($F_{1,9}=4.6$; $p=0.06$). The interaction was non-significant ($F_{1,9}=2.5$; $p=.15$).

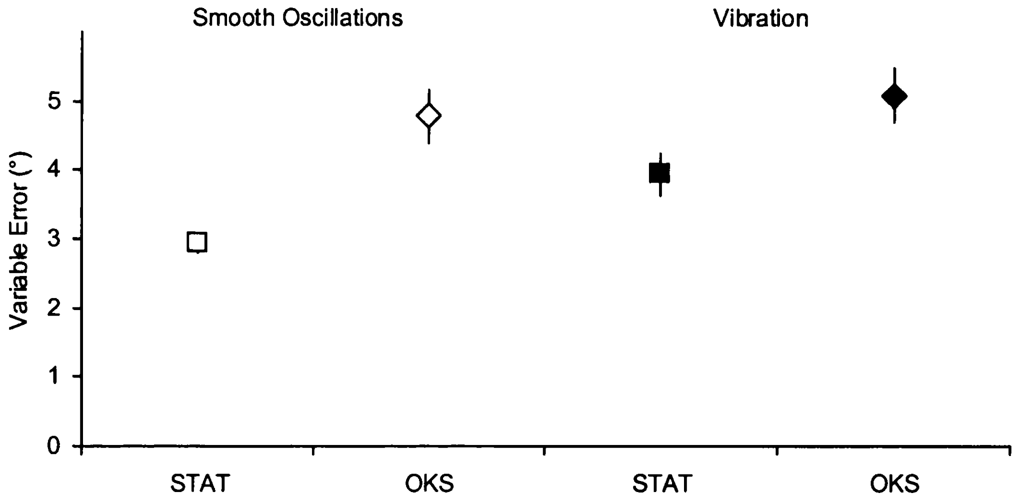

***Figure 6.4** Means and standard errors of variable errors of verticality judgements during stationary (STAT) and rotating (OKS) optokinetic stimulation. Note the tendency for a higher degree of variability during simulator oscillations with superimposed vibration*

Within the verticality judgements obtained during optokinetic stimulation, there was no significant effect of perceptual state ($F_{1,9}<1$) or simulator motion profile ($F_{1,9}<1$) on variable error, nor was an interaction detected ($F_{1,9}=1.0$; $p=0.34$) in a two-way repeated measures ANOVA.

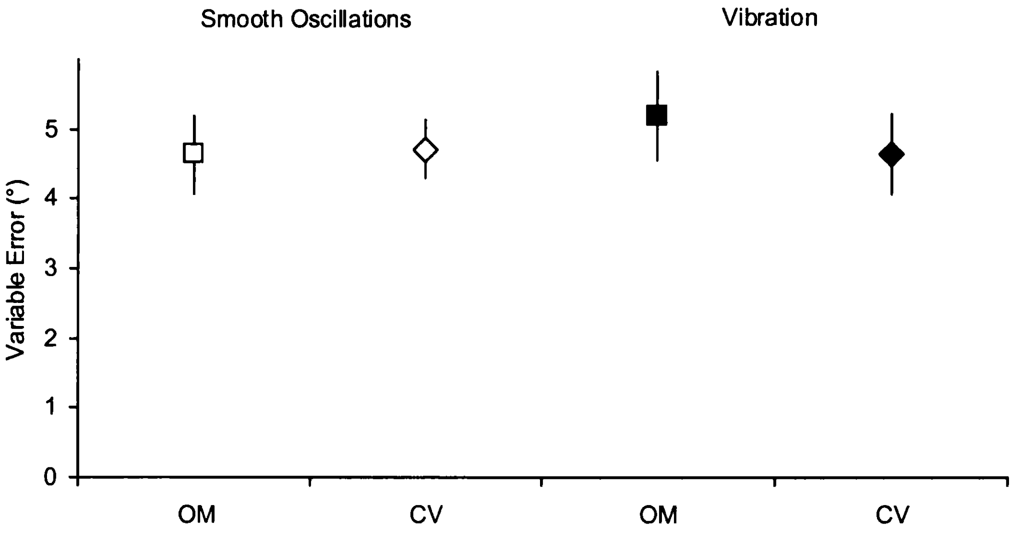

Figure 6.5 *Means and standard errors of variable error of perceived postural verticality during optokinetic stimulation and the concurrent perception of object-motion (OM) or circularvection (CV). Note that neither perceptual state nor simulator vibration increase the variability of participants' ratings*

6.1.4 Discussion

The results of the present experiment are in concordance with previous reports that visual motion in the roll plane biases the perception of postural verticality towards the direction of stimulus rotation (Dichgans et al., 1972; Young et al., 1975; Cheung et al., 1989). There and in numerous other reports it has been assumed that the perception of rollvection coincides with the perception of tilt in the same direction but this assumption has not been tested. The results presented here, in contrast, demonstrate that a dissociation exists between the perceived direction of gravity and the perception of self-rotation. Throughout optokinetic stimulation, subjects' perceived direction of verticality was biased towards the direction of visual stimulus rotation and this was the case irrespective of whether subjects perceived the visual stimulus as originating from object-motion or from self-motion.

An explanation of this phenomenon might be offered by a dual channel hypothesis. If the subsystems processing tilt and rotation were functionally segregated, although both influenced by optokinetic stimulation, a dissociation between the perception of tilt and the differential perceptual states of object-motion versus circularvection could be observed. Primary afferent neurones innervating semicircular canals are indeed anatomically partially segregated from those receiving otolithic input with respect to their point of termination in the vestibular nuclei (Stein and Carpenter, 1967; Gacek, 1969; Carleton and Carpenter, 1984). Visual environment rotation, consistent with a continuous and dynamic reorientation of the body, modulates the firing rate of those vestibular nuclei neurones that receive primary afferents from semicircular canals that would be activated by synergistic contradirectional vestibular stimulation (Dichgans et al., 1973; Henn et al., 1974; Allum et al., 1976; Waespe and Henn, 1977; Waespe and Henn, 1979). In analogy, vestibular nuclear neurones processing otolith input receive a direct modulation by linear visual field translation (Daunton and Thomsen, 1979). The interaction between these types of neurones at the level of the vestibular nuclei indeed appears to be limited, since the population response of otolith-modulated neurones to sinusoidal tilt stimulation was little affected by plugging of all three pairs of semicircular canals (Schor, 1974). Although some convergence of otolith and canal influences onto secondary neurones has been observed, this nevertheless supports the notion of a certain degree of dissociation between the processing of tilt and rotation at the level of the vestibular nuclei (Wilson and Melvill Jones, 1979). In summary, the perceptual dissociation of tilt and circularvection observed here is in concordance with neuroanatomical and neurophysiological evidence about a functional segregation between the processing of tilt versus rotation as signalled by labyrinthine receptors and visual input.

The perception of verticality can not only be assessed posturally but also in the visual modality by asking observers to adjust a straight line about an earth-horizontal axis so that it subjectively coincides with the perceived direction of gravity. A similar influence of torsional optokinetic stimulation on the setting of the visual vertical, inducing a bias in the same direction as the postural vertical, has been reported (Dichgans et al., 1972; Dichgans et al., 1974; Cian et al., 1995). However, a dissociation between modalities can be observed in subjects with acute and chronic peripheral and central vestibular lesions who have a normal perception of the postural vertical but show an enlarged bias of the visual vertical (Bisdorff et al., 1996; Anastasopoulos et al., 1997; Bronstein, 1999). It would therefore be of interest to investigate whether there is a systematic modulation of the visual vertical that is differentially affected by the perceptual states subjects report. Since the visual vertical is partly dependent on the torsional position of the eye in the orbit (Bronstein, 1999), a certain degree of modulation might be obtained as a consequence of the anticipatory shift in torsional eye position when subjects perceive circularvection. If influenced by the anticipatory rotation of the eye, a shift of the visual vertical towards the direction of perceived self-motion, and therefore opposite to stimulus rotation, should be observed. This is counterintuitive, since effectively one should obtain a reduction of visual vertical bias when subjects perceive self-motion, and remains to be tested.

Another finding of the present experiment is that superposition of low-amplitude but high-frequency vibration on the slow flight simulator oscillations increased the bias in perceived verticality brought about by optokinetic stimulation. Furthermore, vibration marginally increased the variability of subjects' judgements. The effects of vibration therefore resemble those of a bilateral vestibular lesion where patients show an enlargement of the sector in which they perceive postural verticality (Bisdorff et al., 1996) as well as an increased dependency on visual cues (Bronstein et al., 1996). Vibration leads to concurrent activation of vestibular and somatosensory graviceptors. Since the vibration itself bears no information about body orientation with respect to gravity, it effectively increases the amount of "noise" or irrelevant signals picked up by these receptors. As a result, visual signals receive an increased weighting or, in other words, carry a higher amount of relevant signal and therefore exert a greater influence on the judgement of verticality similar to when the major graviceptive input from the vestibular system is disturbed or disrupted in disease. In agreement with this view, Aoki et al. (1999) found that vibration increased the ipsilesional bias of perceived postural verticality in unilateral alabyrinthine subjects.

7 General Discussion

The experiments presented in this thesis have investigated a range of physiological and perceptual correlates of the perceptual states occurring in response to large-field visual motion stimulation and succeeded in identifying a number of objective changes that are associated with the subjective phenomenon of circularvection.

Ocular anticipation during the perception of self-motion: Evidence for a shift in spatial attention?

The five experiments of Chapters 1 and 2 have consistently identified that, during circularvection, mean eye position shifts in a direction opposite to visual stimulus motion. This effect can be observed in torsional as well as in horizontal optokinetic nystagmus and might reflect a general oculomotor anticipatory response. There is a large overlap between the cortical substrates involved in the directing of attention as well as in the guidance of eye movements (Corbetta et al., 1998) and the term overt visual attention is often used as a synonym for gaze shifts (Kanwisher and Wojciulik, 2000). Since the physiological relevance of adopting an anticipatory perceptual strategy during the perception of self-motion is evident, it can be speculated that a shift of spatial attention towards the direction of perceived rotation might underlie the observed oculomotor changes. Although it is difficult to conceive how one can perform an overt attentional shift in the roll plane using torsional eye movements this contradiction is resolved when considering the vestigial nature of torsional eye movements in humans and, in support of this view, their importance in lateral-eyed animals and in those that possess a foveal streak instead of a central circular fovea.

If this hypothesis is true, one might expect to find a modulation of performance in certain attentional tasks that is related to the perceptual states observers report during optokinetic stimulation. For instance, it could be assumed that reaction times to visual stimuli presented in the hemifield into which subjects perceive themselves to be rotating during horizontal circularvection should be reduced in comparison to when subjects report the perception of object-motion. Although this prediction might be trivial in part, since the observed deviation of gaze might itself facilitate the detection of objects that are presented in that direction without the involvement of any additional attentional factor. This limitation does, however, not hold for the presentation of stimuli in modalities other than the visual system, for instance for somatosensory or auditory stimuli whose enhanced detection during circularvection could not be accounted for by a change of gaze direction per se. Furthermore, a covert attentional shift during the perception of circularvection might also take place when subjects are presented with optokinetic stimulation whilst keeping their gaze on a stationary and head-centred fixation target. In such a paradigm, the detection of laterally presented visual stimuli would not be confounded with concurrent optokinetic nystagmus and percept-related gaze-shifts, enabling the testing of the attentional-shift hypothesis within the visual modality.

