



53

Vision in near-head space

Ervin Poljac

VISION IN NEAR-HEAD SPACE

Hoe zien we de ruimte rond ons hoofd
(met een samenvatting in het Nederlands)

PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD VAN DOCTOR AAN DE UNIVERSITEIT UTRECHT
OP GEZAG VAN DE RECTOR MAGNIFICUS, PROF. DR. W.H. GISPEN, INGEVOLGE
HET BESLUIT VAN HE COLLEGE VOOR PROMOTIES IN HET OPENBAAR TE
VERDEDIGEN OP MAANDAG 7 MAART 2005 DES MIDDAGS TE 2.30 UUR

DOOR

Ervin Poljac

GEBOREN OP 25 JUNI 1972 TE DERVENTA (Bosnië en Herzegovina)

promotor: **Prof. Dr. A.V. van den Berg**

Faculteit Biologie
Helmholtz Instituut
Universiteit Utrecht

HET IN DIT PROEFSCHRIFT BESCHREVEN ONDERZOEK WERD UITGEVOERD MET FINANTIËLE STEUN
VAN DE NEDERLANDSE ORGANISATIE VOOR WETENSCHAPPELIJK ONDERZOEK (NWO),
GEBIEDSBESTUUR AARD- EN LEVENSWETENSCHAPPEN (810.37.006)

Contents

Chapter 1. Introduction	3
Chapter 2. Representation of heading direction in far and near head space	15
Chapter 3. Perceptual compensation for eye torsion	41
Chapter 4. Localization of the plane of regard in space	61
Chapter 5. Collision judgment of objects approaching the head	77
Chapter 6. Summary and conclusions	99
Samenvatting	105
Curriculum vitae	111
List of publications	113

Introduction

1

To engage in desirable and to avoid threatening situations, knowledge of the environment is required. Our brain embodies such knowledge in the activity of neural circuits. This representation of perceived objects includes various aspects such as shape, color or distance. One of the important and basic features is the information about an object's location. For, to act upon an object we first must determine its position, and in particular, how it relates to ourselves. Even an action seemingly as simple as directing the gaze towards an object, is preceded by estimating at least where the object is located relative to our eyes. More complex actions, like pointing to or grasping the object, require beside the representation of the object itself also knowledge of the location and orientation of the effectors used to execute the action.

This thesis deals with the question how the brain represents an object's location. More specifically, we investigate how objects in the space near the head are defined in the brain. A fast and accurate representation about an object's position is crucial, particularly when the object is in the close proximity of the head. Even more so this holds for objects that are not static, but that are approaching the head, for instance. To introduce the reader to the context from which these specific questions arise we briefly discuss some important issues concerning space representations.

Reference frames

Representations of loci surrounding the observer always refer to one or even multiple *reference frames*. A frame of reference gives the physical location relative to which an object's position is defined. This reference can be another object in space, but also a body part such as the head or the eye, for instance. In the latter case we speak of an eye-centered representation or eye-centric frame of reference (also called retino-centric or oculo-centric), where locations of other objects are expressed relative to the retina. For convenience, a coordinate system within a reference frame is defined. A set of base vectors is chosen for this purpose. Often one uses a *Cartesian* description of a reference frame, in which positions of objects are defined as a triple of distances from the origin (the eye, for example) along three orthogonal axes. But alternative ways to describe the object's position, such as by a single distance relative to the origin and two angles of rotation can also be applied.

Let us take for example an apple lying on the table in front of us. To check if it looks delicious we have to direct our eyes towards it. First, the visual system must determine how the apple's location relates to the eye. A representation of the apple's location in a retino-centric frame of reference is directly given by the pattern of light falling on the retina of a single eye, specifying the direction towards the object, but not its distance. *Binocular* stimulation allows the visual system in principle to also determine the distance from the eyes and even an object's location, just one rotation away from the head's reference frame. Because the two eyes look at 3D objects from different positions, the retinal image of the object will differ slightly in the two eyes. These small differences between the locations of an object's retinal images in the left and right eye, the so-called disparity information, is extracted and used for a three-dimensional percept (Gårding 1995). The *horizontal position* differences between corresponding parts in the images of the two eyes, provide horizontal *disparities*

which are useful for perception of depth relative to the fixation point. They are supplemented by the *vertical disparities* between the corresponding image parts that are found above and below the horizontal retinal meridian. The latter disparities enable a computation of the viewing parameters of the visual scene (Mayhew and Longuet-Higgins 1982), i.e. the way the eyes are oriented relative to the scene. We immediately add, however, that the computation cannot resolve the vertical rotation that is common to the two eyes. The pattern of binocular disparities is ambiguous in this respect, as identical retinal stimulation can arise regardless of vertical orientation of the eyes. To eliminate this ambiguity a reference is needed to account for the vertical eye orientation. One such reference containing the information about eye elevation might be the *plane of regard*. This plane is defined by the two rotation centers of the eyes and the fixation point. By definition it contains the *lines of sight* (lines connecting the fovea and the fixated object) and the *interocular axis*, the axis through the eyes' rotation points, about which it rotates. Therefore, the vertical orientation of this plane is solely dependent on the eye elevation. Motor action needed to orient the eyes towards the apple relies on the retinal representation. The eye movement calculation is based on a difference between the desired and current position (Sparks DL & Mays 1990). The change of orientation from the current fixation direction towards the desired object is performed by a rapid eye movement called *a saccade*. Moreover, most of the time we use visual feedback in order to make a correction if the initial eye movement toward an object is inaccurate. So, if we miss our apple with the first saccade, an additional corrective saccade can be performed to bring its image onto the *fovea*, which is a small depression in the retina at the back of the eye, with the greatest visual acuity.

Identifying the frame of reference in which an object is represented by neural activity is rather straightforward. An object is represented in an eye-centered frame of reference if the response of cells to an object remains constant as long as its image falls on the same location on the retina, independent of the eye's viewing direction. Similarly, an object has (at least) a head-centric representation if it remains stationary relative to the head and the non-resting activities of the cells remain unchanged despite eye movements. An example of such a head-centric receptive field is illustrated in Figure 1. Given that a reference frame is implicit in the neural activity, one can wonder whether the reference frame is unique to each particular sensory modality.

multisensory integration

In natural situations an object is often described in different modalities (for example visual, tactile, auditory). These representations by themselves might be ambiguous, but combined together form a coherent percept of the object. Different modalities interact and sometimes can interfere with the representations of the stimulus originating from other modalities, like in illusions. Shams et al. (2002) describe for instance the sound-induced flash effect in which a single brief visual flash is perceived as a number of flashes when accompanied by multiple auditory beeps. This is a clear illustration of distorted visual representation due to an input from a different, in this case auditory, modality. In general, however, representations in different sensory modalities coming from the same object facilitate each other. This multimodal interaction is called multisensory integration. Auditory information,

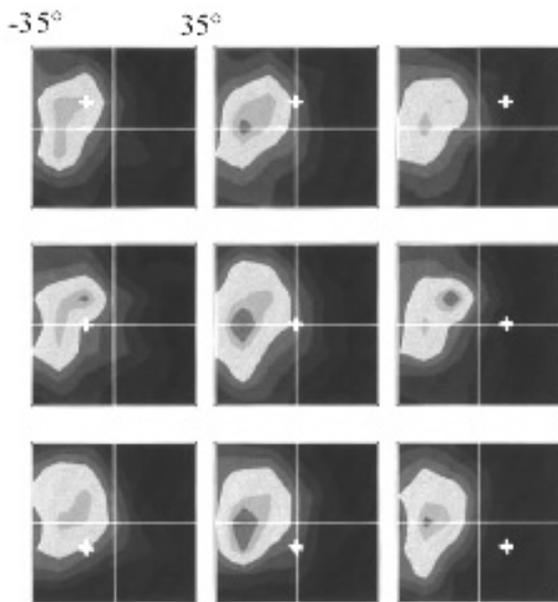


Figure 1. Head-centric visual receptive fields. Data of a single VIP neuron with visual receptive field mappings that are unaffected by eye position. During visual stimulation eyes could be oriented in one of nine directions spaced 20° apart (indicated with white crosses in the figure). The receptive field characteristics of the neuron remained unchanged irrespective of eye orientation. Adapted from Duhamel et al. (1997)

in combination with visual signals for instance, leads to a more confident judgment of an object's location in space (Wallace et al. 2004). Thus, different modalities complement each other when they are related to the same physical object. Accordingly, the percept of our apple will be stronger when we touch it, or smell it for example, while looking at it.

Evidence for multisensory integration comes not only from behavioral, but also from neurophysiological studies. Various neural structures have been identified that contain cells coding for different sensory inputs (Cooke, 2002). Bimodal and multisensory processing is important, and dominant rather than an exception in the brain (Calvert et al. 2004). It is a frequent feature of space coding (e.g. Duhamel et al. 1998, Graziano & Gross 1998). Even primary and secondary areas of visual cortex receive input from early stations of auditory cortex (Falchier et al. 2002). The interaction between different modalities is also observed in objects moving in depth (Kitigawa & Ichihara 2002). For example, tactile information about the location of object's impact on the face is coded by the same groups of (multimodal) neurons that code for visual information about the approaching object (Cooke 2002).

multiple representations

Suppose we now want to see if the apple is firm. To that end we take it in our hand. Moving the hand towards the apple involves a set of commands to joints and muscles. Regardless of the mechanism by which this is accomplished, a representation of the object for the motor action that will bring the hand to the apple must be built. This representation of the object can exist in the brain simultaneously with other definitions of its position. The same apple's location can be described relative to the eye (as initially all visual information is) or relative to the effector, in this case the arm, but also with respect to another object on the table or relative to the table itself.

Which of them is applied may depend on the action that has to be executed. To look at the apple an eye-centric representation would suffice. To reach for it, however, describing it relative to the arm would be more convenient. If one, on the other hand, must judge whether the apple is closer or further away than another object on the table, defining the objects' location relative to each other would be more adequate. Such multiple representations of the same object are not an exception in the brain.

One indication of the existence of different representations is unequal accuracy of an object's location defined in different reference frames. Rine and Skavenski (1997) show that the representation for pointing can be accurate even when the experimenters deliberately distorted the visual signal by prisms. In this case the representation for motor action "outperforms" the object's definition built for visual judgment¹. Subjects were still able to accurately point to the object's location, because, as Rine and Skavenski explain, the extraretinal signals originating from eye-orientation signals were used to make a correct representation for pointing. Another example supporting the notion of the simultaneous existence and dissociation of different reference frames (of the same feature) comes from the study of voluntary and stimulus-evoked saccades (Niemeier & Karnath 2003). Here, different reference frames have been found in which the saccadic system can operate, dependent on whether a saccade is initiated voluntarily (head-centered) or evoked by a salient stimulus (eye-centered).

An important characteristic of these representations is that they are not static, but dynamic. They can change over time (Iriki et al. 1996; Berti & Frassinetti 2000; Maravita & Iriki 2004; Gentilucci et al 2004). Changes in body representations were observed when, for example, macaques used simple tools to reach for objects. Recordings from intraparietal cortex, an area of the brain responsive to somatosensory and visual information, revealed the expansion of the receptive fields of some bimodal neurons. After tool use, these neurons expanded their visual receptive fields to include the entire length of the tool in the body representation (Iriki et al. 1996).

reference frames transformations

Although different representations of our apple's location may be used independently of each other according to the task, as mentioned above, they are not necessarily independent of each other. A nice illustration of this is orienting our eyes toward a sound source, which is a very common action. As auditory information is initially defined in a head-centric reference frame (Cohen & Knudsen 1999) and the location of the sound source must be represented in a frame suitable for the motor action (moving the eyes), a transformation between reference frames is required (Cohen & Andersen 2002). Moreover, this requires a transformation between reference frames originating from different sensory modalities. When multiple encodings of an object's location exist, the transformations are also used to bring them into a common reference frame. A shared frame of reference is convenient, as it may facilitate the exchange of information (Cohen & Andersen 2002). When action is directed towards an object, a common coordinate system may speed up the

¹ Although for pointing, beside an accurate representation of the object's location, a correct representation of the arm is required.

computation of its location and the motor plans needed to direct the effector towards it. Particularly when different effectors are involved in a more complex action such as when looking and pointing to an object.

So, what makes it possible to use for instance a retino-centric representation of the apple in order to grasp it with our hand? Once again, this would require an eye-centric encoding of the apple's location to be transformed into a frame of reference suitable for a motor action. One possible solution might be to have both, the visual representation of the object and that of the effector in a common frame of reference. If the object is described relative to the head, and the effector (the arm) would have the same reference, reaching for that object would mean placing the arm to the same coordinates as that of the object. Alternatively, initial eye centered representation of the object could be used to define the object's location in the effector's coordinate system. Appropriate interaction between not only the retinal representation of the object and the eyes' orientation in the head is then required, but also the orientation signals of the head and the arm with respect to the body.

head-centric representation

Avoiding collision with objects while moving through the environment requires an accurate representation of the approaching objects. We must be able to judge whether they are going to hit or pass by the head. The importance of an accurate and fast encoding of the approaching object's location, particularly if it is potentially harmful, is obvious. This is even more true for objects that are in close proximity, or for objects that we want to bring to a certain location on the face. Therefore, a head-centric representation for the objects would be very convenient. To taste the apple, we have to bring it to the mouth. For an accurate action we have to know where the apple is located relative to the mouth, and how it is moving with respect to the mouth, while bringing it to the face.

Evidence for the existence of head centric representations comes from behavioral and neurophysiological studies (Bremmer et al. 2001; Goltz et al. 2001; Duhamel et al. 1997). Some classes of parietal cells have receptive fields that do not change when eye orientation changes. Such cells code the object's location in a head-centric reference frame (Figure 1). But, how is a head-centric representation created?

One possibility is using eye-in-head position signals to transform an eye-centric representation into a head-centric reference frame. Signals of eye-orientation exist in form of extraretinal signals and are available to the visual system. Following an older notion by Helmholtz, von Holst (1950) proposed the use of the copy of a motor command to the eyes, *efference copy*, by the visual system. To build a head centric representation of objects the retinal representation must be combined with the signals of the eyes' orientation in the head. One such interaction is known to result in an *eye position gain field*, which is the modulation of neuronal activity by eye-in-head position. A gain-modulated, eye-centered representation might be a common mechanism to take into account eye position signals (Duhamel et al. 1997) or head or body position signals (Zipser & Andersen 1988), to transform to various reference frames.

Another possible mechanism is the so-called retinal updating. Contrary to a head-centric representation, visual space remains encoded in retino-centric frame of reference. However, this retinotopic representational map is dynamic, as every shift

of an object's retinal image as a result of an eye movement causes the receptive field of each neuron to also move.

Retinal updating is known to be involved for the encoding of a distant object's location for goal-directed arm movements (Henriques et al. 1998). It is not yet clear, however, whether the location of proximate objects is updated in a retino-centric frame of reference or transformed to a head-centric representation.

Most of the time movement is not limited to our eyes, we move our head and the body, as we walk through the environment. When we move forward, an expanding pattern occurs on the retinae. Although this pattern does not necessarily have to contain an explicit center of expansion (an object), people have no difficulties indicating it (e.g. van den Berg 1996). The centre of expansion is the point we are moving to. Its accurate representation is useful for navigation. As this center in a way resembles an object approaching the head, the question arises how the brain encodes its location and whether the representation of this locus of expansion is transformed in the same way as for approaching objects.

Posterior Parietal Cortex

Posterior parietal cortex is thought to be central to computations underlying coordinate transformations (Andersen & Buneo 1997). It contains many cells where information from different sensory inputs converge. *Ventral intraparietal area* (VIP, Figure 2) within the parietal cortex contains neurons responsive mostly to visual stimuli, but some are bimodal, with both visual and tactile receptive fields. These receptive fields match in size and location. This is revealed by their vigorous response to stimuli approaching the location on the face with corresponding tactile receptive field (where the trajectory of the visual stimulus is directed to; Cooke 2003; Duhamel et al. 1998). So, area VIP might in particular be involved when we take the apple and bring it to the mouth. Although there are several groups of neurons with receptive fields ranging from purely retino-centric to entirely head-centric, bimodal neurons with gaze-independent receptive fields and corresponding tactile receptive fields are prevalent (Duhamel et al. 1997), which means that the azimuth and elevation of a visual stimulus is encoded (at least) relative to the head. In this sense, the activity of visual neurons in VIP likely contributes to multisensory stimulus encoding and multiple spatial representations.

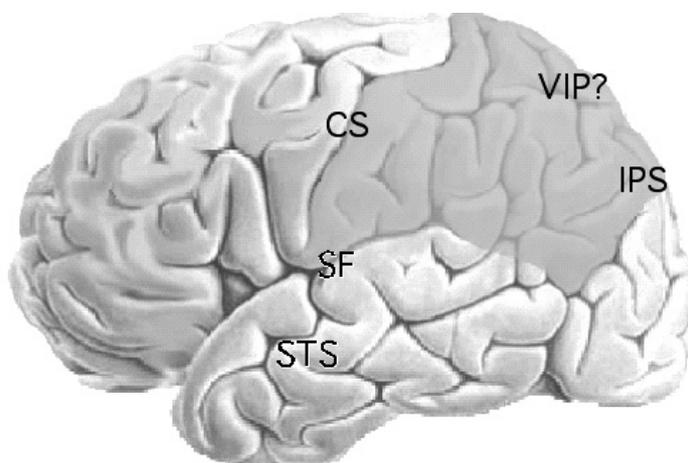


Figure 2. Parietal lobule
IPS intraparietal sulcus
VIP ventral intraparietal area
CS central sulcus
SF Sylvian fissure
STS superior temporal sulcus

far-near space dissociation

As the distance from the body increases, the response of some of the VIP cells decreases. Representations in VIP might be involved in representation of space *near* the body (Duhamel, Colby, Goldberg, 1998) and guidance of movements in *near* space (Bremmer et al 2002). A number of neurophysiological studies have shown this pattern of activity, also outside the parietal cortex. Uka et al 2000 observed “near” and “far” cells in the inferior temporal cortex of the monkey. This dissociation manifests itself also in some neurological disorders; in neglect, stimuli near the body are ignored, while there is a normal response to distant objects (Cowey et al 1994, in Colby & Goldberg 1999). Some neurological patients perform poor on a line bisection task when it is executed in near peripersonal space, but not when stimuli are positioned in extrapersonal space (Halligan & Marshall 1991).

Target distance is known to affect visual responsiveness in several classes of parietal cells (Colby and Goldberg 1999). A head centric representation might be advantageous in response to objects in close proximity of the head. Could it be that the frame of reference is different dependent on the distance of visual stimuli in the environment relative to the head and that the visual stimuli near the head are coded in head centric coordinates?

disorders following a damage to PPC

Posterior parietal cortex plays an important role in construction of spatial representations in different reference frames. Conversely, the disruption of its functions can lead to various disorders. As already indicated in the previous section, a variety of transformation deficits have been observed in patients with damage in the parietal region. An illustration is mirror agnosia that is a very common disorder in case of parietal damage (Ramachandran 1997). Patients with *mirror agnosia* are unable to learn that the mirror-image of an object is not actually there, and continuously try to grasp it. The sensorimotor transformation disorders reveal the prominent role of the parietal cortex as a sensorimotor interface.

The consequences of brain damage in this area lead also to serious behavioral problems such as *neglect*. In this disorder the patients tend to ignore objects in the contralesional half-space, and have difficulties making arm-movements toward visual, auditory or somatosensory stimuli. For example if a neglect patient was asked to pick up an apple lying on the left side of the table, the patient would not be able to do so, because the patient is completely unaware of it. One important characteristic of neglect is that it can occur in all sensory modalities. Rizzolatti and Berti (1990) conclude that neglect is essentially a representational deficit rather than purely due to attentional disturbances that indeed may aggravate the syndrome, which again accentuates the importance of the posterior parietal cortex for space-representations.

Since parietal cortex plays an important role in representing position of objects, the disturbance of its functions can also lead to inability to localize objects accurately. Bisiach et al. (1999) found that patients with parietal damage show erroneous pointing performance, for example. In such *optic ataxia*, patients are unable to accurately direct their eyes or arms toward the target. Damage to certain areas in parietal cortex also compromises grasping behavior (Binkofski et al 1998).

Outline of this thesis

We investigated the human ability to estimate the location of static or moving visual objects in space near the head. Beside the accuracy of the localization of visual stimuli, we were also interested to find out in what reference frame the objects in near head space are represented. This was investigated by a task in which the subjects judged the remembered location of an object after an eye movement. If the object's location is remembered relative to the head, then the judgment should not change in accuracy, irrespective of eye movements. If, however, its location is described relative to the retina, this representation must be updated to compensate for each eye movement. Consequently, in this case we should observe errors associated with the retinal updating mechanism, as found before for distant targets (Henriques, 1998). In this way we can test whether a retinal updating mechanism or a transformation to a head centric map is used to represent the location for an nearby object. In *chapter 2* we describe the study of the representation mechanisms in near-head space and also try to answer the question if localization of the centre of an expanding motion pattern is treated in the same way as localization of single point targets.

When looking at an eccentric object the eyes not only change their horizontal and vertical orientation. They also lawfully rotate around the lines of sight. Rotations of the eye about the line of sight change horizontal and vertical direction from the retina toward all objects in the environment, that are not on the fovea. *Chapter 3* concentrates on compensation for the eye's torsion required to correctly perceive visual directions relative to the head. Moreover, the accuracy of the perception of an object's location relative to the plane of regard is investigated and whether the visual system compensates for torsion when such judgment must be made.

In *chapter 4* we further elaborate on the availability of eye-in-head signals in the visual system. To create a correct representation of objects in head-centric coordinates that is based on object's location with respect to the plane of regard, the orientation of the plane of regard relative to the head is also required. In this chapter we describe a study that examined people's ability to localize the plane of regard in space. Per definition, the plane of regard contains the two lines of sight that intersect at the fixated object. The orientation of the plane of regard is dependent solely on eye-elevation. Hence, if the eye-elevation signals are available, the judgment of its orientation might also be possible.

There is vast evidence from everyday life that an accurate judgment of moving objects relative to ourselves is possible. People catch balls, drive cars with a high speed effectively avoiding collisions, all that seemingly without a large effort. The question we raise in the last chapter is how accurate can we estimate where an approaching object is going to hit the head. Our approach is twofold: We compare a pure perceptual judgment with a motor task, where the location of impact must be indicated by a pointing movement towards it. *Chapter 5* is dedicated to such an analysis of judgments.

Reference

- Andersen RA, Snyder LH, Bradley DC, Xing J (1997) Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annual review of Neuroscience* 20: 303-330
- van den Berg AV (1996) Judgments of heading. *Vision Research* 36(15): 2337-2350
- Berti A, Frassinetti F (2000) When far becomes near: Remapping of space by tool use. *Journal of Cognitive Neuroscience* 12: 415-420
- Binkofski F, Dohle C, Posse S, Stephan KM, Hefter H, Seitz RJ, Freund H-J (1998) Human anterior intraparietal area subserves prehension. A combined lesion and functional MRI activation study. *Neurology* 50: 1253-1259
- Bisiach E, Ricci R, Berruti G, Genero R, Pepi R, Fumelli T (1999) Two-dimensional distortion space representation in unilateral neglect: perceptual and response-related factors. *Neuropsychologia* 37: 1491-1498
- Bock O (1986) Contribution of retinal versus extraretinal signals towards visual localisation in goal-directed movements. *Experimental Brain Research* 64: 476-482
- Bremmer F, Schlack A, Shah NJ, Zafiris O, Kubischik M, Hoffmann K, Zilles K, Fink GR (2001) Polymodal motion processing in posterior parietal and premotor cortex: a human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron* 29(1): 287-96
- Calvert GA, Thesen T (2004) Multisensory integration: methodological approaches and emerging principles in the human brain. *Journal of Physiology Paris* 98: 191-205
- Cohen YE, Andersen RA (2002) A common reference frame for movement plans in the posterior parietal cortex. *Nature Reviews Neuroscience* 3: 553-562
- Cohen YE, Knudsen EL (1999) maps versus clusters: different representations of auditory space in the midbrain and forebrain. *Trends in Neurosciences* 22: 128-135
- Colby LC, Goldberg ME (1999) Space and attention in prietal cortex. *Annual Review of Neuroscience* 22:319-49
- Collewijn H, van der Steen J, Ferman L, Jansen TC (1985) Human ocular counterroll: assessment of static and dynamic properties from electromagnetic scleral coil recordings. *Experimental Brain Research* 59: 185-196
- Cooke DF, Taylor CSR, Moore T, Graziano MSA (2003) Complex movements evoked by microstimulation of he ventral intraparietal area. *Proceedings of the National Academy of the Sciences of the United States of America* 100(10): 6163-8
- Duhamel JR, Bremmer F, BenHamed S, Graf W (1997) Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature* 389: 845-848
- Duhamel JR, Colby CL, Goldberg ME (1998) Ventral intraparietal area of the macaque: Congruent visual and somatic response properties. *Journal of Neurophysiology* 79: 126-136
- Enright JT (1995) The non-visual impact of eye orientation on eye-hand coordination. *Vision Research* 35(11):1611-1618
- Falchier A, Clavagnier S, Barone P, Kennedy H (2002) Anatomical evidence of multimodal integration in primate striate cortex. *Journal of Neuroscience* 22(13): 5749-5759
- Fetter, M., Haslwanter, T., Misslisch, H., & Tweed, D. (1997). *Three-dimensional kinematics of eye, head and limb movements*. Amsterdam: Harwood Academic Publishers.