Would the change in oculomotor strategy be preserved following right-hemisphere brain damage?

Lesions of the right parietal and parieto-occipital lobe in right-handed humans frequently induce the clinical condition of unilateral neglect, an impairment in the ability to direct attention to stimuli presented in the left hemispace, or a deficit in disengaging attention from the right hemispace (Mesulam, 1981; Vallar and Perani, 1986; Heilman et al., 1993). Recently, it has been reported that patients with lesions in the right hemisphere, most of which presented with unilateral neglect, lack a certain type of anticipatory eye movements. In healthy subjects, rotation of the torso about the longitudinal axis relative to the stationary head elicits the cervico-ocular reflex composed of small-amplitude horizontal nystagmic movements of the eyes and a deviation of mean eye position in a direction opposite to movement of the torso (Bronstein and Hood, 1985; Bronstein and Hood, 1986; Bronstein, 1992). In addition, when rotation of the torso is carried out at angular velocities and accelerations below the threshold of vestibular detection, an illusory sensation of head rotation in the direction opposite to torso rotation is induced in healthy volunteers (Gurfinkel and Levik, 1993; Ivanenko et al., 1999). In contrast to normal as well as left brain-damaged subjects, patients with a lesion in their right hemisphere do not show this anticipatory oculomotor orienting response although most of them report the perception of illusory head rotation when their torso is turned passively (Ivanenko et al., 2000). If the anticipatory gaze shifts during the perception of circularvection and those accompanying illusory head rotation in a cervico-ocular reflex paradigm are mediated by common underlying mechanisms, patients with unilateral neglect should exhibit an impairment in both.

Relation between symptoms of unilateral neglect and optokinetic stimulation

Another observation in patients with unilateral neglect is of interest for the interpretation of the results presented here. A number of studies have subjected right brain-damaged patients with unilateral neglect to horizontal optokinetic stimulation. Leftwards optokinetic stimulation has consistently been found to reduce biases in the perception of the subjective straight ahead transiently (Pizzamiglio et al., 1990), of limb position (Vallar et al., 1993; Vallar et al., 1995) and in motor deficits (Vallar et al., 1997). Rightwards optokinetic stimulation did either not affect the symptoms or deteriorated them. In contrast to these reports, the finding of an anticipatory orientation of gaze, and therefore probably attention, during the perception of circularvection would predict that a reduction of left unilateral neglect symptoms should, if at all, be achieved through horizontal optokinetic stimulation towards the right, since this induces the sensation of rotation towards the left, neglected, side. However, this apparent contradiction is resolved when considering that the optokinetic stimulus used in these studies was only subtending the central part of the visual field and therefore presumably less likely to induce the perception of self-motion.

Transient and sustained responses in striate, extrastriate and vestibular cortex

Using functional magnetic resonance imaging, it was possible to measure regional cerebral blood flow during optokinetic stimulation and to compare activity levels obtained during the perception of object-motion with those obtained during circularvection. Previous attempts to identify the neural correlates of self-motion perception have utilised the fact that locomotion through a stationary visual environment generates coherent optic flow on the observer's retina (de Jong et al., 1994; Cheng et al., 1995; McKeefry et al., 1997; Brandt et al., 1998; Previc et al., 2000; Greenlee, 2000). It was reasoned therefore that the comparison between the perception of self-motion and that of object-motion could be performed by presenting observers with patterns of coherent versus incoherent optic flow. This approach, however, confounds a change of perceptual state with different visual stimulus attributes. The paradigm used here differs from the ones used previously in that observers were presented with one and the same continuous optokinetic stimulus, rotating at a sustained velocity throughout, causing observers to alternate spontaneously between the differential perceptual interpretations.

By contrasting activity levels obtained during the perception of object-motion with those obtained during circularvection, it was found that early visual as well as parieto-insular vestibular cortex act in synergy by deactivating. On the contrary, higher order temporo- and parieto-occipital areas retained elevated, but identical, levels of activation across both perceptual states. Event-related analysis demonstrated that within this sustained response, those areas displayed transient activations in response to each perceptual transition reported by the observers. This points to the possibility that these areas might be highly sensitive to, or responsive to, the perceptual instability during optokinetic stimulation. Correlative approaches like functional imaging cannot determine the causality of activity changes observed and it remains to be determined whether and in what way the perceptual transitions between object- and self-motion perception would be affected by a transient interference with the normal neural processing in those brain regions.

Does the modulation of activity in primary visual cortex result from top-down processes?

Furthermore, and perhaps separately from an involvement in the switching between perceptual states, the transient and sustained activity differences observed in striate and extrastriate cortex might be related to the shift in spatial attention that has been speculated to occur following perceptual transitions. Using functional imaging, event related potentials and single unit recordings, attentional modulation of neural activity has repeatedly been found to occur throughout extrastriate cortical areas (for review, see (Kanwisher and Wojciulik, 2000). More recently, a number of studies has demonstrated that spatial attentional modulation of neural processing can also occur as early in the visual pathway as in primary visual cortex (Watanabe et al., 1998; Somers et al., 1999; Gandhi et al., 1999). The modulation of activity is likely to be caused by top-down influences on calcarine cortex through feedback processes from higher, extrastriate areas (Martinez et al., 1999) as well as through feedforward modulation via the thalamus (Guillery et al., 1998).

The findings of Experiment 4.2 are in support of the results obtained using functional imaging. Pattern reversal evoked potentials obtained during a stationary peripheral visual field did not differ from those recorded during torsional optokinetic stimulation. This demonstrates that the modulation of activity in calcarine cortex observed before is not merely due to the facilitation of torsional optokinetic nystagmus and a reduced retinal slip during the perception of self-motion. Furthermore, when contrasting the potentials obtained during the different perceptual states following optokinetic stimulation, a reduction of negativity in the early components of the evoked potential was observed. This is likely to indicate an overall decrease of the number or amplitude of excitatory postsynaptic potentials of stellate cells (Schroeder et al., 1991) which receive afferent input not only from the thalamus but also from other striate and extrastriate neurones. This reduced negativity could therefore result from a change in top-down, or feedback, processes acting upon primary visual cortex.

Functional segregation within vestibulo-autonomic pathways?

In the experiment of Chapter 5 cardiovascular parameters were measured in response to real lateral whole-body tilt and to the perception of circularvection around the sagittal axis. A pressor response, consisting of increased peripheral blood pressure and reduced peripheral blood flow, presumably due to sympathetically mediated enhanced vasoconstriction, was found following real tilt. On the contrary, no indicators of a change in autonomic nervous system activity were obtained when comparing the onset of visually induced perception of self-motion with the preceding period of perceived stationarity, as reported by the subjects.

Although the finding of an upregulation of sympathetic activity in response to a reduction of the pressure differences along the vascular column may be considered somewhat counterintuitive, it was reliably obtained. Furthermore, this observation is in agreement with other studies reporting pressor responses in human subjects following translational and rotational stimulation which have claimed that the responses obtained were likely to be of vestibular origin (Yates et al., 1999; Radtke et al., 2000; Aoki et al., 2000).

Vestibular nuclear neurones responding to vestibular stimulation also exhibit a synergistic modulation of their firing rate following contradirectional optokinetic stimulation (Henn et al., 1974; Waespe and Henn, 1977; Waespe and Henn, 1979). It is in part those neurones that are thought to mediate vestibulo-autonomic adjustments via projections to subcortical centres involved in autonomic regulation (Yates et al., 1994; Balaban and Beryozki, 1994). In light of this evidence, the observation of a dissociation between autonomic responses following real tilt and those, or their absence, in response to illusory self-motion prompts the question whether a functional segregation exists within the vestibulo-autonomic pathways resulting in different onwards processing of labyrinthine and visual motion stimulation.

Although real lateral rotational stimulation differs from the perception of rollvection, for instance due to a different perception of acceleration across conditions, the torsional optokinetic stimulus used here should nevertheless mainly activate neurones that receive their primary afferent input from hair cells in the vertical semicircular canals. The vestibular stimulus of Experiment 5.1, however, only consisted of a short and transient rotational component, stimulating the vertical semicircular canals, and was followed by a sustained lateral tilt of the body and head resulting in a static deflection of mainly the utricular otolith membranes. As a result, different neuronal subpopulations in the vestibular nuclei would have been activated in the two conditions. During postural reorientations, blood shifts in the vascular system as well as deflections of the otolith membranes are caused by changes in gravitoinertial forces. Since this itself does not induce endolymph flow in the semicircular canals, it is likely that vestibulo-autonomic responses predominantly originate in neurones receiving input from otolith organs. These neurones, however, are not likely to modulate their firing rate following visual environment rotation since they do not code for congruent labyrinthine stimulation following real head rotation either (Gacek, 1969; Carleton and Carpenter, 1984). Therefore, instead of claiming a segregation of autonomic nervous responses following optokinetic versus vestibular stimulation, a simpler explanation is that the differences found might be merely due to the activation of different neuronal subpopulations following real tilt and torsional optokinetic stimulation. To ultimately clarify this relationship, however, further animal experimentation is required performing single-unit recordings in the vestibular nuclei as well as in autonomic nervous system centres comparing responses to congruent vestibular and optokinetic stimulation.

Although it has been well documented that visual motion stimulation accesses vestibular nuclear neurones (Dichgans et al., 1973; Henn et al., 1974; Dichgans et al., 1974; Allum et al., 1976; Waespe and Henn, 1977; Waespe and Henn, 1979), it is not known whether differential firing patterns are exhibited when observers perceive object-motion versus circularvection during optokinetic stimulation. Despite of the suggestion that circularvection might originate in the vestibular nuclei (Straube et al., 1987), it can be conceived that the vestibular nuclei might only act as a relay station where visual motion signals are made available for further vestibular processing. If the vestibular nuclei were not involved in the perceptual interpretation about the origin of retinal image motion lying in environment- or self-motion, which is in agreement with the model by Wertheim (1994), one would not expect subsequent autonomic neurones to respond differentially to perceptual transitions. It is difficult to determine the behaviour of vestibular nuclear neurones during different perceptual states since there is no clear objective measure indicating the subjective experience of a laboratory animal. However, it is likely that the advancement of brain stem functional imaging techniques will make it possible to address this questions in human observers where perceptual reports can be obtained more reliably.

Is circularvection a valid model for the perception of lateral tilt?

It has frequently been assumed that rollvection around an earth-horizontal axis coincides with the simultaneous perception of whole-body tilt (Dichgans et al., 1972; Dichgans and Brandt, 1978). In the experiment of Chapter 6, subjects were exposed to torsional optokinetic stimulation and had to continuously indicate their perceived direction of postural verticality. The results confirmed that optokinetic stimulation biases the postural vertical towards the direction of optokinetic stimulus rotation. However, when contrasting subjects' ratings of verticality during the perception of object-motion with those obtained during circularvection, it became evident that there is no differential perception of verticality across perceptual states. Hence, visually induced perception of self-rotation about earth-horizontal axes is not a suitable model for the perception of static lateral body tilt.