- Freund H-J (2001) The parietal lobe as a sensorimotor Interface: A perspective from clinical and neuroimaging data. *NeuroImage* 14: 142-146
- Gårding J, Porrill J, Mayhew JEW, Frisby JP (1995) Stereopsis, vertical disparity and relief transformations. *Vision Research* 35(5):703-722
- Gentilucci M, Roy AC, Stefanini S (2004) Grasping an object naturally or with a tool: are these tasks guided by a common motor representation? *Experimental Brain Research* 157: 496-506
- Graziano MSA, Gross CG (1998) Spatial maps for the control of movement. *Current Opinion in Neurobiology* 8: 195-201
- Halligan PW, Marshall JC (1991) Spatial compression in visual neglect: a case study. *Cortex* 27: 623-629
- Henriques DYP, Klier ME, Smith MA, Lowy D, Crawford JD (1998) Gaze centered remapping of remembered visual space in an open-loop pointing task. *Journal of Neuroscience* 18:1583-1594
- Iriki A, Tanaka M, Iwamura Y (1996) Coding of modified body schema during tool use by macaque postcentral neurons. *Neuroreport* 7(14): 2325-30
- Kitigawa N, Ichihara S (2002) Hearing visual motion in depth. *Nature* 416: 172-174
- Maravita A, Iriki A (2004) Tools for the body schema. *Trends in Cognitive Sciences* 8(2): 79-86
- Meredith M.A, Nemitz JW, Stein BJ (1987) Determinants of multisensory integration in superior colliculus neurons. I. Temporal factors. *Journal of Neuroscience* 7: 215–3229
- Mayhew JEW, Longuet-Higgins HC (1982) A computational model of binocular depth perception. *Nature* 297:376-378
- Niemeier M, Karnath H-O (2003) Stimulus-driven and voluntary saccades are coded in different coordinate systems. *Current Biology* 13: 585-589
- Ramachandran VS, Altschuler EL, Hillyer S (1997) Mirror agnosia. *Proceedings of the Royal Society of London series B: Biological Sciences* 264: 645-647
- Rine R, Skavenski AA (1997) Extraretinal eye position signals determine perceived target location when they conflict with visual cues. *Vision Research* 37(6):775-787
- Rizzolatti G, Berti A (1990) Neglect as a neural representation deficit. *Review of Neurology Paris* 146: 626-634
- Shams L, Kamitani Y, Shimojo S (2002) Visual illusion induced by sound. *Brain Res Cogn Brain Res.* 14(1):147-52
- Sparks DL, Mays LE (1990) Signal transformations required for the generation of saccadic eye movements. *Annual Review of Neuroscience* 13: 309-36
- Uka T, Tanaka H, Yoshiyama K, Kato M, Fujita I (2000) Disparity Selectivity of Neurons in Monkey Inferior Temporal Cortex. *Journal of Physiology* 84: 120-132
- Wallace MT, Roberson GE, Hairston WD, Stein BE, Vaughan JW, Schirillo JA (2004) Unifying multisensory signals across time and space. *Experimental Brain Research* 158: 252-258
- Zipser D, Andersen RA (1988) A back-propagation programmed network that stimulates response properties of a subset of posterior parietal neurons. *Nature* 331: 679-684

Representation of heading direction in far and near head space¹



¹ *adapted from:* Poljac E, van den Berg AV (2003). Representation of heading direction in far and near-head space. *Experimental Brain Research* 151:501-513

Abstract

Manipulation of objects around the head requires an accurate and stable internal representation of their locations in space, also during movements such as that of the eye or head. For far space, the representation of visual stimuli for goal-directed arm movements relies on retinal updating, if eye-movements are involved. Recent neurophysiological studies led us to infer that a transformation of visual space from retinocentric to a head centric representation may be involved for visual objects in close proximity of the head. The first aim of this study was to investigate if there is indeed such a representation for remembered visual targets for goal directed arm movements. Subjects had to point towards an initially foveated central target after an intervening saccade. Subjects made errors that reflect a bias in the visuo-motor transformation that depends on eye displacement rather than any head-centred variable. The second issue addressed was if pointing towards the centre of a wide field expanding motion pattern involves a retinal updating mechanism or a transformation to a head centric map and if that process is distance dependent. The same pattern of pointing errors in relation to the gaze displacement was found independent of depth. We conclude that for goal directed arm movements, representation of the remembered visual targets is updated in a retinal frame, a mechanism that is actively used irrespective of target distance, stimulus characteristics or the requirements of the task.

Introduction

Manipulating objects around the head is an activity that requires care and competence. Shaving one's beard and bringing a parcel of food to one's mouth are typical examples of activities that are under visual control and involve skilled movements around the head. Initially, visual stimulus location is encoded in a retinal frame, and preserved in this form in several different retinotopic cortical maps. For directed arm movements, motor commands must at some point refer to the joints of the arm. It has been argued that an internal representation of stimulus location has to be built from the visual signals to achieve appropriate motor commands for movement towards a target (Flanders et al. 1992). If so, it would seem essential for both perception and motor control to use a coherent internal reference frame for visuospatial representation of the environment and maintenance of the integrity of this frame during eye movements. Because the head's dimensions set boundaries on hand movements around it, it would seem that a head centric representations of the visual environment might be involved. How could such a representation arise?

The transformation from retinal coordinates into a head centric representation requires appropriate interaction between the retinal signal of the object-position relative to the eye and an efference copy of the eye-in-head position. Zipser and Andersen (1988) suggested that the multiplicative interaction between visual and eye-orientation signals serves as a first step for such a transformation towards a head centric visual representations of the environment. Such an interaction results in a so called *eye position gain field* which means that the retinal receptive field (RF) is maintained but the cell's response to the visual stimulus within the RF is modulated by the eye position. Such response properties are ubiquitous in the extra-striate cortex (Salinas and Thier 2000). Note, however, that a map of such cells still carries a retinotopic code. Several different proposals have been made to build a head centric representation out of such a gain-modulated representation (Zipser and Andersen 1988; Olshausen et al. 1995; Beintema and van den Berg 1998).

Recent neurophysiological studies in the monkey have identified an area (VIP) in the posterior parietal cortex that contains cells with head centric receptive fields (Duhamel et al. 1997). Although the receptive fields are wide and often largely overlapping for different cells, an array of such cells provide a head centric code of the visual stimulus that can be much more precise than suggested by the diameter of the receptive field. To what extent the representation in VIP is used for the control of hand movement is unknown. A human homologue of monkey VIP has been found in fMRI studies (Bremmer et al. 2001; Goltz et al. 2001). There is also evidence that pointing related activity in human rostral IPS was modulated by eye position in the orbit suggesting that this region may be involved in transforming the visual signal for pointing to a non-retinotopic representation (DeSouza et al. 2000). Hence, the neural machinery to base movement control on a head-centric visual map of space is available in principle.

There is, however, an alternate strategy for visual control of movement: *retinal updating*. Visual signals remain in essentially a retino-centric format, but for motor control the retina-based signals are updated to take the displacements of the eye into account (Colby and Goldberg 1999). For example, to point towards the mid-sagittal

plane of the head, while looking to the left or right one does not necessarily require a head centric map of visual space. If the retinal locus of straight ahead is known for every possible eye-position one can perform this task. Provided the finger is visible one merely needs to align the finger with the retinal location of the straight-ahead. Thus, one only needs to update this location for every eye movement. Recent behavioural experiments have suggested that remembered visual targets for goal directed arm movements, such as pointing, are encoded in a retinal frame (Henriques et al. 1998; Batista et al. 1999). This form of representation is maintained, with certain well-known distortions in the retinotopic maps of the various brain areas. In support of this view, the current position of the hand appears to be coded in an eye-centred frame (Batista et al. 1999; Buneo et al. 2002).

One of the distortions of the retinotopic representation of visual stimuli mentioned above is the retinal eccentricity overestimation (Bock 1986; Henriques et al. 1998), when gaze direction deviates from target direction so that extra-foveal retinal information is involved. Pointing towards objects aligned with the current direction of gaze is something human subjects can do accurately (Flanders et al. 1992). However, when pointing to a target after an intervening eye-movement human subjects tended to overestimate retinal eccentricity of the target, even if the target was viewed only foveally before the eyes moved (Henriques, 1998), leading to the conclusion that this effect is a result of misinterpretation of target location in a retinal frame rather than the consequence of eye position relative to the head.

Thus, pointing experiments (Bock 1986; Henriques et al. 1998) seem to support the retinal updating rather than the transformation scheme. The neurophysiological studies in the monkey, on the other hand, could support a transformation theory. The apparent conflict between those two collections of data is less sharp when a distinction is made between near-head space and distant spatial tasks. The clinical and behavioural studies used pointing tasks to more distant targets. The neurophysiological results, on the other hand, refer to stimuli that specify the approach of, or near hits of a target with the head.

Target distance is known to affect visual responsiveness in several classes of parietal cells (Colby and Goldberg 1999). Could it be that the frame of reference is different dependent on the distance of visual stimuli in the environment relative to the head and that the visual stimuli near the head are coded in head centric coordinates? A head centric representation might be advantageous to respond to objects in close proximity of the head. To see one's daddy's hand and spoon approach relative to one's hand may tip the balance between porridge in the mouth and a mess on the table.

The first aim of this study is, then, to investigate if there is a head centric representation of remembered visual targets for goal directed arm movements, such as pointing, in the near-head space. We examine the hypothesis that transformation to a head centric representation of visual space may be limited to visual objects in close proximity of the head, whereas more distant visual space is represented through a basically retinal code that is updated with eye movement signals.

In addition, we wished to move beyond the direction representation of static visual stimuli and their frame of reference. Moving stimuli around the head can hit us and cause injury. Equally important then is the accurate representation and estimation of direction of moving, for example approaching, stimuli. This requires

competence in estimating the direction of approach or conversely the direction of motion of our head relative to the object or environment (heading judgement). Movement of the head through space produces optic flow with a focus of expansion in the direction of translation (Gibson 1966). Humans can perceive this direction of heading with typical accuracy of about 1 degree at walking speeds over ground (Warren et al. 1988). Performance is not degraded if visual structure is absent at the centre and there is surprisingly little effect of noise (Warren et al. 1991; van den Berg 1992) The accuracy is high (< 1 degree) if the centre of flow is presented in the fovea with a sharp drop off to about 1 degree right outside the fovea. For larger eccentricity the heading discrimination threshold rises much less steep (Crowell et al. 1993). Because the latter data were collected with straight ahead fixation one cannot determine whether the eccentricity dependence is head or retino-centric. Nevertheless one can conclude that the heading direction is based on spatial motion integration of a large part of the visual scene and that it does not require visual structure at the heading direction. This is distinct from the coding of small target location, through small receptive fields that must contain visual structure. We wondered then, whether pointing towards the heading direction involves the retinal updating mechanism or a transformation to a head centric map and if that process is distance dependent.

Materials and methods

Subjects

Eight subjects participated in the experiment. Two of them did not take part in all six conditions. One subject (EP) was aware of the design and purpose of the experiments, the rest of the subjects were naïve. This study has been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. Participation was voluntary and all the subjects gave their informed consent prior to their inclusion into the study.

Apparatus

Subjects were seated in complete darkness and looked at a projection screen located at approximately 110 cm in front of the subject's eyes (Figure 1). Images were generated by a Macintosh 8500 computer with Graphics acceleration (Formac) and backprojected on the screen through a video-projector (InFocus). To reduce the amount of projected light a neutral density filter was placed in the light path of the video-projector. Covers carefully masked any stray light from the projector. Hence no visible structure was present apart from the light projected on the screen.

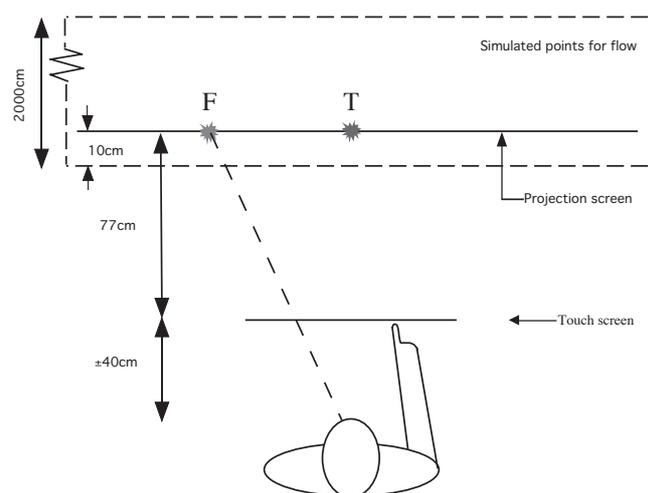


Figure 1. The layout for experiment 1. Subjects fixated target F and pointed towards target T (or towards themselves from T in experiment 2, see Figure 2.) when both targets were extinguished. The pointing response was registered through a touch screen. Presentation was dichoptic. Targets at 110 cm simulated distance or visual flow of dots between 100 cm and 2000 cm simulated distances from the eyes, were shown.

A transparent touch screen was placed on a distance of 77 cm in front of the projection screen, about 40 cm from the subjects. The touch screen was used for the recording of the right index-finger position. The subject's head was stabilized, by means of a dental bite-board that was mounted on the table and adjustable in height. Eye orientations and movements were measured using a camera-based measurement of the eye's pupil orientation (SMI EyeLink- inc. Teltow, Germany). When ocular fixation criteria, as described below, were not met, a trial was discarded online and repeated. The subjects wore a red filter in front of the left eye and a green filter in front of the right eye. Presentation of red and green images resulted in independent stimulation of left and right eyes (dichoptic stimulation). Either image was updated every frame. Precise location of each eye in front of the screen was determined before the session started, using the triangulation procedure (van den Berg 1996). This was required to present the correct image of the scene for each eye as seen from that eye's perspective. The centre of the projection of the image for each eye was aligned vertically and horizontally with that eye. In this way a 3D scene in stereoscopic perspective was created.

The stimuli consisted of stereo images of optic flow patterns or of single points. The flow stimuli consisted of 512 dots, which were arranged in a cloud. The simulated world extended in depth from 1 to 20 m in front of the subject's eyes in the far condition and from 0.1 to 2 m in the near condition (see Experiment 3). Self-motion was simulated by fixed displacement of all the dots of the simulated scene and recomputing the perspective projection of the dots on the screen for each stimulus frame. The dots moved towards the subject causing an expanding pattern of motion on the screen. Subjects perceived heading towards the centre of expansion. The simulated speed of forward self motion was 4000 mm/sec in the far condition and 400 mm/s in the near condition. The velocity of the dots on the screen was in this way kept similar for both distances. Each dot had a fixed diameter of 0.5 degrees. The dots did not scale with distance. The constant magnitude is at odds with real world approach of a scene but the constant size of the dots provided only a minor conflict cue and did not interfere with the heading percept. The points were randomly located in the viewing box and the majority of the points were visible throughout the motion sequence. The horizontal and vertical boundaries of the simulated world remained invisible. The distance of the fixation points relative to the subjects was 110 cm in the far condition and 15 cm in the near condition for all stimuli kinds.

Procedure

The procedure was inspired by a previous experiment (Henriques et al. 1998). Subjects were asked to point as accurately as possible toward a point target straight in front of the head while maintaining their fixation toward one of the fixation points. Their heads were always oriented towards the centre of the projection screen. The arm movement was made when all the stimuli disappeared from the projection screen and therefore in the complete absence of visual cues. Straight ahead was defined as the direction perpendicular to the interocular axis, and intersecting that axis halfway between the eyes.

Calibration

Each paradigm started with a calibration procedure in which subjects pointed towards five possible target points, while fixating them. Only one target at a time was visible. Subjects had no other visual reference. The position and order of target point presentation was fixed for all calibrations: 30° left, 15° left, 0°, 15° right, 30° right, all relative to straight ahead. The subjects made five repeats for each target. When subjects touched the touch screen at a certain position, the coordinates of that position was saved in a file, as well as the eye position data. Pointing errors that we report later, are computed as the pointing position relative to the corresponding pointed position during calibration.

Experiment 1. Pointing away from the head: Distant targets or distant radial flow

Two experimental paradigms were used, a ‘static’ and ‘dynamic’. In the ‘static’ paradigm the eyes did not move during the trial and did not fixate the target. Subjects were asked to look continuously at a possibly eccentric fixation point. A trial was started by the subject through a key press, at which time the (eccentric) fixation point appeared. When 0.7 sec had passed after the initial mouse click, the central target point appeared for another 0.7 sec and then both lights disappeared. Subjects subsequently pointed to the remembered location of the central target, while keeping gaze fixed at the location of the now absent fixation point. The subject’s pointing at the touch screen terminated the trial. Thus, subjects were asked to point toward a retinally peripheral, but craniotopically central, remembered target.

In the second, ‘dynamic’ paradigm, subjects looked initially at the central pointing target for 750 ms. The moment that target disappeared, the fixation target appeared at an eccentric location, and subjects were required to saccade towards it. 750 ms later the fixation stimulus disappeared, and subjects had to point toward the remembered position of the pointing target prior to the eye displacement. In this case the memory of the pointing target was created when the eye was looking at that target.

A mean value of the last ten eye-position samples before the fixation point disappeared was taken and compared with every new sample of the eye position during the remainder of the trial. If gaze eccentricity drifted to a value below 90% or above 110% of the value measured before the fixation point disappeared then the trial was rejected and repeated. We repeated each condition until ten ‘accepted’ trials were collected. Then the next fixation condition was tested. On average, ten percent of the trials had to be rejected and repeated because of inaccurate fixation.

We tested a wide range of fixation positions along the horizontal meridian. In addition we investigated the dynamic task with two additional pointing target positions: 15° left and 15° right. The order of fixation positions and targets in each experiment was identical: 30° left, 15° left, 0°, 15° right, 30° right, always with the same central target in static paradigm. Different order of presentation, 30° right to 30° left, did not affect the performance, as the results of a pilot study have shown. In the dynamic paradigm the order was 30° left, 15° left, 0°, 15° right, 30° right, with central target; 30° left, 15° left, 0°, 15° right, with target 15° left and finally 15° left, 0°, 15° right, 30° right, with the target positioned 15° right. This fixed order of presentation has been used because a random display of fixation positions in this dynamic condition proved to be almost impossible to do, causing a large increase in time needed for a proper fixation, as reported by subjects in a pilot session. The order of paradigms did not affect the performance, as we found in a pilot experiment.

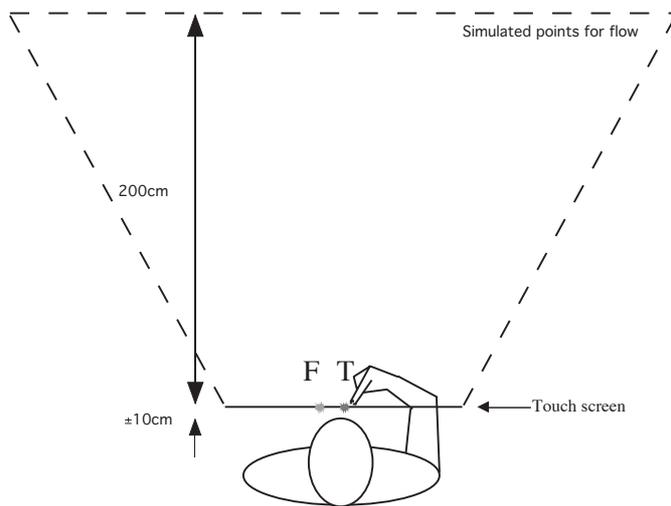


Figure 2. The arrangement for experiment 3. Nearby targets were presented dichoptically and projected on the touch screen. Point targets for fixation and pointing were simulated at the screen distance (about 10 cm in front of the eyes; this varied across subject). Angular position of the target was computed on the basis of precise localization of the eyes re. to the screen through a triangulation procedure. Dichoptic visual flow of dots between 10 cm and 200 cm simulated distances was shown. Subjects pointed towards themselves moving the index finger along a straight line through the target and the self.

Experiment 2. Pointing towards the head. Distant targets or distant flow

In the second experiment the touch screen was positioned very close (± 10 cm) to the bite board so subjects almost touched the screen with their nose (Figure 2). Again, the triangulation procedure (van den Berg 1996) was used to determine precise location of each eye in front of the screen. The touch screen was reversed in orientation because it was now placed between the subjects' head and his arm, so the subject touched the back of the screen.

The subject's task was to point with their index finger from the observed target point towards themselves (their ego-centre), touching the screen at the locus where the line, that connected the seen target point with their ego-centre, intersected the screen. During the calibration this same pointing task was performed while the target remained visible. All the paradigms, stimuli and the order of display were the same as in the first experiment.

Experiment 3. Pointing towards the head. Nearby targets or nearby flow

The whole procedure of the Experiment 2 was repeated, this time with the projection on the touch screen itself instead of using the distant projection screen. In this case the visual stimuli were projected very close to the subject's head, which avoids the conflict between accommodation and vergence for simulation of nearby targets.

All the three experiments were repeated with the target-point replaced by a radial flow pattern that was centred on the target point. In this case the subjects had to point towards the centre of expansion even though there was not a visible object to point to. The fixation points had the same characteristics as in the experiments without flow.

Experiment 4. Indicating visual direction without pointing

In a control experiment, we sought to eliminate the effect of sensorimotor distortions by using a paradigm that did not required sensorimotor transformation. We made a few modifications in the experimental setup. A computer screen was used (Sony 19" FD Trinitron CRT) instead of the video-projector, at a distance of approximately 30 cm in front of the subject's eyes. The touch screen was not used any more. The same set of target and fixation conditions was used in our two paradigms, static and dynamic, as in previous experiments. We excluded the trials

with eccentric target positions of the dynamic paradigms (15° left and 15° right). In other words, only trials with central target position were presented. Only dots are used as targets.

After a period of 200 ms subsequent to the disappearance of fixation point and the target, a mouse cursor appeared at a random position along the horizontal axis at eye level. We asked our subjects to reproduce the location of the previously presented target by repositioning the mouse cursor, while maintaining fixation towards the fixation point. For each subject we determined the variable error (SD = standard deviation) per fixation direction and the bias. Eye position was measured in the same way as in the pointing experiments to make sure that the subjects fixated correctly.

Then the procedure was repeated, but instead of the mouse cursor a test dot was presented. The position of this test dot varied randomly within the determined error range around the central target. There were five different positions of the test dot, 2 SD right or left of the target, 1 SD right or left, and a position identical to that of the target position. So, for each subject there was a specific range within the test dot was presented and this range (magnitude) could also vary for different fixation directions. The task the subjects had to do is to estimate for each trial if the test dot appeared on the right or left relative to the target. From these data the visual contribution to the pointing error was determined.

Results

Experiment 1. Pointing away from the head: Distant targets or distant flow

In the first experiment we tried to replicate the study by Henriques et al. (1998) to establish whether the use of a touch screen to measure the pointing response would affect the pointing errors. We added the new condition of pointing towards the perceived centre of flow to investigate if implied (centre of flow carries no visible target) and explicitly marked (the point target) visual directions cause the same type of pointing errors. Below we will use the phrases ‘explicit’ and ‘implicit’ targets as defined above.

Figure 3 shows the performance of pointing towards implicit and explicit targets for the static paradigm, averaged across subjects. In the static paradigm subjects pointed towards the remembered location of the briefly presented (central, relative to the head but usually eccentric on the retina) target, while keeping gaze fixed at the location of the extinguished fixation point.

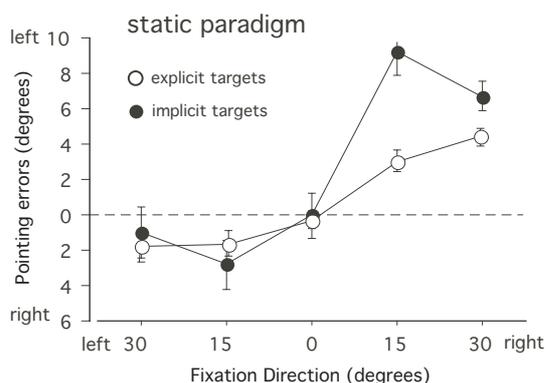


Figure 3. Results of Experiment 1. Pointing towards a remembered central target (T) with *static* fixation. Pointing error is averaged over 6 subjects (10 trials per subject). Error bars indicate ± 1 SE. Fixation to the left of T caused pointing errors to the right and v.v. This occurred for pointing towards single point targets and towards centres of flow (implicit targets).

Consistent with findings of Henriques et al. (1998), subjects pointed left of the central target when fixating right and vice versa. Statistical analysis (ANOVA) showed a significant effect ($p < 0.0001$, $F(4,50) = 27.268$) of fixation direction on pointing error, for all eccentric fixation directions (left and right), except for 30° left fixation and pointing towards the centre of the flow ($p = 0.4655$, error not significantly different from 0). The pointing errors differ significantly ($p < 0.0001$) between the most eccentric left and right fixation directions, 30° left and 30° right, in case of explicit stimuli.