This finding offers another explanation for the failure to obtain an autonomic nervous correlate of self-motion perception in Chapter 5. If the onset of self-motion perception in roll does not coincide with the perception of tilt, the perceptual effects of vection are not comparable to the effects elicited by the vestibular stimulus used. As has been detailed before, vestibular stimulation consisted of a short transient roll-motion of the subjects followed by sustained lateral body tilt. The major stimulus component of lateral tilt was therefore not mimicked by the perception of circularvection and might thus explain the absence of a cardiovascular adjustment. The findings of Chapter 6 might suggest that the onset of optokinetic stimulation, instead of circularvection, might present a better model for the visually induced perception of tilt. Yet, although the bias in perceived verticality obtained during optokinetic stimulation was consistent, it presumably is too small to elicit detectable, and physiologically significant, compensatory cardiovascular adjustments. Secondly, although sustained optokinetic stimulation in roll can act as a model of lateral body tilt, the present data do not support the conclusion that the onset of optokinetic stimulation does so as well. It is possible that, similar to the perception of self-motion, there is a time delay between the onset of optokinetic stimulation and the first perception of tilt with a sustained perception of tilt thereafter and concurrent transitions between self- and object-motion perception.

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9 Appendix

9.1 Publication of Experiment 2.3

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RESEARCH ARTICLE

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Torsional eye movements are facilitated during perception of self-motion

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Abstract Visual motion in the roll plane elicits torsional optokinetic nystagmus (tOKN) with intermittent periods of illusory, contradirectional self-motion (circularvection, CV). The CV may also have a component of whole-body tilt if the axis of stimulus rotation is not aligned with the direction of gravity. We report how the characteristics of tOKN are affected by the presence of CV. Subjects had their eye movements recorded by VOG whilst viewing a full-field stimulus rotating at 30–60°/s about their naso-occipital axis. They were tested in upright and supine posture and signalled the presence-absence of CV with a pushbutton. In both postures, during CV, tOKN slow-phase gain was found to be enhanced and average torsional eye position shifted in the direction opposite to stimulus rotation. When supine, slow-phase gain was greater than when upright both during the perception of object-motion and during CV. The effects may be explained in terms of a relegation of restraining vestibular input to the torsional oculomotor system during CV and illusory tilt.

Key words Circularvection · Eye movements · Graviceptive conflict · Vestibular nuclei · Visual-vestibular interaction

Introduction

Visually induced sensations of self-motion have been studied for more than one century, e.g. by Mach (1875) and by Helmholtz (1896). The stimuli usually consist of large-field objects (e.g. rotating drum) or projected patterns which either move linearly past or rotate around the observer. The self-motion phenomena elicited by these stimuli have been termed linearvection or circularvection, respectively (Fischer and Kornmüller 1930; Tschermak 1931). The nystagmic eye movements they provoke are often referred to as 'optokinetic'.

Visual stimuli only provoke pure circularvection when their axis of rotation is aligned with the gravitational vector. An upright observer seeing a visual field which rotates about his sagittal or x-axis may, after a time, report the perception of whole-body rotation (rollvection) and also a simultaneous perception of body tilt opposite to the direction of stimulus motion (Dichgans et al. 1972; Young et al. 1975). This ambiguous combination of circularvection and perception of lateral tilt is due to the stimulus creating a so-called graviceptive conflict between different sensory channels. The otolith and somatosensory pathways provide the central nervous system with the information of a stationary body orientation with respect to gravity whereas the visually induced perception of self-rotation is not in line with the sensed gravity vector (Dichgans and Brandt 1978). Another characteristic feature of rollvection is that, once reached, the sensation of self-rotation does not continue uninterruptedly but is rather interspersed with phases in which vection ceases and pure stimulus motion without involvement of the observer's body is perceived (see, e.g. Finke and Held 1978; Cheung et al. 1989; Cheung and Howard 1991).

Brecher (1934) was the first researcher to discover the presence of binocular torsional nystagmus under visual roll stimulation by observing conjunctive blood vessels of the subjects' eyes via a telescope. Since then, optokinetically induced torsional eye movements have been investigated by numerous groups with systematic varia-

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tions of head and body position (Merker and Held 1981; Morrow and Sharpe 1993), in microgravity (Young et al. 1981; Cheung et al. 1995), with modifications of several stimulus features (Kertesz and Jones 1969; Wade et al. 1991), at different stimulus velocities (Collewijn et al. 1985) and using stimuli rotating continuously or oscillating sinusoidally (Cheung and Howard 1991; Cheung et al. 1995). A significant attribute of torsional optokinetic nystagmus is that it is involuntary since naive normal subjects have little voluntary influence over their torsional eye movements.

Only few studies have examined whether the shift between the perception of visual motion as egocentric (object-motion) and exocentric (self-motion) coincides with changes in induced optokinetic eye movements and their results differ. Finke and Held (1978), studying torsional eye movements by means of afterimages, found eye movements and perceptual state to be independent. Similarly, using scleral search coils, Cheung and Howard (1991) reported that they could find no correlation between the onset or offset of rollvection and changes in quality of torsional eye movement but did not provide evidence for this assertion. In contrast, a recent study using video-oculography (Thilo et al. 1998), which permits long recording epochs, found the gain of torsional nystagmus slow-phase velocity evoked by a stimulus velocity of 60°/s significantly increased when subjects started to feel vection. In view of the latter positive findings, the object of the present study was to assess the behaviour of torsional eye movements related to the presence or absence of vection using stimuli at different velocities. Responses to stimuli inducing roll-tilt vection (observer upright) and pure rollvection (observer supine) were compared.

Materials and methods

Subjects

Two women and four men, from 23 to 50 years of age (mean 33.5 years), without history of relevant neurological or sensory disease, consented to participate in the experiment according to the guidelines of the local ethics committee. All had normal vision or were mildly myopic, and had no difficulty in fixating the stimulus without the need of corrective lenses. Written consent had been obtained from all subjects prior to the start of the experiment.

Apparatus

The stimulus (see Fig. 1) consisted of a cone whose maximum diameter was 58 cm with a depth of 25 cm. The inside of the cone was painted black and eight stripes of fluorescent tape, each 20 mm wide, had been fixed radially to the inner surface. The stripes joined at the apex of the cone, where a black circle of 20 mm diameter was fixed. Prior to each session, the fluorescent stripes were charged by 10 s illumination with a 60-W light bulb at approximately 80 cm distance. Sessions started 30 s after illumination had terminated. In darkness, the luminance of the black background was below 0.01 cd/m^2. As shown in Fig. 2, the luminance of the fluorescent stripes decayed according to the power function $y=1.31x^{-0.61}$, with a determination coefficient $r^2=0.96$. The corresponding contrasts calculate as 0.89 for the beginning of the recording and 0.67 for the end.

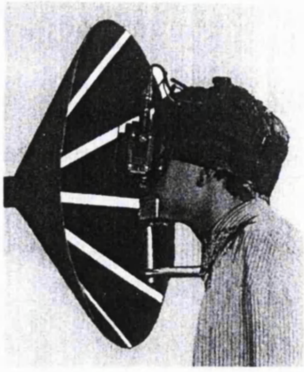

Fig. 1 Upright subject wearing the video-oculography spectacles sitting in front of the optokinetic stimulation device

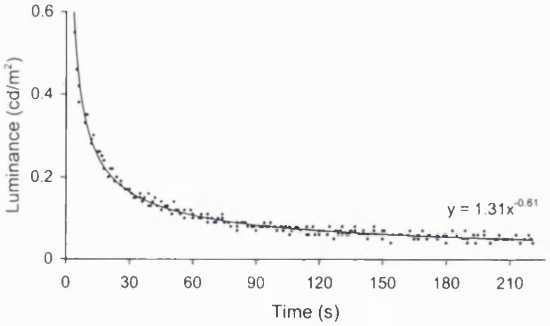

Fig. 2 Luminance decay of the fluorescent stimulus elements after termination of 10 s illumination at 60 W. The power function $y=1.31x^{-0.61}$ fits the data with $r^2=0.96$. Optokinetic stimulation lasted from 30 s until 210 s

The cone was driven by an electrical 12 V current-servo motor, which was fixed at the back of the apex. Angular speed was regulated and kept constant by a standard power supply. Subjects were either sitting upright with their head on a chin rest or lying supine with their head resting in a mould. In either condition, the axis of rotation of the stimulus cone could be rotated into alignment with the subjects' line of sight. The apex of the cone was maintained at a distance of 28 cm from the viewer's nasion.

Eye movement recording

Continuous monocular recording of the subjects' left eyes was obtained by means of an infrared camera and infrared light-emitting diodes mounted in a headframe as shown in Fig. 1. The eye was illuminated and filmed via a dichroic mirror, so that the recording equipment was invisible for the subject. At an eye-to-eye distance of 69 mm, the aperture of the recording device allowed non-restricted vision of approximately 90° width and 70° height. Camera signals were recorded at the PAL/CCIR standard of 50 fields/s. Three-dimensional eye movement analysis was carried out offline, using the SensoMotorics Instruments (Teltow, Germany) system resampling at 25 frames/s and with a spatial resolution of approximately 0.1° for torsional eye movements and below 0.3° for horizontal and vertical eye movements.

Procedure

Subjects were tested on two consecutive days, with three sessions per day. Sessions consisted of 30 s baseline and of 3 min clockwise optokinetic stimulation at a stimulus velocity of 30°/s, 45°/s and 60°/s, respectively. Eye movements were recorded for the duration of a session. The sequence of velocities was varied according to a Latin square and reversed on the following day. Sessions were interspersed with a rest period of 5 min. Half of the subjects were tested sitting upright on the first day and lying supine on the following day. The other half were tested in the opposite order.

Subjects viewed the stimulus with both eyes and were instructed to fixate the spot in the centre of the cone and to avoid eye blinks during recording. They signalled the perception of rollvection by depressing a pushbutton. During the 5 min rest, they were asked to keep their eyes closed and during this time the fluorescent stripes were recharged.

Data analysis

Torsional eye position recordings were displayed on a personal computer and subjected to further offline analysis. Over all oculomotor recordings acquired, every single torsional nystagmus slow phase was identified visually and fitted with a linear regression line, the slope of which equals the mean eye velocity during the corresponding slow phase. For each session and subject, the obtained regression slopes were pooled with respect to whether their slow phases were performed during perception of object motion or during CV. Accordingly, two average slow-phase velocities were computed, one for the sensation of stimulus motion, one for the sensation of vection. Subsequently, for each average slow-phase velocity, gain was calculated as torsional oculomotor slow-phase velocity over angular stimulus velocity.

Mean torsional eye position data were computed automatically by averaging the eye position values with respect to the perceptual state in which they were recorded. Again, per condition and subject, one average was obtained for vection, one for egocentric motion perception.

As a control of gaze direction, standard deviations of horizontal and vertical eye position were computed for each subject and session.

Results

Psychophysical data

Subjects reported perceiving self-motion, albeit intermittently, at all stimulus velocities and in both body positions. The average number of vection onsets per session and subject was 5.9, with an average duration of 14.8 s. On average, the onset latency of the first perception of rollvection per session was 31.6 s. These values showed a high interindividual variability and did not differ significantly between body positions or stimulus velocities in two-way repeated measures ANOVAs (all $F<1$). A detailed listing of the psychophysical parameters measured in the experimental conditions is given in Table 1.

Table 2 shows the psychophysical variables grouped by the number of session during which they were obtained. One-way repeated measures ANOVAs with time as within-subjects factor detected no significant effect of time on onset latency of the first CV reported ($F_{5,25}=1.8$; $P>0.15$) or on average duration of CV ($F_{5,25}<1$). In contrast, the average number of vection sensations per session changed significantly over time from 7.8 in session 1 to 5.3 in session 6 ($F_{5,25}=4.5$; $P<0.01$).

Oculomotor responses

Torsional nystagmus

The rotating cone evoked a typical pattern of torsional optokinetic nystagmus with slow phases in the direction of cone rotation and fast phases in the counterdirection. Means and standard errors of torsional nystagmus slow-phase gain under the different combinations of body positions, stimulus velocities and perceptual states are displayed in Fig. 3 and are listed in Table 3. During vection, gains increased by factor 1.46 at a stimulus speed of 30°/s, 1.47 at 45°/s and 1.61 at 60°/s when subjects were sitting upright while viewing the stimulus. In sessions with subjects lying supine, the according gain enhancement factors during vection were 1.33, 1.45 and 1.49. The main effect of vection on gain was significant in a three-way repeated measures ANOVA ($F_{1,5}=33.0$;

Table 1 Means and standard errors (*in brackets*) of the psychophysical parameters measured at different combinations of optokinetic stimulus velocity and body position

Body position	Upright			Supine		
Stimulus velocity (°/s)	30	45	60	30	45	60
Number of illusions	5.5 (1.5)	6.0 (1.5)	6.3 (1.6)	5.3 (1.7)	5.8 (1.2)	6.2 (1.4)
Onset latency (s)	26.1 (5.7)	24.7 (15.2)	30.2 (21.4)	51.3 (27.0)	19.2 (5.4)	38.2 (19.2)
Average duration of rollvection (s)	15.5 (2.3)	18.8 (9.1)	13.9 (5.9)	17.0 (3.1)	10.2 (3.1)	13.6 (2.7)

Table 2 Time course of means and standard errors (*in brackets*) of the psychophysical parameters

Session number	1	2	3	4	5	6
Number of illusions	7.8 (0.9)	5.0 (1.6)	7 (1.4)	6.5 (1.4)	5.8 (1.4)	5.3 (1.5)
Onset latency (s)	13.1 (3.5)	62.6 (28.3)	32.4 (12.9)	15.8 (5.8)	32.8 (21.0)	32.9 (15.0)
Average duration of rollvection (s)	10.6 (1.8)	12.3 (3.3)	13.0 (3.8)	18.4 (7.3)	18.2 (6.7)	16.3 (9.9)

Table 3 Means and standard errors (*in brackets*) of torsional optokinetic nystagmus gain obtained at both object-motion and self-motion perception, during the six experimental conditions

Body position	Upright		Supine	
Perceptual state	Egocentric	Exocentric	Egocentric	Exocentric
30°/s	0.092 (0.012)	0.134 (0.020)	0.110 (0.014)	0.146 (0.020)
45°/s	0.059 (0.004)	0.087 (0.009)	0.086 (0.010)	0.124 (0.017)
60°/s	0.046 (0.003)	0.074 (0.009)	0.069 (0.008)	0.102 (0.013)

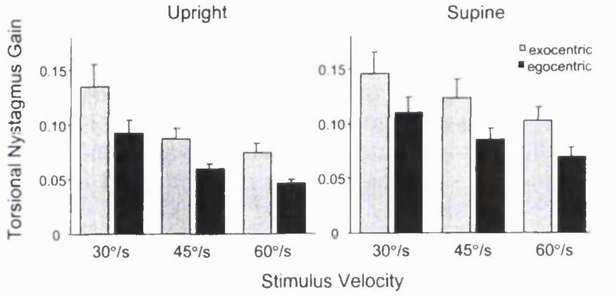

Fig. 3 Changes in torsional optokinetic nystagmus gain between perception of object motion (egocentric) and self-motion (exocentric) at various stimulus velocities. Note the gain-enhancing effect of supine body position

$P<0.01$). Figure 4 demonstrates the gain increase during vection in an example of raw recordings.

At increasing stimulus velocities, torsional nystagmus slow-phase velocity also increased at both body positions and perceptual states, respectively. However, as slow-phase velocities rose slower than stimulus velocities, the actual gain decreased significantly with faster stimulus revolutions ($F_{2,10}=24.5$; $P<0.01$; see Table 3).

The supine body position resulted in a significant enhancement of torsional nystagmus gain, compared to when subjects were watching the stimulus while sitting upright ($F_{1,5}=11.6$; $P<0.05$). The absolute mean increase of gain was 0.024 between upright and supine, which is a relative enhancement of 29%.

Grouped by time of recording, torsional nystagmus slow-phase velocities did not show any relation with the sequence of sessions in a one-way repeated measures ANOVA ($F_{5,25}=1.1$; $P>0.38$).

Eye position

During egocentric motion perception, mean torsional eye position deviated counterclockwise, i.e. in the direction of the fast phase. On average, this deviation was −0.19° at the upright body position and −1.49° when lying supine. During vection, eye position shifted further in the direction of the fast phase at either body position. The average eye shift was −1.35° when viewing upright and −1.38° when supine. A two-way repeated measures ANOVA revealed a significant main effect of body position ($F_{1,17}=8.0$; $P<0.05$), and a highly significant effect of vection ($F_{1,17}=33.7$; $P<0.01$). Figure 5 shows the effects of body position and perceptual states on average torsional eye position. The raw recordings in Fig. 4 also give an example of torsional eye position shift during vection.

No significant effect of time on mean torsional eye position was obtained in a one-way repeated measures ANOVA ($F_{5,25}=1.0$; $P>0.43$).

Subjects managed to maintain fixation of the target throughout the stimulation. The mean standard deviation was 0.86° for horizontal, and 1.12° for vertical eye position.

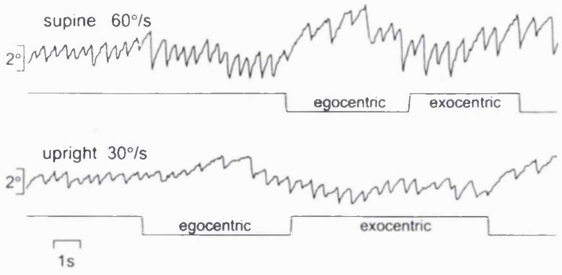

Fig. 4 Raw recordings of optokinetic torsional nystagmus demonstrating the changes in slow-phase velocity as well as the shift in average eye position across the different states of motion perception. The *upper trace* was recorded at a stimulus velocity of 60°/s with the observer lying supine. The *lower trace* shows torsional eye movements in an upright-sitting subject watching a stimulus revolving at 30°/s

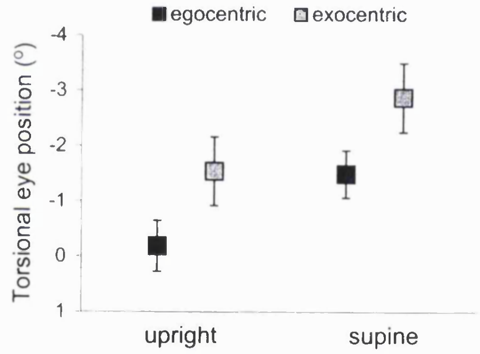

Fig. 5 Means and standard errors of torsional eye shift during egocentric vs exocentric motion perception in upright and supine body positions

Discussion

This study demonstrates that visually induced perception of rotary self-motion around the x-axis coincides with a systematic increase in the slow-phase velocity of torsional optokinetic nystagmus. Enhanced torsional slow-phase velocity during rollvection was present irrespective of whether subjects were upright or supine and average eye position deviated in the direction of the nystagmus fast phase during self-motion sensation. Furthermore, all slow-phase velocities at either perceptual state tended to be faster when subjects were supine. Over the course of the experimental sessions, a mild perceptual adaptation effect could be observed with the average number of rollvection sensations reported during each optokinetic stimulation decreasing over time. The oculomotor variables, however, did not show any detectable temporal dynamics. It is tempting to draw parallels between the nystagmus seen with and without rollvection and 'look' and 'stare' nystagmus observed for horizontal optokinetic stimulation (Hood and Leech 1974), but their characteristics do not correspond. In 'stare' nystagmus the fast phases are more anticipatory, beating away from the torsional primary position towards the newly appearing visual environment. In addition, 'stare' nystagmus has a lower slow-phase velocity than 'look' nystagmus, in which slow phases track the visual flow with the fast phases returning the eyes to their primary position. For torsional nystagmus, also all fast phases are anticipatory, but more so during rollvection where slow phases are faster. The results raise two questions: Why is the nystagmus slow-phase velocity enhanced when supine, and why does slow-phase velocity enhance with fast-phase anticipation during vection?

In answer to the first question; the upright observer receiving visual roll stimulation in his frontal plane has to integrate two competing demands on gaze strategy. First, in order to maintain an upright retinal image, the torsional eye position needs to be adjusted to earth-vertical, as sensed by the otoliths. Second, at a rotating visual environment, optokinetic reflex mechanisms counteract this impulse by inducing torsional nystagmus with the slow phase in the direction of stimulus rotation. For the supine observer, however, otolithic inputs onto the oculomotor system cannot contribute to the torsional positioning of the eyes to earth-vertical, as the axis of eye rotation is aligned with the direction of gravity. Hence, they exert less suppression or restraint on the torsional oculomotor system and, consequently, slow-phase gain is high. This effect also becomes evident in the average torsional eye position under upright and supine body positions. When lying supine, overall torsional eye position deviates considerably towards the nystagmus fast phase during either state of motion perception. Neurophysiological evidence is in accord with this explanation based on disinhibition. Single-unit recordings in monkeys have shown that the multidirectionally oriented hair cells of the utricle have a reduced overall depolarisation rate when the otolith membrane is deflected backwards, as is the case at a supine body position (Löwenstein 1974).

The enhancement of slow-phase velocity with increased saccadic anticipation during vection may be explained by the relegation of signals in sensory channels other than the visual motion input. If we assume that the rotating visual stimulus accesses the mechanisms of vestibular space perception through vestibular nuclei neurons innervated by primary afferents from the vertical canals, then, presumably, vestibular and somatosensory inputs fail to provide a parallel confirmatory signal of roll motion as head and body remain stationary. In order to perceive self-motion in the roll plane, rather than object-motion, we have to assume that there is some suppression, or neglect, of these signals. Thereby, their restraint on the optokinetic-vestibular input to the torsional oculomotor system might be attenuated and the resulting eye movement is a fully developed response to spatial reorientation with anticipatory saccades and disinhibition of nystagmus slow phases. This explanation is in accord with studies reporting inhibitory interactions between various sensory systems serving spatial orientation (Berthoz et al. 1975; Probst et al. 1985, 1996; Loose et al. 1996; Wenzel et al. 1996).