There was considerable variability between the error magnitudes of individual subjects, as can be seen in Figure 4 (example subjects ErP, JD and JG), but no qualitative differences between the error patterns could be identified. There was no significant difference in magnitude of pointing errors between explicit and implicit targets, except for 15° right fixation ($p = 0.0014$). The latter causes the small interaction effect shown by the two way ANOVA ($p = 0.0486$, $F(4,50) = 2.578$).

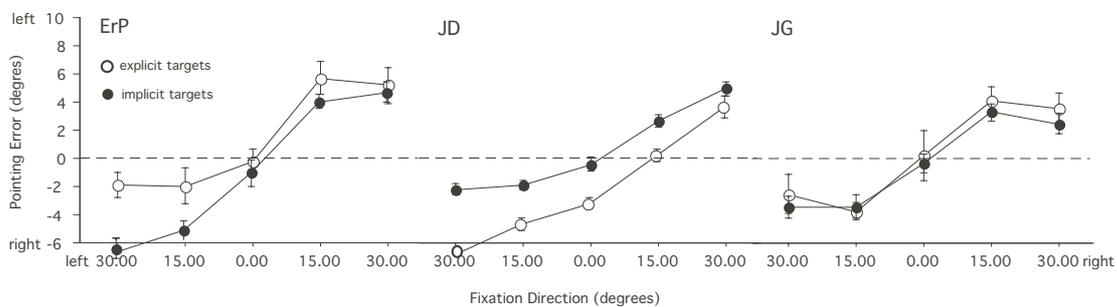


Figure 4. Individual differences in Experiment 1. Pointing towards a remembered central target with *dynamic* fixation, for three subjects. Error bars indicate ± 1 SE. Initial fixation is on the pointing target. The fixation direction in the figure denotes the fixation direction after the saccade away from the extinguished pointing target towards a flashed fixation target.

We investigated if subjects would show errors when pointing towards a remembered, foveally presented target, after that subject made an intervening saccade. Figure 5 shows the error diagrams for each of the three different targets (15° left, central and 15° right relative to the head) of this dynamic paradigm.

Qualitatively similar errors are made as in the static condition; subjects point left of the target when fixating to the right of it and vice versa. Significant pointing errors occur for all the three targets and all eccentric fixation conditions, with exception of 30° left fixation for the flow arising from the screen centre, for the 15° right target and for the central target (15° right target: mean pointing error -1.314° , $p = 0.1932$; central target: mean pointing error -0.323° , $p = 0.7478$). Also, subjects performed poorly when pointing towards the flow centre to the left (15 deg) when fixating in the same direction ($p < 0.0001$, mean pointing error -4.675°)

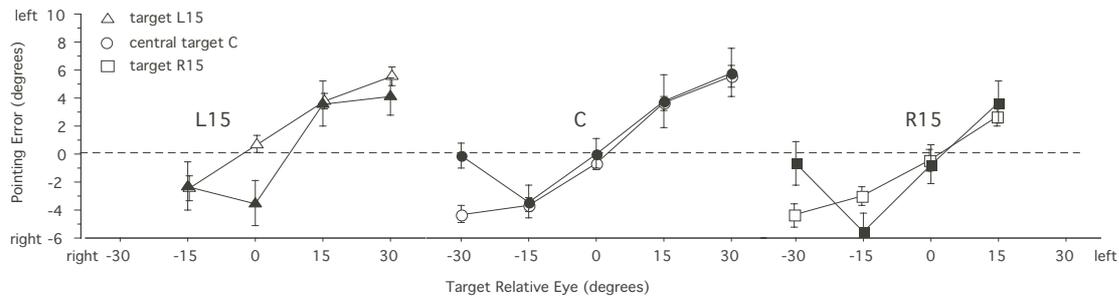


Figure 5. Three targets of Experiment 1. Pointing error as a function of the remembered target position relative to the fixation direction and target type for three different pointing targets (left: L15; central, straight ahead: C; right: R15). Fixation was dynamic. The data are pooled across subjects.

Subjects show very similar patterns of pointing errors in both paradigms, for explicit and for implicit targets. Both the static paradigm and the dynamic paradigm produced the characteristic pattern of eccentricity overestimation as a function of final fixation position.

In the same way, there were no significant differences between the error patterns of the three targets of the dynamic paradigm. When plotted as a function of gaze displacement relative to the target (Figure 6) the same error pattern occurs for all three target positions.

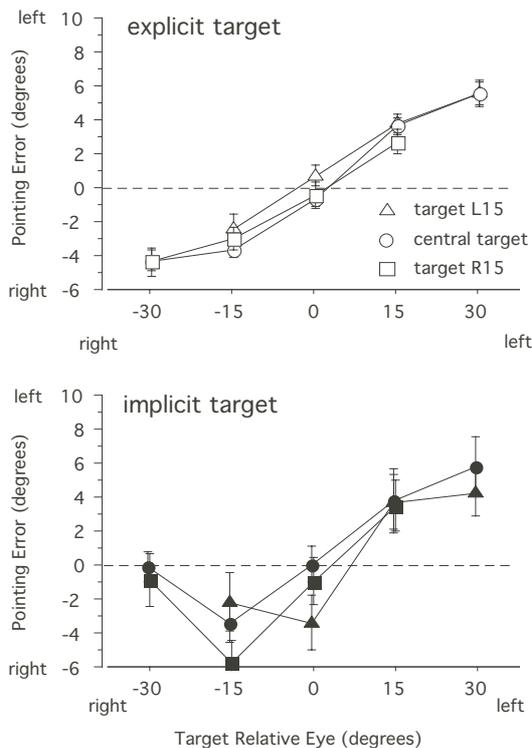


Figure 6. Implicit and explicit targets in Experiment 1. Pointing error as a function of the target position relative to the fixation direction and target location for two different target types. The data of panel c are rearranged to emphasize the similarity of the error function for different target locations if plotted against the remembered target location relative to the current fixation direction.

Experiment 2. Pointing towards the head. Distant targets or distant flow

In our second experiment the same set of stimuli was presented in our two paradigms, static and dynamic, but the subjects had a different task. The subjects were asked to point with their index finger from the observed target point towards themselves (their ego-centre), touching the screen at the locus where the line, that connected the seen target point with their ego-centre, intersected the screen.

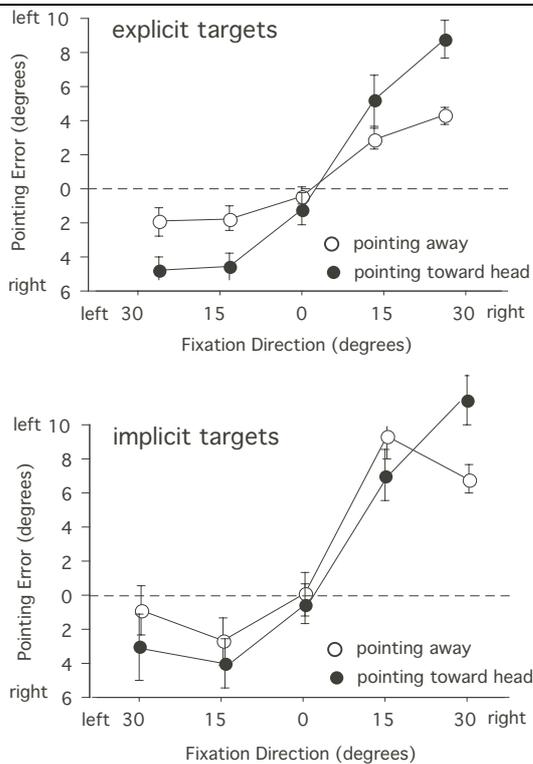


Figure 7. Pointing task effect. Pointing error for static fixation, pooled over all subjects. Data for pointing towards the head (Experiment 2) and pointing away (Experiment 1) are compared for single point targets in the dark (explicit targets) and for centre of flow (implicit). Flow and point targets were shown on the distant screen and simulated distant objects.

As can be seen in Figure 7, changing the task did not result in different performance of pointing toward explicit and implicit targets in the static paradigm. In this static paradigm, pointing toward implicit and explicit (retinally eccentric, central relative to the head) targets was again inaccurate. Averaged across subjects, it was similar to the results of our first experiment. Subjects tend to point left of the central target when fixating right, and vice versa. Even larger pointing errors for the eccentric fixation directions could be observed, relative to our first experiment, when subjects were pointing toward explicit targets. This was not the case for the implicit targets. In general, larger errors were made when subjects were fixating to the right relative to the target than to the left (for pointing toward the head).

When the target was foveally presented and subjects were asked to point after an intervening saccade (dynamic paradigm), they made an overestimation of the target eccentricity in all cases of the eccentric fixation directions. There was no significant difference between this second paradigm and our first, static paradigm, if a comparison is made for the central (To) target ($p=0.5029$).

Regardless of the target position relative to the head (15° left, central or 15° right), subjects, again, tend to overestimate the eccentricity of the target. In Figure 8 we see that the pattern and the magnitude of the pointing errors made in the second experiment is nearly the same as in the corresponding paradigms of our first experiment.

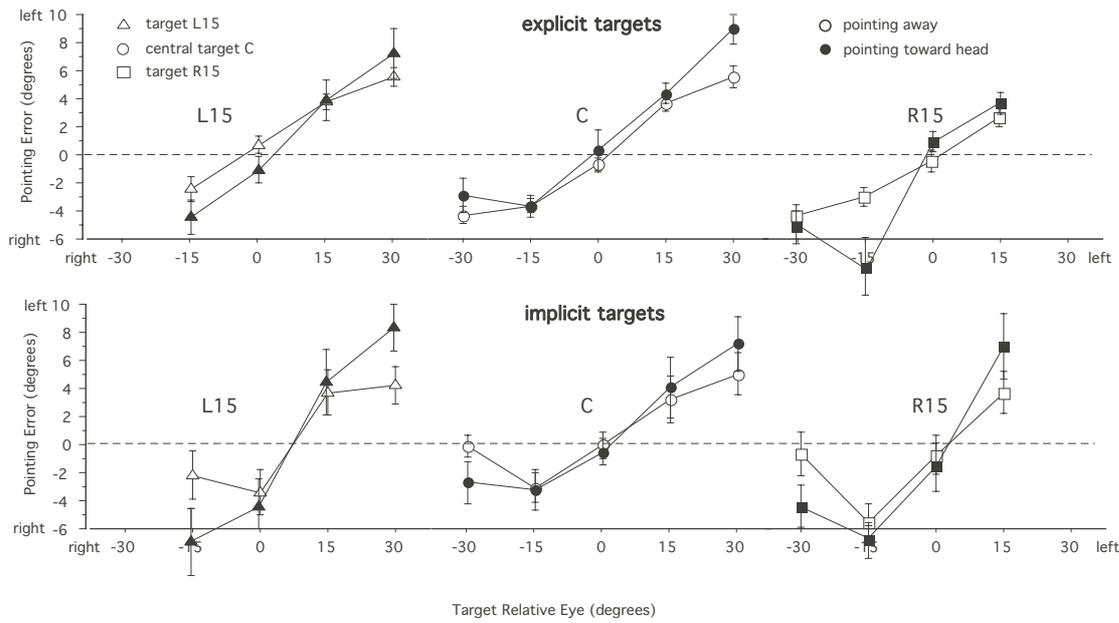


Figure 8. Pointing task effect, three targets and two target types. Pointing errors for dynamic fixation compared for the effect of the pointing task and target type. Data for three pointing targets are shown (L15, C, R15). See also legend of figure 5.

Also, when the three targets are compared to each other, like in the analysis of our first experiment, we see a similar eccentricity overestimation effect (Figure 9). This suggests that retinal displacement, rather than eye position, plays an important part as far as the pointing errors in our paradigms is concerned.

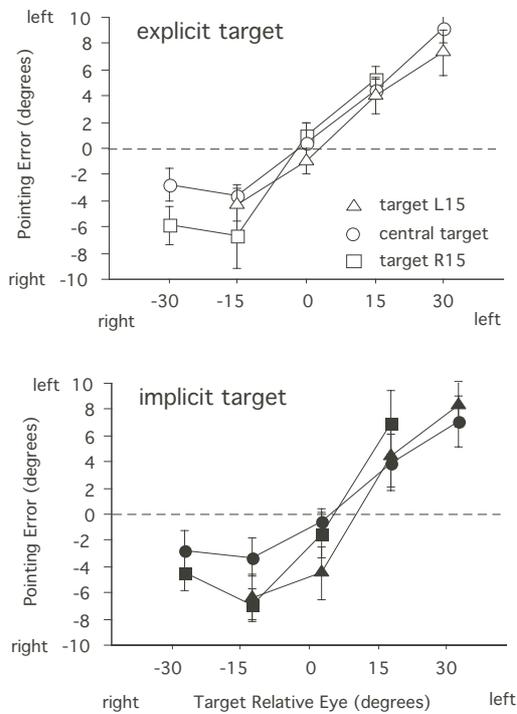


Figure 9. Pointing task effect. Pointing errors of Figure 9 compared for three different targets.

Experiment 3. Pointing towards the head. Nearby targets or nearby flow

The preceding results were consistent with the outcome in Henriques' experiments (predictions of the oculocentric model). As we stated in the introduction, distance of the presented visual stimuli seems to affect responsiveness in several classes of parietal cells. Could it be the case that the transformation of visual information from retina based to other reference frames (such as head centric frame) may be limited to certain depth ranges? In particular, could it be limited to visual targets near the head?

For this reason, we measured perceived direction of flashed targets at a distance of approximately 12 cm. The task that the subjects had to perform was the same as in our second experiment. Figure 10 illustrates the mean pointing orientation in the static paradigm of the third experiment (near-condition) compared to the performance of the same paradigm of the second experiment (far-condition) for both, explicit and implicit targets.

Although ANOVA shows a significant effect of the fixation direction ($p < 0.0001$, $F(4,50) = 10.753$), it is clear that this effect is much smaller if compared to our second experiment. Two of the subjects (ErP and JD, see Figure 11) seem to be able to point very accurately towards the explicit targets regardless in which direction relative to the target they are fixating. However, their performance in the dynamic paradigm is affected by the fixation direction. The rest of the subjects show less accurate pointing in both paradigms, with overestimation of eccentricity, although the magnitude of pointing errors is still much smaller than in the same paradigm of our second experiment (far condition).

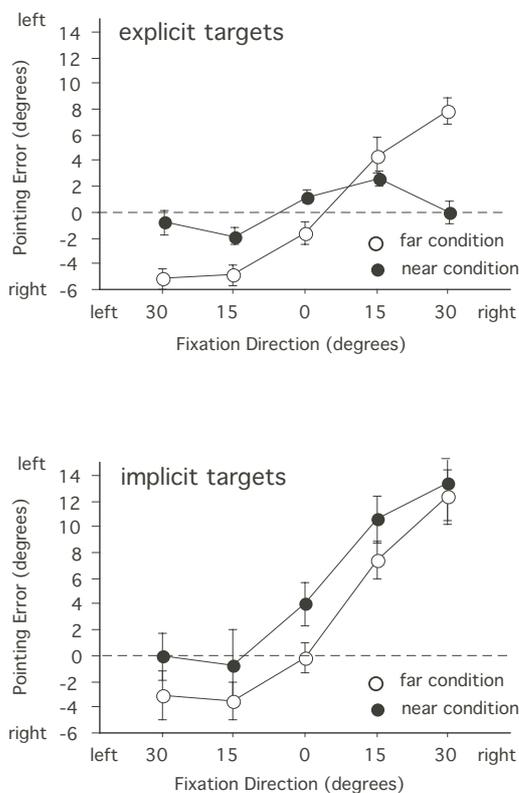


Figure 10. Target distance effect. The mean pointing orientation in the static fixation of Experiment 3 (near condition) compared to the performance of the same paradigm of the Experiment 2 (far condition) for both explicit and implicit targets. In the near condition, the stimuli were projected on the touch screen, very close to the subject's head. The pointing errors are smaller for the explicit targets in the near condition than in the far condition, but not for the implicit targets. The data are pooled across subjects.

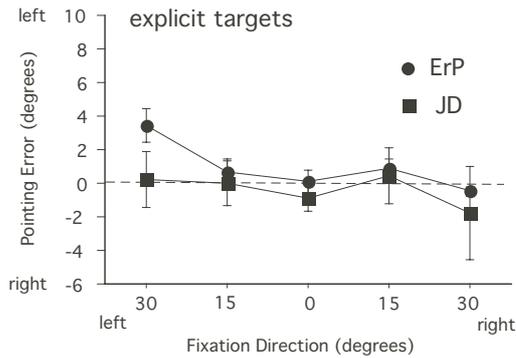


Figure 11. Accurate pointing in two subjects (ErP and JD). Two of the subjects (ErP and JD) point very accurately towards explicit targets in the static paradigm of the near condition.

For the implicit targets, changing the stimulus distance does not seem to affect the pointing behaviour, as can be seen from the pattern of pointing errors (Figure 10), which is qualitatively almost indistinguishable for the two conditions, far and near the head. But, subjects made large pointing errors when fixating to the right relative to the target and very small errors when fixating to the left (30° left: $p=0.2730$, 15° left: $p=0.2589$). Moreover, subjects were inaccurate when pointing to the central target and fixating in the same direction (mean pointing error 4.225° , $p<0.0001$). The pointing error curve for the near condition is shifted to the left compared to the far-condition curve.

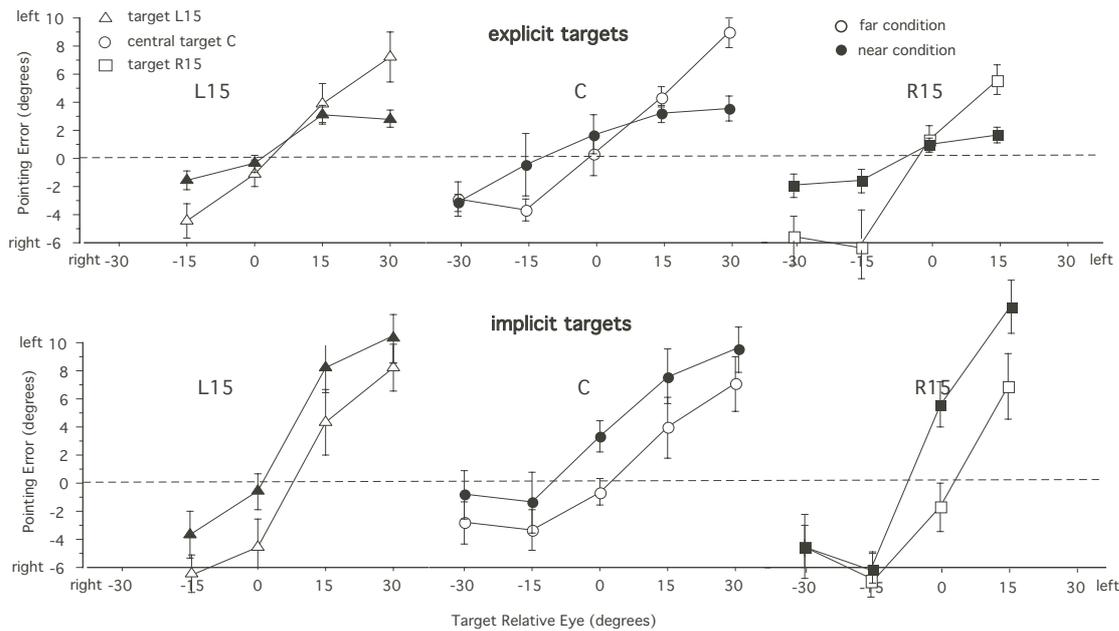


Figure 12. Target distance effect. Pointing errors compared for the effect of target distance for dynamic fixation. Data for three pointing targets (L15, C, R15) for both, explicit and implicit targets are shown. Qualitatively similar errors are made for eccentric fixation positions regardless of target position relative to the head. The pointing errors for implicit targets are very similar for the two experiments. The data are pooled across subjects.

The dynamic paradigm produces, again, the patterns similar to those seen in static paradigm (Figure 12). When pointing toward a remembered, foveally presented target after an intervening saccade (dynamic paradigm) qualitatively similar errors are made for eccentric fixation positions, regardless of target position relative to the head. For the explicit targets (dot-targets) the magnitude of pointing errors is smaller than in the same paradigm of our second experiment, far-condition ($p<0.0001$),

except for the fixation 15° left ($p=0.059$). As to the implicit targets, the pointing errors are very similar for the two experiments. For all implicit target-positions applies that the subject are making larger errors when fixating right of the target.

Similar effects occur when the three targets of the dynamic condition are compared to each other. Here, we observe a much larger variability for pointing toward implicit targets. Still, there is a strong correspondence between the patterns of errors (Figure 13).

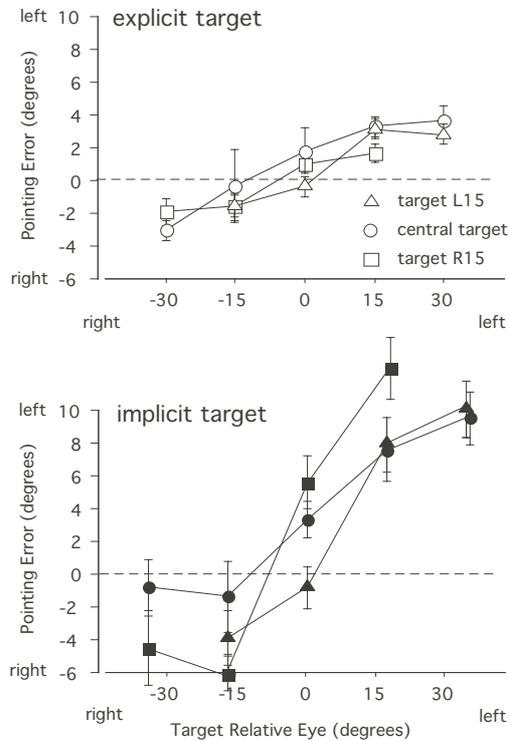


Figure 13. Three targets compared. Pointing errors of Experiment 3, compared for three different targets.

Experiment 4. Indicating visual direction without pointing

Our results so far show that even for nearby targets a majority of our subjects show pointing errors not unlike these reported before. This suggests that the visuo-motor transformation for pointing does not profit from the head centric representation of nearby visual targets. This raises the question if the visual representation of nearby targets shows similar errors. Thus we investigated localisation bias in a task that relies on pure visual judgements.

First, we determined the error range of the perception of the visual stimuli by asking our subjects to reproduce the location of the previously presented target by repositioning the mouse cursor, while maintaining their fixation toward the fixation point. Figure 14a shows the performance of pointing with the mouse cursor. Averaged across subjects, the pointing errors towards the remembered location of briefly presented central targets are very small in both, the static and the dynamic paradigm. ANOVA does not show a significant effect of the fixation direction. In other words, subjects are very accurate in positioning the mouse cursor in the direction of the remembered target.

The second and in fact the main task subjects had to do is to decide in each trial if the test dot appeared on the right or on the left relative to the target. The same set of stimuli was presented in our two paradigms, static and dynamic. The bias in their responses was measured as it depends on the fixation direction. In Figure

14b the mean bias, averaged across subjects, is plotted for five fixation directions. There is no significant effect of the fixation direction. This is true for both of our paradigms (static: $p=0.0952$; dynamic: $p=0.2455$).

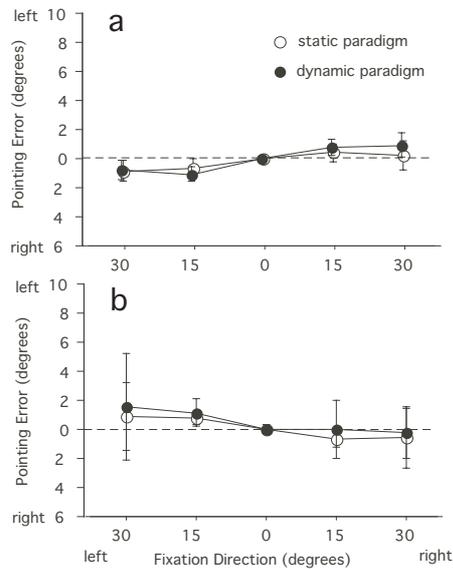


Figure 14. Visual experiment. (a) Performance of pointing with the mouse cursor in the two experimental paradigms. Pointing error is plotted as a function of the remembered target position as indicated with the mouse cursor, relative to the fixation direction. Pointing error is averaged over 4 subjects (10 trials per subject). Error bars indicate ± 1 SE. (b) The bias measured in the two alternatives forced choice discrimination task. The pointing error reflects the accuracy of the perceived position of the test dot relative to the remembered position of the target.

Pointing-time

We analysed the duration of the time needed to perform the movement toward the target in the dynamic paradigm to investigate if it affected performance. This period, that we called response time, was defined as the period between onset of the saccade toward the eccentric fixation point and time of contact with the touch screen. Figure 15 shows that performance was not affected by this response time, as the smaller durations of the onset of the pointing movement after the intervening saccade did not result in more accurate pointing behaviour and vice versa.