A number of animal experiments has shown that optokinetic stimulation increases the firing rate of vestibular nuclei type I units in several species and it has been suggested that enhanced activity in the vestibular nuclei is the neural basis of circularvection (for a detailed review, see Dichgans and Brandt 1978). This is in agreement with our hypothesis, as an increase in vestibular nuclei neuron firing rate might well be modulated by non-vestibular structures converging on the vestibular nuclei. Straube and Brandt (1987) suggested the hypothesis that circularvection occurs under excitation of the vestibular nuclei innervated by a descending projection from motion-sensitive areas of the primary visual cortex. Also, the vestibular nuclei are a highly integrative structure, being innervated by primary vestibular, optic, somatosensory and proprioceptive afferents, with a strong and direct connection to subcortical oculomotor areas.

Our experimental design does not allow the inference of a causal relationship between the observed changes in eye movements and the perception of vection. Although the vestibular nuclei possess afferent connections with oculomotor nuclei (Carleton and Carpenter 1983; Carpenter and Cowie 1985), it seems plausible to assume that the enhancement of torsional nystagmus slow-phase velocity is a result of vection rather than the cause of it. This view is supported by the findings of Brandt et al. (1973), who found that eye movements were not a necessary condition to elicit horizontal circularvection in an observer. Subjects are able to perceive visually induced self-motion when gaze is being kept stable by presentation of a fixation target and, furthermore, circularvection is even elicited when the direction of horizontal optokinetic nystagmus is being reversed by pursuing a small superimposed central pattern moving in the opposite direction to the surrounding large-field stimulus.

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9.2 Publication of Experiment 3.1

Thilo, KV, Guerraz, M, Bronstein, AM, Gresty, MA. Changes in horizontal oculomotor behaviour coincide with a shift in visual motion perception. Neuroreport 11: 1987-1990.

Changes in horizontal oculomotor behaviour coincide with a shift in visual motion perception

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During full-field rotation of the visual field, subjects commonly experience an initial perception of object-motion which 'switches' to a perception of self-motion. We studied the characteristics of the horizontal optokinetic nystagmus responses evoked by a moving visual stimulus in these two perceptual states over a range of stimulus velocities. During self-motion perception mean eye position was found to shift more in the direction of the newly appearing stimulus elements with a slight reduction in slow phase gain in comparison to the nystagmus evoked during object-motion perception. The results may reflect a modified strategy of spatial attention with increased emphasis on anticipatory eye movements during visually induced self-motion perception. *NeuroReport* 11:1987–1990 © 2000 Lippincott Williams & Wilkins.

Key words: Circularvection; Horizontal optokinetic nystagmus; Perceptual ambiguity; Visual attention; Visual motion; Visual–vestibular interaction

INTRODUCTION

Relative motion between an observer and the visual environment is a potent stimulus to elicit the sensation of self-motion, an everyday example being the illusion of self-translation induced by perchance sighting of a moving train through the window of a stationary one. In a laboratory setting visually induced perception of self-motion is elicited by a patterned stimulus subtending a large area of the visual field. A stimulus that is moving linearly past an observer will lead to the illusory perception of translational self-motion, termed linearvection, in a direction opposite to which the stimulus is moving. Correspondingly, rotation of visual scenery around an observer induces the perception of contradirectional angular self-motion, or circularvection [1].

During transient self-motion, visual, vestibular and somatosensory signals are mutually corroborative. However, when motion is sustained vestibular and somatosensory inputs decay or adapt and visual signals maintain the perception of motion, perhaps via a slow build up of visual velocity signal in the vestibular system [2]. It is this slow build up that is thought to provoke the perception of self-motion in a stationary subject. Consequently, the visual motion stimuli used in the laboratory initially provoke the perception of object-motion after which a spontaneous and involuntary transition to a perception of self-motion takes place [3].

A frequent feature of stimuli tending to elicit self-motion perception is their property of inducing involuntary nystagmic eye movements. This optokinetic nystagmus consists of alternating slow and fast phases. During the slow phase the eyes follow the visual motion whereas the fast phase is a saccadic repositioning of the eyes in the orbit during which visual motion perception is reduced in order to minimize visual blur that would result from an eye movement in a direction opposite to that of stimulus motion [4].

We have recently investigated circularvection in the frontal plane induced by an optokinetic stimulus revolving around the line of sight and found that subjects' torsional optokinetic nystagmus was enhanced when they entered into self-motion perception [5].

There are mechanical and physiological differences between torsional and horizontal eye movements: in contrast to ocular torsion, horizontal eye movements are largely under voluntary control, can cover a much wider amplitude and originate from different neuroanatomical structures [6]. The purpose of the present study was therefore to investigate the interrelationships between oculomotor dynamics, object-motion perception and circularvection during optokinetic stimulation in the horizontal plane.

MATERIALS AND METHODS

Subjects: Three women and five men, aged 22–31 years (mean 26.3 years), without neurological or oculomotor abnormalities consented to participate in the study according to the guidelines of the local ethics committee. Subjects had uncorrected Snellen acuities of at least 6/9 and had clear vision of the stimuli.

Stimulus: The apparatus was a servo-motor controlled optokinetic drum, 190 cm high with a diameter of 150 cm, which rotated about its vertical axis. The inner surface was covered in alternating black and white vertical stripes, 9 cm and 4 cm wide respectively. Indirect illumination of the stripes rendered the corresponding luminances 0.12 cd/m^2 and 6.08 cd/m^2. The subject's head was held in position by a chin rest so that the distance between the nasion and the stripes was 65–70 cm.

Eye movement recording: Continuous recording of the subjects' right eyes was obtained by infrared Videooculography (SensoMotorics Instruments). The device allowed non-restricted vision of ~90° width and 70° height. Digitisation of the signal was carried out offline, re-sampling at 50 Hz with a spatial resolution of 0.2° for horizontal eye movements.

Procedure: After eye movement calibration, subjects were exposed to 12 trials of optokinetic stimulation. The sequence of drum rotation velocities (30°/s, 45°/s, 60°/s and 70°/s) was counterbalanced across subjects according to a Latin square. The direction of motion was alternated between trials. Each trial lasted for 30 s with an inter-trial interval of 90 s. Between trials, subjects were kept in darkness and eye movement recording was paused. Subjects were instructed to passively gaze at the stripes, which they viewed binocularly, and to try to avoid blinking. They signalled their perceptual states by flicking a hand-held switch between two positions.

Data analysis: For all oculomotor recordings acquired, every nystagmus slow phase was identified automatically and fitted with a linear regression line, the slope of which equals the mean eye velocity during the corresponding slow phase. For each subject and stimulation condition, the obtained regression slopes were pooled with respect to whether they were performed during the 5 s period that preceded or followed the transition from object- to self-motion perception. Because the onset of circularvection is known to vary considerably between subjects and often commences as early as 7–12 s after stimulation [7], periods of only 5 s pre- and post-onset of circularvection were available for the analysis in order to ensure that equal amounts of data would be obtained during each perceptual state for all trials and subjects. Accordingly, two average slow phase velocities were computed, one for the sensation of stimulus motion, one for the sensation of circularvection. Subsequently, for each average slow phase velocity, gain was calculated as slow phase velocity over angular stimulus velocity.

Mean eye position was computed by averaging all sampled eye position values during the according periods as above. Again, per condition and subject, one average was obtained for object-motion perception, one for circularvection.

Statistical comparisons of means were made computing two-way repeated measures analyses of variance.

RESULTS

Slow phase velocity: Onset of visual motion evoked an immediate nystagmic oculomotor response that was sustained throughout stimulation. As can be seen in Fig. 1, stimulus velocity had a highly significant main effect on horizontal nystagmus slow phase gain, decreasing from 1.02 at a velocity of 30°/s to 0.73 at 75°/s during object-motion perception ($F(3,21) = 14.9$; $p < 0.01$). During circularvection, slow phase gain was reduced by an average of 0.04 which is considerably small but was sufficiently consistent across subjects and velocities to give rise to a significant main effect of perceptual state ($F(1,7) = 7.7$; $p < 0.05$). No interaction between velocity and perceptual state could be detected ($F(3,21) = 1.1$; $p > 0.35$). Table 1 gives a detailed listing of slow phase gain values obtained at different stimulus velocities and perceptual states.

Eye position: With respect to primary gaze, visual motion stimulation led to a deviation of mean eye position in the direction opposite to stimulus motion during all velocities as shown in Fig. 2. Over all velocities tested, mean eye position shifted 6.6° in the direction contrary to stimulus motion during the perception of object-motion. Comparison of mean eye position between perceptual states revealed an additional significant deviation in the same

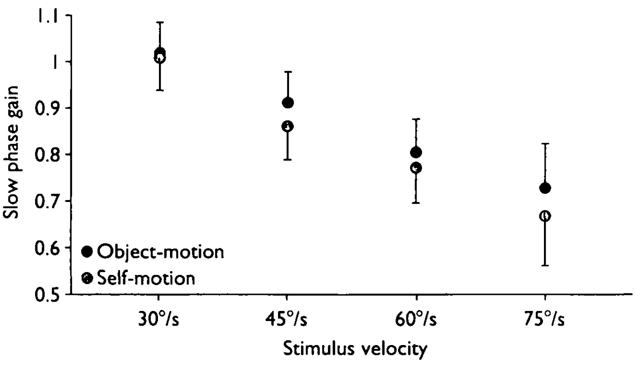

Fig. 1. Means and s.e. of horizontal optokinetic nystagmus slow phase gain during both perceptual states at various stimulus velocities.

Table 1. Means and s.e. (in brackets) of horizontal optokinetic nystagmus slow phase gain during object-motion and self-motion perception during the different optokinetic drum velocities.

	Stimulus velocity			
	30°/s	45°/s	60°/s	75°/s
Object-motion	1.02 (0.06)	0.91 (0.07)	0.80 (0.07)	0.73 (0.10)
Self-motion	1.01 (0.07)	0.86 (0.07)	0.77 (0.08)	0.67 (0.11)

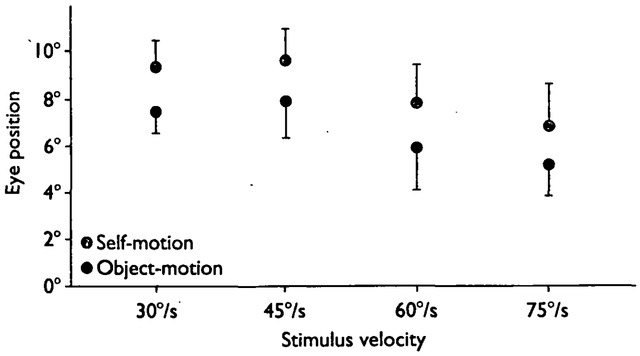

Fig. 2. Means and s.e. of horizontal eye position during the perception of object-motion *vs* self-motion at a range of optokinetic drum velocities. Eye position values are normalised according to the direction of visual motion stimulation with positive values denoting a deviation from primary gaze in the direction opposite to stimulus motion.

direction during circularvection ($F(1,7) = 9.8$; $p < 0.05$). Averaged over all velocities, this deviation was a further 1.8 (27%) in the anticipatory direction. No main effect of stimulation velocity on eye position could be detected ($F(3,21) = 1.8$; $p > 0.18$), nor an interaction between velocity and perceptual state ($F(3,21) < 1$). Individual eye position values are listed in Table 2.