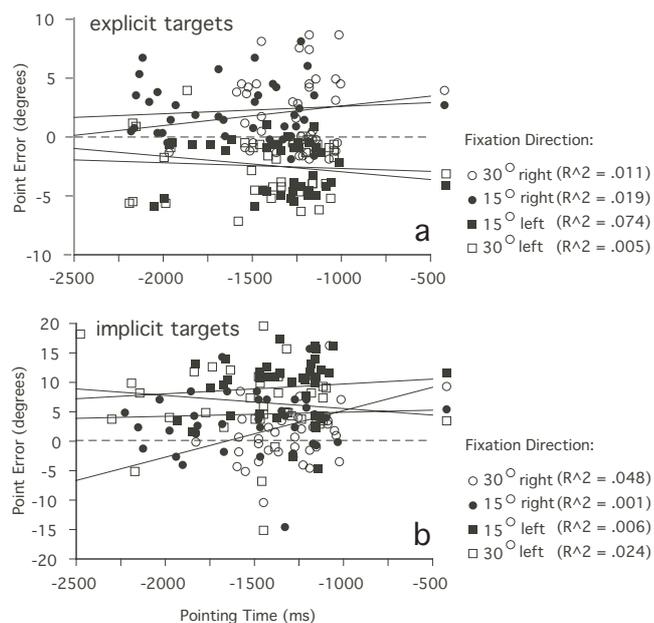


Figure 6. Pointing-time. Duration of the time (in ms) needed to perform the pointing movement after the saccade is plotted against the pointing error. Figures show all trials of the 4 subjects in the dynamic paradigm, separately for different fixation directions. (a) Data for explicit targets. (b) Data for implicit targets (centres of flow)

Discussion

No use of a head-centric frame for pointing to nearby targets

The conclusions from recent neurophysiological studies led us to infer that the transformation of visual space from retinocentric to a head centric representation may be limited to visual objects in close proximity of the head, whereas more distant visual space is represented through a basically retinal code that is updated with eye movement signals. The current findings, however, largely go against this idea. Our study demonstrates that most subjects make systematic errors in locating remembered targets when gaze is directed away from the pointing target, regardless of the distance of that pointing target to the head. Only two subjects showed a marked reduction of the pointing error when the target was close to the head and when they were required to point towards their head. However, this effect was limited to explicit targets in the static paradigm. Their pointing performance in the dynamic paradigm was affected by the fixation eccentricity in the same way as for the other subjects. We have no explanation for the accurate pointing behavior of these two subjects in the static paradigm.

Localization error of the target is defined as the difference between the target direction and the direction of the motor output. It is therefore difficult to attribute errors to a specific part of the sensorimotor loop and to differentiate errors that occur during visual perception, memorization or motor execution.

A certain number of error sources can be eliminated by our data. The pointing errors are not based in judgement errors of the target's *retinal* eccentricity. First, the errors are virtually absent for a visual judgement task as shown by our control experiment (Experiment 4). Subjects are able to discriminate very accurately the remembered direction of the target from the direction of subsequent visual object, which implicates a correct visual memory of the direction of the visual stimuli. Similar results have been found in other experiments (D'Avossa and Kersten 1996, see their Figure 4). Mergner et al. (2001) used a task, very much like our control experiment, to investigate if the perception of the eccentric target is accurate. In his experiment subjects had to indicate the remembered location of a previously presented eccentric target using a remotely controlled light source, after a memory period of twelve seconds. Estimation of the position of the eccentric target was accurate regardless of the eye movements, or even head or trunk movements prior to that judgement.

Second, the pointing error remains in the dynamic paradigm when the target is flashed at the fovea and subjects point after an intervening saccade, showing that the error arises even in the absence of retinal eccentricity at the time of memory formation.

Furthermore, the pointing errors do not arise from the motor task per se, because the errors vary in accordance to the gaze position while the pointing task is invariant. The subjects in our experiment were asked to point as accurately as possible toward a central target, a point straight in front of the head, making the same arm movement toward the touch screen. By using a constant central pointing target and only varying eye-position, the pure arm-related motor-effect was excluded as the possible cause of the error.

Finally, it is also unlikely that the errors originate from eye movement as such. In contrast to arm pointing, open-loop saccadic eye pointing (saccades to the location of a remembered target) is accurate, even after intervening eye and head movements (Karn et al. 1997). Even in a double-step task (Mays and Sparks 1980, in Colby and Goldberg 1999) human subjects seem to have no trouble to point to a target location very accurately, after they made a first saccade. In this task the subjects have to remember two locations and to adjust the direction and amplitude of the second saccade using position information of the first target. This finding suggests that the saccadic system has accurate access to either the position of the target in head centred coordinates or has access to accurate retinal updating mechanisms (Colby and Goldberg 1999). Below we wish to discuss two possible explanations for the different errors of arm and eye-pointing.

The first is a temporal one. For arm-pointing, the time needed to perform the movement to the target is longer. After memorization, the target position has to be updated because of the eye-movement. The visual system has to compensate for the displacement of the eye. Possibly, the retinally updated information is preserved and accessible for a short period. If the movement is performed after this short period, distortion of the updated information for movement may occur. The duration of this period does not affect the *visual* memory for target location, as Mergner et al (2001) showed. However, it could have an effect on the transformation of visual representation of the target into coordinates for pointing. In the double-step eye-pointing, saccadic movements towards the target occur with short latency and, compared to arm pointing, the probability that the accurate information about the target position is still accessible at the time of pointing is higher. If this is true, then one would expect for smaller durations of the onset of the pointing movement after the intervening saccade to result in better pointing performance. We could not find a relation in our data in support of this proposal. The time needed to perform the pointing movement with the arm is possibly already beyond the period within which the updated information for movement toward the target is accurately preserved.

The second possibility that could explain the difference between arm-pointing and eye-pointing has a geometrical basis. Remapping updates the internal representation of space (i.e. remembered locations of flashes, remembered locations of body markers like the nose the brows, the subjective straight ahead etc.) in conjunction with eye movements so that it remains in correspondence with the current eye position. Location information is thereby maintained in eye-centred coordinates. An eye-centred representation has the advantage, compared to other reference frames, that it is already in the coordinates of the effector system that will be used to acquire the target (Colby and Goldberg 1999) *if one plans an eye movement*. However, the nodal point of the eye, where all the light paths intersect, lies in front of the rotation point of the eye. Due to that difference the retinal angle of target eccentricity is larger than the required eye rotation for fixation of the target if the target is very nearby as in our experiments; for the distant targets the difference is insignificant (Steinman et al. 1982). The transformation to the coordinates for the shoulder or arm, or finger movement toward the target is more complex compared to the transformation into coordinates for the eye-movement. To reach the target with the finger, for instance, the system has to know the precise orientation of all the joints involved in the movement. This makes the likelihood for errors larger and

might be another reason of the saccadic pointing being more accurate than arm pointing.

We conclude, in line with Henriques' view, that the errors reflect a bias in the visuo-motor transformation that involves eye displacement rather than eye position relative to the head at the time of the target flash or any other head-centred variable. Errors arise when the remembered visual targets for goal directed arm movements are updated in a retinal frame irrespective of target distance. The implication of these results, that the brain does not appear to use a stable map of absolute space (Henriques, 1998) for the control of pointing movement, applies also to near head space.

Task effects

Due to limitations set by physical characteristics of our experimental setup, our task for the proximate targets was different from that employed by Henriques et al. (1998). In that study subjects pointed towards distant targets. In our study, subjects approached the remembered nearby target point from the back as if to push it towards themselves. Thus, our task emphasizes the direction towards the ego-centre explicitly. We hoped in this way to provoke a head-centric response. In Experiment 2 we compared for distant targets, pointing from the target towards the self and the other way around and found no difference in performance. Thus, the task by itself did not affect performance for the distant targets.

Pointing errors for near targets were similar as for the distant targets and are consistent with the very recent findings of Medendorp et al. (2002). In his experiment subjects made pointing movements towards target at 2 m distance and reaching movements for the targets at 15 cm or 42 cm distance, while fixating an eccentric position. The reaches were directed so as to grasp the invisible object. In their study the task refers to the object's location without reference to the subject's ego-centre and could be solved in any reference frame provided it contains a representation of both hand and object. Despite the dissimilarity of the tasks, Medendorp et al. (2002) and we found similar pointing errors. Exaggeration of the eccentricity of the final fingertip position was present also in all conditions of Medendorp's experiment.

For the proximate targets a small shift to the left occurs in some of our subjects. This effect was also visible in Medendorp's data. In the absence of visual input, the subjective medial plane of the head is shifted toward the direction of eccentric gaze (Pierce 1901, in Lewald and Ehrenstein 1999). We presented the central pointing target at the geometrical straight ahead position, i.e. at a location straight in front of a position midway between the eyes. The leftward pointing bias irrespective of gaze is consistent with a shift of the perceived straight ahead towards the right for nearby targets. This might be related to the pointing arm, which was always the right arm in our experiments.

Explicit and Implicit targets

We also investigated errors for pointing towards the centre of a wide field expanding motion pattern. The locus of a small visual object has an explicit representation in the retinal map in the primary visual cortex. Such an object will stimulate a bounded region in area V1. In contrast, an expanding flow pattern stimulates the whole retina, the display being filled with moving dots. The centre of the pattern, the heading direction, is implicit in the visual field as there need not be a visual structure at that locus. In fact, our stimuli never contained a target point into the direction of heading. Although the information about the position of the object at the focus of expansion, if present, is used to guide locomotion (Warren et al. 2001; Rushton et al. 1998) it is not critical for determination of the heading direction (Warren et al. 1986). In that sense, leaving the focus of expansion unmarked was not disadvantageous for the performance.

We found the same pattern of pointing errors in relation to the gaze displacement for explicit and implicit targets and independent of depth in either case, except for one condition. When pointing towards distant explicit targets, significantly larger errors were found when fixating to the most eccentric right fixation direction than when looking to the most eccentric left fixation. Flanders et al. (1992) suggested that the origin of the coordinate system for the neural representation of direction is shifted towards the shoulder, prior to the production of pointing arm movement. This would mean that the measured error curve would also be shifted to right, if right arm is used for pointing, irrespective of gaze. We do not see this effect in our data. Scherberger et al. (2003) found that monkeys preferred to reach towards targets right of the mid-sagittal plane of the head when they used their right arm. Eye fixation direction modulated this preference in an opposite manner, increasing reaching preference for targets left of fixation if the monkey looked rightward. If we assume that the humans and monkeys prefer to reach for targets that are perceived as “nearer” one would expect a smaller error for rightward fixation in our study on the basis of Scherberger’s data. Thus, neither study can explain the larger error for pointing towards the centre when the subject looks 30° rightward compared to 30° left fixation.

For point targets our control experiment excludes judgement errors of the target’s *retinal* eccentricity as the cause for the pointing error. Does that hold also for the judgment of the centre of flow? Human subjects are known to estimate their heading from optic flow with constant errors of about 1° of visual angle (Warren et al 1988; van den Berg 1992). Also, subjects estimate correctly the direction when asked to walk toward the centre of expansion (Warren et al. 2001). Some other studies have reported larger bias up to 10 degrees (D’Avossa and Kersten 1996; Llewelyn 1971). Importantly, however, the bias was directed towards the fixation point, hence opposite to the pointing errors we found. Thus, if anything, the visual contribution to the pointing error towards the centre of flow would lead to undershoot not overshoot. This point is also supported by the findings of Hooge et al. (1999). Subjects were asked in that study to search for the direction of heading in an optic flow display by making saccades. The first saccade was made after about 0.5 sec and usually undershot the centre of the expanding flow. In combination with the results of our study this again suggests that the transformation of visual into motor signals introduces errors that are primarily dependent on the effector system (eye or

arm) and not the visual representation of the goal.

Above we excluded the time interval between the saccade and the pointing movement as a determinant of the pointing error. We wondered if a limitation of visual processing time for heading direction could have increased the errors for pointing towards the centre of flow. Flow patterns and point targets were shown for 750 ms. This is ample time for localization of a point target, but is it for the heading direction? Processing time for the heading direction, when saccadic eye-movement is involved, is estimated by Hooge et al. (1999) at about 430 ms (error saturated at about 500 ms), others estimated the time needed even lower (~ 300 ms; Crowell et al. 1990, te Pas et al. 1998). So, it is unlikely that the difference in error between explicit and implicit targets is caused by presentation time duration.

We used the same procedures for pointing towards the explicit and the implicit targets. Hence the arguments against a head centric or pure retinal cause of the error apply also to the case of pointing towards the centre of flow. This suggests that also the perceived direction of heading is updated into a retinal reference frame. It is well known that specific sensitivity to patterns of radial motion is found in the extra-striate cortex areas MST, VIP, and area 7a (Tanaka et al. 1989; Schaafsma and Duysens 1996, Bremmer et al. 2000, Siegel and Read 1997). Microstimulation of area MST (Britten and van Wezel 1998) affects heading judgments by the monkey. Hence, at least for this area we know that it is involved in the assembly of neurons that supports such judgments. Our finding then suggests that the mechanism of retinal updating is placed beyond the level of area MST. Indeed, a number of neurophysiological and neuroimaging studies have concluded that reach related activity in the monkey (Batista et al. 1999) and human (deSouza et al. 2000) parietal cortex is modulated by eye position signals. Remembered target positions as well as the initial hand position appear to be encoded in eye-centred coordinates in the parietal reach region (Buneo et al. 2002). Such a frame of reference for the hand is consistent with a retinal updating mechanism.