DISCUSSION

The results of the present study are consistent with previous reports showing a decrease in optokinetic nystagmus slow phase gain with increasing stimulation velocities [8,9]. Comparison of the two states of motion perception reveals an enhancement of anticipatory deviation of overall eye position with a simultaneous decrease of nystagmus slow phase gain during the perception of circularvection at all stimulus velocities.

Hood and Leech [10] investigated the effect of different perceptual strategies on horizontal optokinetic nystagmus. When subjects were instructed to actively pursue the stimulus, mean horizontal eye position deviated in the direction towards which the stimulus was moving with nystagmus fast phases resetting the eyes towards primary gaze. In contrast, when subjects gazed passively at the stripes, nystagmus slow phases were reduced in velocity and fast phases were anticipatory with the slow phases returning the eyes towards primary gaze. In our experiment, all responses were characteristic of passive viewing with greater anticipation during circularvection.

An anticipatory shifting of gaze, and thereby attention, towards the direction from which new visual elements are appearing enables early detection of relevant changes in the visual environment. When visual motion is perceived to be originating from actual self-motion, however, an orienting response towards the direction of heading would be of even greater relevance, especially when there is no need to pursue the visual scene. An attentional shift of such kind may be reflected by our finding of enhanced passive nystagmus characteristics during circularvection. The gaze shift towards the fast phase would correspond to an increase in anticipation and the decrease in slow phase velocity would result from a reduced emphasis on active pursuit. It should be noted that the latter reduction in horizontal optokinetic nystagmus slow phase gain accounts for a relative change of an average 4.8%. This effect only constitutes a small expense for ocular tracking accuracy since during a pursuit period of 300 ms, retinal slippage would increase by an average 0.12° of visual angle at a stimulation velocity of 30°/s and by 1.35° at 75°/s which lies well within the size of the fovea and would, hence, presumably be of little consequence for visual motion perception. Although this decrease in slow phase gain is small it has additional significance because it is in the opposite direction to Alexander's law from which one would expect an increase in slow phase velocity with larger amplitude decentring saccades [6].

It appears that the anticipatory characteristic of both horizontal and torsional optokinetic nystagmus is enhanced when the subject enters circularvection [5]. However, torsional slow phase gain also enhances during circularvection whereas that of horizontal optokinetic nystagmus does not. This discrepancy may be resolved when the different natures of torsional and horizontal eye movements are taken into account. The torsional optokinetic reflex in humans is largely vestigial and its slow phase more than thirty times smaller than that of horizontal optokinetic nystagmus [11]. Its main purpose is a static one, namely to maintain an upright retinal image during motion in the roll plane and it does not shift the orientation of the fovea with respect to the visual environment. Horizontal optokinetic eye movements, however, largely reduce retinal slip and anticipate the direction of heading. Torsional nystagmus may be enhanced during circularvection because the threat of the body tilting makes maintenance of orientation imperative.

Recent evidence from functional imaging on the central nervous correlates of the two states of visual motion perception, found an interaction in haemodynamic responses of early visual and multisensory vestibular cortices. Parieto-insular vestibular cortex underwent a deactivation during circularvection as compared to object-

Table 2. Means and s.e. (in brackets) of horizontal eye position during both perceptual states obtained at various stimulus velocities. Values are normalised with respect to the direction of optokinetic drum rotation so that positive values indicate an ocular deviation in the direction contrary to drum rotation.

	Stimulus velocity			
	30°/s	45°/s	60°/s	75°/s
Object-motion	7.4 (0.9)	7.9 (1.6)	5.8 (1.8)	5.2 (1.3)
Self-motion	9.3 (1.1)	9.6 (1.4)	7.8 (1.7)	6.8 (1.8)

motion perception whereas occipital cortex showed an inverse response pattern [12,13]. It had been suggested previously that visually induced perception of self-motion might involve a descending projection from motion-sensitive visual cortical areas to the vestibular nuclei in the brain stem [14]. This view is in agreement with a number of electrophysiological studies demonstrating a modulation in firing rate of monkey vestibular nuclei neurons in response to optokinetic stimulation which gave rise to the hypothesis that enhanced neural activity in the vestibular nuclei may lead to the perceptual interpretation of visual motion as originating from self-motion [15–17]. The vestibular nuclei are closely coupled with subcortical oculomotor areas, which form the neural substrate of the vestibulo-ocular reflexes and are therefore the earliest, although not the only, central nervous structure in which a perception-related modulation of oculomotor behaviour may occur.

CONCLUSION

This study found that the characteristics of optokinetic responses to visual field motion become more anticipatory when subjects switch from perceiving object-motion to self-motion with the eyes deviating more towards the oncoming visual field during circularvection. We presume that the optokinetic behaviour during object-motion perception has a monitoring function whereas, during circularvection, the response is tuned to exploration of, or orientation to, the emerging environment. This finding also is a demonstration of a physiological marker which corresponds to a change of perceptual state during otherwise constant visual stimulation.

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9.3 Publication of Experiment 5.1

Aoki, M., Thilo, KV, Burchill, P, Golding, JF, Gresty, MA. Autonomic responses to real versus illusory motion (vection). Clin Autonom Res 10: 23-28.

Research Paper

Clinical Autonomic Research 2000, **10**:23–28

Autonomic response to real versus illusory motion (vection)

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This study explored the cardiovascular responses to illusions of self-motion (vection) induced in normal subjects according to the hypothesis that vection may be a model for vertigo in vestibular disease. Responses were obtained from 10 men who were exposed to rapid tilts of 20° and 30° rolling from the upright position down to the right or left shoulder. These responses were compared with those evoked during the illusion of roll-tilt vection provoked by a torsionally rotating visual field. Comparisons were made between 10-second data epochs before and after stimulus onset. In response to vection, blood pressure (BP) in the radial artery rose consistently in six subjects, and in all of these, a pressor response to real tilt was also observed. The remaining four subjects consistently had decreased BP in response to vection, and their BPs were affected little by tilt. Subjects whose BP increased with vection and tilt may have been dominated by tendency to arousal, whereas those whose BP decreased may reveal the more appropriate response to tilt from the upright position, which is a decrease in BP. This may reflect individual stereotypes and differences in the relative contributions of somatosensory and vestibular control of autonomic regulation.

Key words: vertigo, vection, tilt, blood pressure, optokinetic.

The profound vasovagal consequences of vestibular vertigo are ample evidence that the labyrinth has significant implications for autonomic function. However, it is only recently that animal studies have demonstrated possible mechanisms in the form of direct projections from vestibular nuclei serving cardiac and respiratory regulation [1]. The present study intended to gain insight into the autonomic responses accompanying vertigo by using vection in normal subjects as a model of vertigo caused by vestibular disease.

Vertigo is illusory self-motion caused by disordered vestibular activity, which wrongly signals that the head is moving. Vection is an illusory self-motion induced by a moving visual field, which is familiar to readers in the "railway carriage" illusion of self-motion provoked by seeing a train go by. Vection is attributed to a summation of visual motion signals and vestibular signals in vestibular nuclei type I neurones. These neurones give an output which the brain may interpret as self-motion [2–4], even though their input may be only from visual motion. Therefore, both vection and vertigo arise through activity in the vestibular nuclei, which causes a false perception of self-motion that is at odds with other sensory inputs. *A priori* one would expect individual differences in the autonomic responses to vection because normal subjects' reactions to induced dizziness, on fairground rides or during caloric irrigation, for example, vary from exhilaration to fear.

To provoke substantial autonomic responses, we studied roll-tilt, which is tilting from the upright position down to either shoulder. Illusory roll-tilt is provoked in the form of a roll-tilt vection by a torsionally rotating visual field. While viewing the rotation, the observer first sees object motion and then, after a delay, may experience the illusion of rotating and being tilted in the direction opposite to field rotation.

Material and methods

Apparatus and tilting
Subjects were seated with head upright in a flight simulator (SEGA, Tokyo, Japan) that executed discrete tilts from the upright position by rolling subjects about an anteroposterior, horizontal axis aligned through the midline of the trunk at the level of the heart (Fig. 1). Head, trunk, and limbs were supported and restrained with foam padding. Peak velocities of tilt were 20° per second with settling times of 2.5 and 3.0 seconds. Tilts were maintained for 30 seconds, after which the machine returned to the upright position with a similar velocity profile. Subjects closed their eyes during tilts.

Optokinetic stimulus inducing vection
A motorized cone with a diameter of 58 cm and a depth of 25 cm was mounted in the flight simulator at a distance of 28 cm from the nasion (Fig. 1). The subjects looked into the

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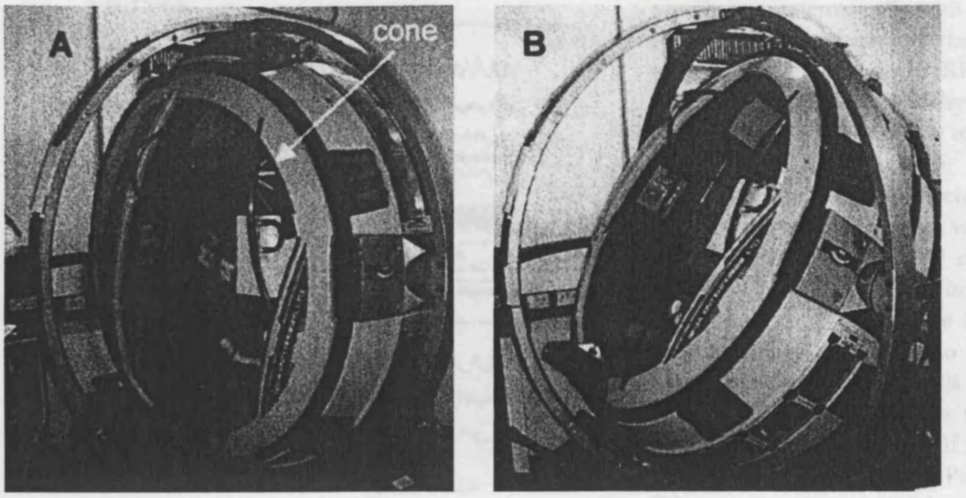

Figure 1. (A) SEGA flight simulator in upright position with optokinetic cone visible within the cockpit. **(B)** SEGA tilted 30° rightward.

cone, fixating the apex. The inside was matte black with radially oriented stripes of charged fluorescent tape 20 mm wide. The stripe/background contrasts were 0.89 at the beginning of testing and decayed to 0.67. To provoke vection, the cone rotated about its principle axis at 40° per second. Subjects indicated the onset and offset of vection with a foot switch. During and immediately prior to this procedure, the cockpit was in darkness.

Autonomic recordings

The electrocardiogram (ECG) was recorded by a BP-508 (Colin Corporation, Komaki, Japan), which also recorded continuous tonometric arterial blood pressure (BP) from a robotic sensor positioned over the left radial artery, approximately 20 mm from the wrist line. The forearm was fully supported and restrained to exclude mechanical shocks, and it was semi-abducted so that the BP sensor was on the axis of tilt. Pulsatile blood flow measure was obtained by photoelectric plethysmography (Model PPS; Grass, Boston, MA, USA) from the index finger of the right hand and high pass filtered with a time constant of 3 seconds. Galvanic skin resistance (GSR) was obtained from solid state electrodes (ARBOTM Neonaten, Hamburg, Germany) mounted on the second and third fingers of the right hand. Respiration was recorded as the measure of airflow from a thermocouple in the left nostril. Instantaneous heart rate (HR) and R-R interval time (RRt) were derived in analog form from the raw signal with a Grass tachograph. Signals were sampled for processing at 125 Hz, and averages were taken of HR, RRt, diastolic arterial blood pressure (DAP), systolic arterial blood pressure (SAP), and peak-to-peak beats of the plethysmograph. All measurements were taken for 10 seconds before and 10 seconds after the onset of stimuli (tilt, vection, and cone motion). GSR amplitude was measured from baseline to peak in ohms attained during the 10 seconds after stimulus.

Background information questionnaire

Subjects completed a validated questionnaire that probed headache, ear and eye diseases, and optical correction; susceptibility to motion sickness; susceptibility to startle, shock, blushing, and fainting; introversion–extraversion; physical activity and attitude to physical risk and amusement parks; and use of social and prescribed drugs. Relevant medical history was sought by questioning.

Experimental design

Ten healthy adult men (age range, 29–52 y; mean, 36.2 y; standard deviation, 6.4) consented to the study according to the guidelines of the local ethics committee. None were smokers. None had unusual ingestion of drugs or unusual life events over the previous 24 hours. Testing was performed midmorning or midafternoon.

Stimuli were given in a balanced design: five subjects were exposed to real tilts followed by optokinetic stimulation with a rest period of 10 minutes between tests. The remainder underwent the inverse sequence.

Tilts of 20° and 30° to the right and left shoulders were given in a balanced design with two trials at each amplitude. Timing of tilts was varied to be unpredictable, and at least 30 seconds elapsed before and between tilts.

Vection stimuli included alternating 1 minute of rotation to the right or left shoulder (two times each way) followed by a 1-minute pause and stimulation in the opposite direction. During testing, the door of the simulator was closed.

Data analysis

Data were collected continuously for at least 30 seconds before and after any stimulus to decide whether the baseline was stable enough to identify responses (Fig. 2).

Responses were often small, so we adopted the following tactic: first, responses that were visible in stable baselines were identified. Thereafter, measurements were taken on all records with similarly stable baselines. This procedure included both obvious and minimally sized responses.

Vection occurred intermittently. The first onset of vection could be as early as 10 to 20 seconds after cone motion onset in susceptible subjects and could come and go thereafter. Because cone motion onset induced transient responses that could last up to 10 seconds, we decided that, as

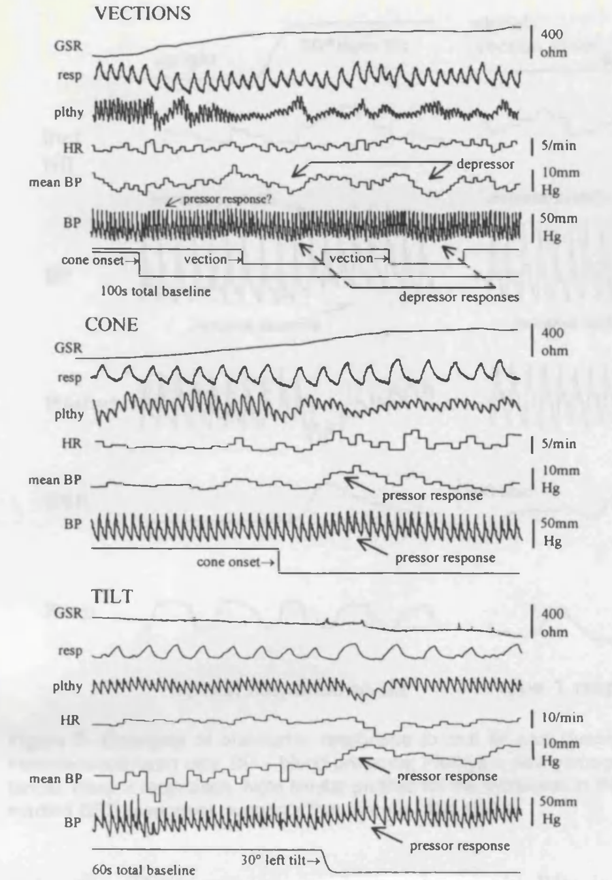

Figure 2. Extended data records showing baselines for responses to vection (upper traces with two examples of the depressor response), pressor response to cone onset (middle traces), and pressor response to tilt (lower traces). GSR = galvanic skin response; resp = respiration; plthy = plethysmograph; HR = heart rate; BP = blood pressure.

a precaution against collecting overlapping responses, we could only accept vection responses that occurred more than 20 seconds after cone motion onset or that were spaced 20 seconds after the offset of the last episode of vection (Fig. 2).

After failures to achieve vection and rejection of overlapping responses and unstable baselines, data from three vection trials were obtained for each subject. Tilting occasionally produced artifacts (usually a spontaneous arm movement) that had to be rejected.

Because of the temporal constraints on vection, comparative measurements and statistical analyses were performed on 10-second epochs before and after stimulus or vection onset.

Results

General characteristics of responses

On inspection of the records, we found that SAP and DAP increased in nine subjects on real tilt down (Figs. 2,3). HR appeared to initially increase and then decrease. In response to the onset of illusory tilt (vection), six subjects appeared to have increased DAP and/or SAP, whereas four subjects appeared to have decreased DAP and/or SAP (Fig. 3). RRt did not change systematically with illusory tilt. Both the return to the upright position and the onset of cone rotation gave more variable responses in RRt, DAP, and SAP with no consistent pattern. The plethysmograph showed decreased peripheral volume of variable magnitude in most subjects in response to all of the stimuli.

For each of the six subjects who appeared to have increased DAP and/or SAP (of which two had short peaks in BP and four had rises in BP sustained over 10 seconds), t tests showed significant rises in the 10 seconds after vection onset in comparison with the 10 seconds before ($p <0.05$). For subjects who appeared to have decreased DAP and/or SAP after vection, the results of t test results on the 10 seconds before vection versus the 10 seconds after vection were significant ($p <0.05$). Of most importance, the distribution of rising and falling BPs was unequivocally bimodal. When responses were visibly evident, subjects were consistent in showing either a rise or fall, never both (see Fig. 2, raw records, and Fig. 4, DAP and SAP). Absolute amplitude of increases in diastolic BP in type 1 ranged from 0 to 7.5 mm Hg across the six subjects, and absolute amplitude of systolic BP ranged from 0 to 14 mm Hg. In type 2, diastolic BP decreased by up to 8 mm Hg, and systolic BP decreased by up to 8.5 mm Hg.

Using χ^2 goodness-of-fit tests, we rejected the null hypothesis of normally distributed diastolic BP changes for $n = 30$ observations at $\chi^2 = 7.2$ ($df = 1$, $p <0.01$). Similarly, systolic BPs were not normally distributed ($\chi^2 = 26.1$, $df = 3$, $p <0.001$). Because BP responses to vection were continuously distributed and their behavior was consistent within subjects, we tentatively classified subjects as type 1 (BP rising during illusion or pressor response) and type 2 (BP falling during illusion or depressor response) (see also Fig. 3).

Averages of subjects' responses were taken and grouped as types 1 or 2. These are shown in Figure 4 for 10 seconds preceding and 10 seconds following stimuli (averaging epochs are short because vection comes and goes). The averages included all vection over 10 seconds in duration. The latencies of vection after onset of visual stimulus were 20.3 ± 6.6 seconds in type 1 subjects and 18.2 ± 4.1 seconds in type 2 subjects, with durations of 30.5 ± 12.3 seconds and 39.0 ± 16.2 seconds, respectively. Mean ages of the two groups were 34.0 ± 7.0 years in type 1 and 37.6 ± 5.6 in type 2 (mean ± standard deviation). There were no differences between the two groups in latency, duration of vection, or age (analysis of variance, $p >0.05$).

Repeated analyses of variance were performed on RRt, DAP, SAP, plethysmographic responses, and respiratory frequency seen in the 10 seconds before and 10 seconds after stimulation (or onset of vection) using the factors before and after stimulus (or vection) onset, trial number (first, second, third), and group (type 1, type 2). For tilt down, DAP and SAP increased by 4.8 and 8.9 mm Hg in type 1 subjects ($p <0.01$), for whom there were also significant plethysmographic responses. For type 2 subjects as a group, there were no significant changes in BP or plethysmographic response, although individual subjects' BP did increase on

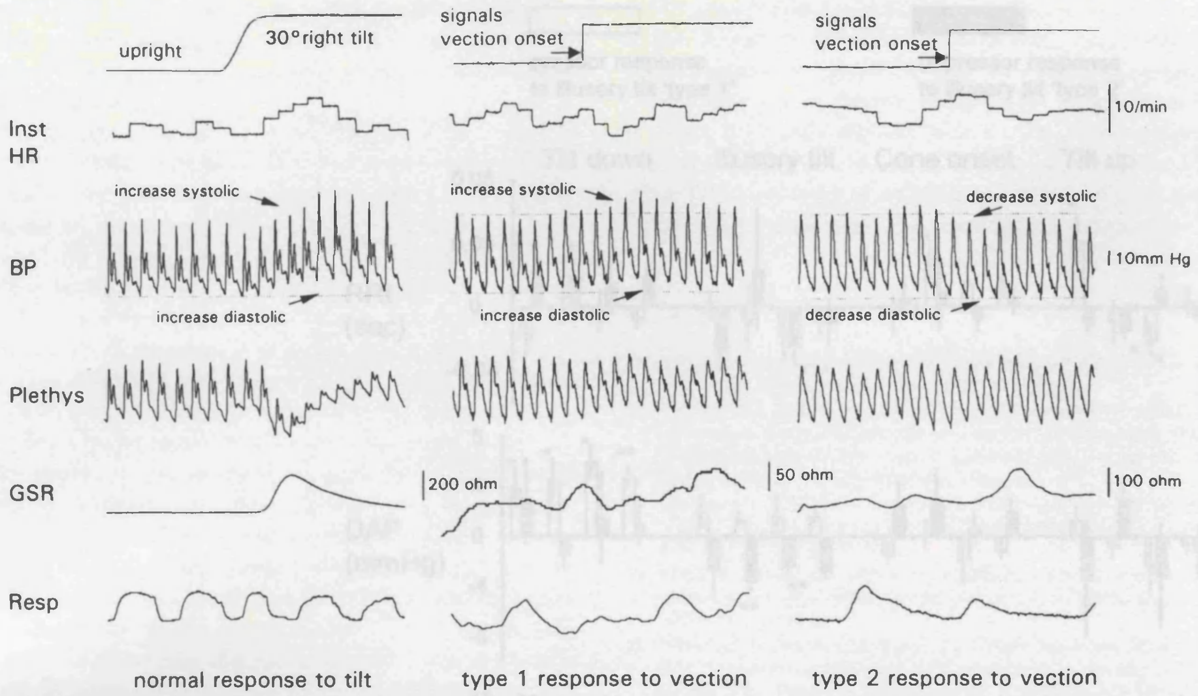

Figure 3. Examples of autonomic responses to real tilt and illusory tilt comparing 10 seconds before and after stimulus onset. Inst HR = instantaneous heart rate; BP = blood pressure; Plethys = plethysmograph; GSR = galvanic skin resistance (shown in Siemens, units of conductance); Resp = respiration. Note similar profiles for the increases in BP in real tilt and in the type 1 response to vection. Note that the absence of marked GSR responses suggests that there is little startle.

some tilts. There were no consistent changes in RRt in either group. Onset of vection provoked an increase of 3.5 mm Hg in SAP in type 1 subjects and a decrease in DAP (-2.8 mm Hg) and SAP (-2.2 mm Hg) in type 2 subjects ($p < 0.05$, Fig. 4). For tilt up, there were no systematic autonomic responses in either subject type. Onset of cone motion provoked only a decrease in plethysmographic response in type 2 subjects ($p < 0.05$).

Respiratory frequency in type 2 subjects was significantly higher in response to cone motion onset and significantly lower during vection ($p < 0.05$). However, based on averages, respiratory responses were unrelated to cardiovascular responses.

There were no differences in GSR response between stimulus conditions (analysis of variance, $p > 0.05$). During vection, type 1 subjects had a weak increase in conductance, whereas type 2 subjects had a marked increase in conductance (Fig. 4).

Latencies of response

Based on type 1 subjects whose BP increased during tilt, the latency of the increase in BP was 2.5 seconds. Plethysmographic changes had a latency of 3.0 seconds. Latencies of responses to illusory tilt are impossible to estimate because the onset of the illusion is difficult to pinpoint. Latencies to the peak of the GSR responses to tilt down, recorded as mean ± standard deviation, were 4.3 ± 0.4 seconds for type 1 and 4.5 ± 0.4 seconds for type 2. Latencies of response to cone motion were 3.8 ± 0.5 seconds for type 1 and 3.8 ± 0.5 seconds for type 2 (no differences between subject types).

Estimates of response novelty, adaptation, or startle components

Decreases in the magnitude of plethysmographic response were found on the first three trials (analysis of variance, $p < 0.05$) for type 1 subjects but only on the first trial for type 2 subjects.

Repeated analyses of variance on the peak amplitudes of GSR responses in the 10 seconds after tilt, cone motion, or vection onset showed no differences ($p > 0.05$) in response among the first three trials.

Response consistency

A type 1 subject and a type 2 subject have recently been retested 6 months after the original study and have produced pressor and depressor responses respectively to vection, as they did originally.

Discussion

The key finding in this study was that rapid roll tilt provoked a pressor response that one might expect as an arousal-readiness response to significant spatial reorientation, whereas with vection, some subjects' BP increased (type 1) and others' BP decreased (type 2). These responses to vection persisted with repeated exposure. Type 1 subjects' BP also significantly increased over the 10 seconds after tilting the body. Bigger GSR and plethysmographic response were observed in real tilt, and plethysmographic response in vection was variable and weak. No relationships were found between BP and HR in any stimulus condition.

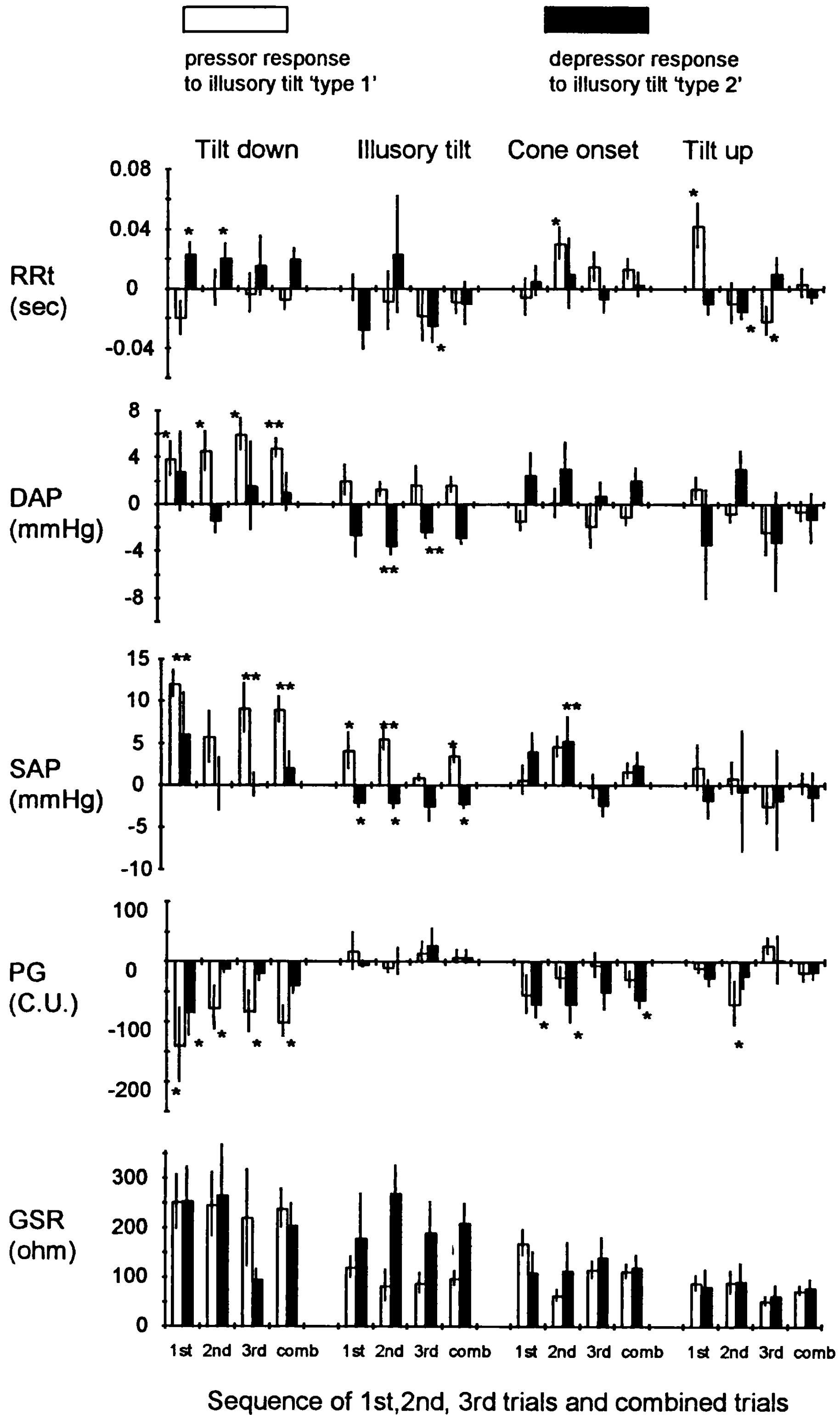

Figure 4. Autonomic responses to tilt down, illusory tilt, cone motion onset, and tilt up showing the changes in averages over 10 seconds pre-stimulus as compared with 10 seconds post-stimulus. The first three successful trials and their average are shown. Type 1, unfilled columns; type 2, filled columns. **, *, significant differences from 10-second pre-stimuli recording at $p < 0.01$ and $p < 0.05$, respectively. RRt = R-R interval time; DAP = diastolic arterial blood pressure; SAP = systolic arterial blood pressure; PG = plethysmograph; C.U. = computer unit; GSR = galvanic skin resistance. Each column shows mean ± standard error of mean.

Our attempt to classify subjects according to whether they had pressor or depressor responses to vection is in accord with a recent study on a visually induced illusion of tilt from the supine position toward the upright position, which found two classes of subjects, those who failed to respond and those whose BP increased [5]. It is not surprising that BP responses to illusory motion varied among individuals because vestibular stimulation (eg, calorics or rotation) does not induce stereotypical responses in humans [6]. We have observed that such intersubject variability is also characteristic of patients' responses to vertigo. Furthermore, even when subjects feel motion sickness, autonomic responses are not systematic [7,8]. However, in the present study, none of the subjects reported any discomfort as a consequence of the experiment, which would indicate that motion sickness had been provoked, so it is unlikely that the types of responses we observed were related to motion sickness susceptibility.

In absolute terms, the observed changes in BP, either to tilt or to vection, were small. Effects of similar magnitude in humans have been reported for other forms of vestibular stimulation, for example, tilt of the head [9] or inertial force vector [10], typically below 5 mm Hg. Although they may have statistical significance, one might query the functional significance of such diminutive changes. The reason vection provokes small responses is probably that it inputs to normal closed loop autoregulation so that its effect is minimized by other regulatory mechanisms that fail to corroborate that a major spatial reorientation has taken place.

In respect to the mechanisms mediating the responses observed, animal studies have demonstrated that somatosensory inputs, including body movement, initially increase BP. For vestibular-canal input (calorics or rotation), some studies have shown a decrease in BP [11,12], whereas others have shown the opposite pressor effect [13]. Otolithic [14] stimulation in humans appears to raise BP (note the profile of the BP response to linear acceleration is identical to our type 1 response to rapid tilt). Hence, we may speculate on the mechanisms of response variability. For example, the increased BP response to real tilt could be derived from somatosensory or vestibular otolithic inputs. The depressor response during the vection in type 2 subjects may be induced by activation of the vestibular system by the visual flow (*nota bona,* no somatosensory input in vection). The pressor response during vection in type 1 may be associated with the cortical sympathetic output, which is induced by onset of vection. This suggestion is supported by the finding that during vection there was a significant increment of systolic arterial BP without a change in HR. Seen from another perspective, it may be that subjects whose BP increased with vection and tilt may be dominated by tendency to arousal, whereas those whose BP decreased may reveal the more appropriate response to tilt from the upright position, which is a decrease in BP. In sum, individual subjects' responses to real or illusory reorientations may reflect the relative weightings of somatosensory and vestibular modes of autonomic control and/or their preferred response tactic.

Although the central mechanism of sympathetic outflow is still unclear, tilt could excite sudomotor neurons through the vestibular and/or somatosensory systems [15]. The higher GSR response during real tilt (higher than during visual stimulation or vection) might be because of the congruent multisensory input driving the response. Animal studies show the importance of the medullary reticular formation as well as influences from midbrain, hypothalamus, and limbic structures [16]. With respect to the GSR responses in both tilt and vection, it is known that vestibular input directly activates the sudomotor nerve in animals and may therefore do the same in humans [17].

No relationship could be found between subjects' autonomic responses and their profiles from questionnaires, which suggests the possibility that individual responses to illusion represent a relatively independent idiosyncratic factor, as is apparently the case with motion sickness susceptibility, for example [18,19]. It remains to be shown what these individual types of response in normal subjects imply for symptoms associated with pathological vertigo.

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9.4 Declaration in accordance with note 6 of the University of London PhD Examination Entry form

Note 6

"... a candidate shall not be precluded from incorporating in a thesis covering a wider field work which he/she has already submitted for a degree (...) of this or any other university (...), provided that he/she attaches full details to this form and also indicate in the thesis any work which has been so incorporated."

Declaration

Experiment 2.3 presented in this thesis was used for the report of an undergraduate research project ('Diplomarbeit') which formed part of my undergraduate degree in Psychology ('Diplompsychologe') awarded in 1998 by the University of Düsseldorf, Germany. The data have since been further processed, analysed and interpreted and only form part of Chapter 2 in this thesis.