In conclusion, for goal directed arm movements representation of the remembered visual targets is updated in a retinal frame. Retinal updating is a mechanism that is actively used for the representation of the direction of visual targets irrespective of target distance, stimulus characteristics or the requirements of the task.

Reference

- Batista AP, Buneo CA, Snyder LH, Andersen RA (1999) Reach plans in eye-centred coordinates. *Science* 285: 257-260
- Beintema JA, van den Berg AV (1998) Heading detection using motion templates and eye velocity gain fields. *Vision Research* 40: 549-566
- van den Berg AV (1992) Robustness of perception of heading from optic flow. *Vision Research* 32(7): 1285-96
- van den Berg AV (1996) Judgments of heading. *Vision Research* 36(15): 2337-2350
- Bock O (1986) Contribution of retinal versus extraretinal signals towards visual localisation in goal-directed movements. *Experimental Brain Research* 64: 476-482
- Bremmer F, Duhamel JR, Ben Hamed S, Graf W (2000) Stages of self-motion processing in primate posterior parietal cortex. *International Review of Neurobiology* 44: 173-98
- Bremmer F, Ilg U J, Distler T C, Hoffmann KP (1997) Eye position effects in monkey cortex.1. Visual and pursuit related activity in extrastriate areas MT and MST. *Journal of Neurophysiology* 77: 944-961
- Bremmer F, Schlack A, Shah NJ, Zafiris O, Kubischik M, Hoffmann K, Zilles K, Fink GR (2001) Polymodal motion processing in posterior parietal and premotor cortex: a human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron* 29(1): 287-96
- Britten KH, van Wezel RJ (1998) Electrical microstimulation of cortical area MST biases heading perception in monkeys. *Nature Neuroscience* 1998 1: 59-63
- Buneo CA, Jarvis MR, Batista AP, Andersen RA (2002) Direct visuomotor transformations for reaching. *Nature* 416: 632-6
- Colby LC, Goldberg ME (1999) Space and attention in parietal cortex. *Annual Review of Neuroscience* 22:319-49
- Crowell JA, Banks MS (1993) Perceiving heading with different retinal regions and types of optic flow. *Percept Psychophys* 53(3): 325-37
- Crowell JA, Royden CS, Banks MS, Swenson KH, Sekuler AB (1990) Optic flow and heading judgments. *Investigative Ophthalmology & Visual Science* 31:522
- DeSouza JFX, Dukelow SP, Gati JS, Menon RS, Andersen RA, Vilis T (2000) Eye position signal modulates a human parietal pointing region during memory-guided movements. *Journal of Neuroscience* 20: 5835-5840
- D'Avossa G, Kersten D (1996) Evidence in human subjects for independent coding of azimuth and elevation for direction of heading from optic flow. *Vision Research* 36: 2915-2924
- Duhamel JR, Bremmer F, BenHamed S, Graf W (1997) Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature* 389(6653): 845-848
- Flanders M, Tillery SI, Soechting JF (1992) Early stages in a sensorimotor transformation. *Behavioral and Brain Sciences* 15: 309-362
- Gibson JJ (1966) *The perception of the visual world*. Boston, Mass.: Houghton Mifflin
- Goltz HC, Dukelow SP, DeSouza JF, Culham JC, van den Berg AV, Goossens HH, Menon RS, Vilis T (2001) A putative homologue of monkey area VIP in humans. *Society of Neuroscience abstract*

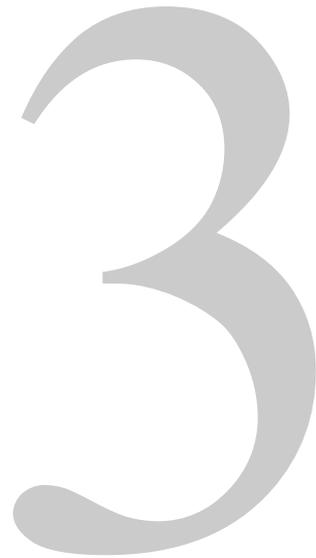
- Henriques DYP, Klier ME, Smith MA, Lowy D, Crawford JD (1998) Gaze centred remapping of remembered visual space in an open-loop pointing task, *Journal of Neuroscience* 18: 1583-1594
- Honda H (1989) Perceptual localisation of visual stimuli flashed during saccades. *Perception & Psychophysics* 45: 162-174
- Hooge IThC, Beintema JA, van den Berg AV (1999) Visual search of heading direction. *Experimental Brain Research* 129: 615–628
- Karn KS, Moller P, Hayhoe MM (1997) Reference frames in saccadic targeting. *Experimental Brain Research* 115: 267–282
- Lappe M, Bremmer F, van den Berg A V (1999) Perception of self-motion from visual flow. *Trends in Cognitive Science* 3: 329–336
- Lewald J, Ehrenstein WH (2000) Visual and proprioceptive shifts in perceived egocentric direction. *Vision Research* 40: 539-547
- Llewellyn KR (1971) Visual guidance of locomotion. *Journal of Experimental Psychology* 91(2): 245-61
- Medendorp WP, Crawford JD (2002) Visuospatial updating of reaching targets in near and far space. *Neuroreport* 13: 633-636
- Mergner T, Nasios G, Maurer C, Becker W (2001) Visual object localisation in space. *Experimental Brain Research* 141: 33-51
- Olshausen BA, Anderson CH, Van Essen DC (1995) A multiscale dynamic routing circuit for forming size- and position-invariant object representations. *Journal of Computational Neuroscience* 1995 2(1): 45-62
- Rushton SK, Harris JM, Lloyd MR, Wann JP (1998) Guidance of locomotion on foot uses perceived target location rather than optic flow [Brief communication]. *Current Biology* 8: 1191-1194
- Schaafsma SJ, Duysens J (1996) Neurons in the ventral intraparietal area of awake macaque monkey closely resemble neurons in the dorsal part of the medial superior temporal area in their responses to optic flow patterns. *Journal of Neurophysiology* 76: 4056-68
- Salinas E, Thier P (2000) Gain modulation: a major computational principle of the central nervous system. *Neuron* 27(1): 15-21
- Scherberger H, Goodale MA, Andersen RA (2003) Target selection for reaching and saccades share a similar behavioral reference frame in the macaque. *Journal of Neurophysiology* 89: 1456–1466
- Siegel RM, Read HL (1997) Analysis of optic flow in the monkey parietal area 7a. *Cerebral Cortex* 7: 327-46
- Steinman RM, Cushman WB, Martins AJ (1982) The precision of gaze. *Human Neurobiology* 1: 97-109
- Tanaka K, Hikosaka K, Saito H, Yukie M, Fukada Y, Iwai E (1986) Analysis of local and wide-field movements in the superior temporal visual areas of the macaque monkey. *Journal of Neuroscience* 6(1): 134-44
- te Pas SF, Kappers AML, Koenderink JJ (1998) Locating the singular point in first order optical flow fields. *J Exp Psychol: Hum Percept Perform* 24:1–17
- Warren WH Jr, Blackwell AW, Kurtz KJ, Hatsopoulos NG, Kalish ML (1991) On the sufficiency of the velocity field for perception of heading. *Biological Cybernetics* 65(5):311-20

Warren WH Jr, Morris MW, Kalish M (1988) Perception of translational heading from optical flow. *Journal of Experimental Psychology: Human Perception and Performance* 14(4): 646-60

Warren WH Jr, Kay BA, Zosh WD, Duchon AP, Sahuc S (2001) Optic flow is used to control human walking. *Nature Neuroscience* 4: 213-216

Zipser D, Andersen RA (1988) A back-propagation programmed network that stimulates response properties of a subset of posterior parietal neurons. *Nature* 331: 679-684

Perceptual compensation for eye torsion¹



¹ *adapted from:* Poljac E, Lankheet M, van den Berg AV (2004) Perceptual compensation for eye torsion. *Vision Research* 45(4): 485-96

Abstract

To correctly perceive visual directions relative to the head, one needs to compensate for the eye's orientation in the head. In this study we focus on compensation for the eye's torsion regarding objects that contain the line of sight and objects that do not pass through the fixation point.

Subjects judged the location of flashed probe points relative to their binocular plane of regard, the mid-sagittal or the transverse plane of the head, while fixating straight ahead, right upward, or right downward at 30 cm distance, to evoke eye torsion according to Listing's law. In addition, we investigated the effects of head-tilt and monocular versus binocular viewing.

Flashed probe points were correctly localized in the plane of regard irrespective of eccentric viewing, head-tilt, and monocular or binocular vision in nearly all subjects and conditions. Thus, eye torsion that varied by ± 9 degrees across these different conditions was in general compensated for. However, the position of probes relative to the midsagittal or the transverse plane, both true head-fixed planes, was misjudged.

We conclude that judgment of the orientation of the plane of regard, a plane that contains the line of sight, is veridical, indicating accurate compensation for actual eye torsion. However, when judgment has to be made of a head-fixed plane that is offset with respect to the line of sight, eye torsion that accompanies that eye orientation appears not to be taken into account correctly.

Introduction

To move an object to a certain position on the face, it would be very convenient to have the object's position described in head centric coordinates, the same coordinates as the place it is relocated to. Neurophysiological studies have identified brain areas in the monkey containing cells with head centric receptive fields (Duhamel et al. 1997). Areas with similar properties may exist also in human brain (Bremmer et al. 2001) as revealed by fMRI. According to a widely accepted view, such a visual head centric representation arises from a retinal representation of the object, taking the eye orientation relative to the head into account. Helmholtz (1910) illustrates the use of eye orientation signals by patients in which certain eye muscles have suddenly been paralyzed to make the eye powerless to move any longer in a certain direction. When the patient tries to turn the eye in that particular direction, the patient reports apparent motion. Apparently, a shift of the viewing direction is expected, and since no change has taken place in the positions of the images on the retina of the paralyzed eye, the patient gets the impression as if the objects shared the supposed movements of the eye. Similarly, eye position is taken into account when judging slant, for example. James et al. (2001) used prisms to alter the sensed eye position, which led to changed slant judgments. Thus, slant and location of the object can be represented relative to the head if the position of the eyes in the orbit is available and combined with the retinal coordinates of the object.

A retinal image depends not only on vertical and horizontal, but also on the torsional component of eye orientation. Fixation of an eccentric direction causes the eyes to rotate around the lines of sight in accordance with Listing's law (Fetter et al. 1997). This law states that eye torsion depends on the fixation direction, and specifies the amount of torsion for a given fixation direction. So, to correctly transform an eye-centered representation of a visual object to a craniotopic representation, the information about 3D eye position is required (Flanders et al. 1992; Crawford & Guitton 1997).

From earlier studies we know that the brain accounts for torsional orientation of the eye (Haustein & Mittelstaedt 1990; Bockisch & Miller 1999; Smith & Crawford 2001). Klier and Crawford (1998) reported high accuracy of horizontal saccades between pairs of lights located symmetrically with respect to the midline. The eye movement started at an eccentric position (tertiary eye position) at different elevations. Because of the eye's torsion relative to the plane of regard at an elevated starting position with horizontal eccentricity, the horizontally displaced (i.e. relative to the head) goal of the impending saccade was not imaged at the horizontal retinal meridian. The high accuracy of the subject's movements was in accordance with the reference frame transformation hypothesis (from eye centered into a head centered representation), which led the authors to conclude that brainstem saccade generator must compensate for 3D eye orientation when generating saccades to make a correct transformation. Such compensation needs to occur also for the ocular counterroll that arises when a head tilt is introduced. This is the consequence of the fact that as we move, not only our eyes, but the head also changes orientation constantly. In the same study (Klier & Crawford 1998) found only partial compensation when radial saccades had to be made from counterrolled positions. Medendorp et al. (2002) asked subjects to make saccades to targets after head or eye rotations to tertiary

positions, and they were surprisingly accurate. This is an indication of compensation for the torsional offset at the start of the movement.

The saccade-studies we mention here tested motor function. However, perception might have different neuronal processes that are underlying the process of compensation for eye torsion. Evidence for perceptual compensation for torsion comes from studies of perception of the vertical during head or body tilt. Subjects that were asked to set two illuminated points orthogonal to the mid-sagittal plane of their heads, with head and body upright or tilted 90° to the right or to the left, can do so, albeit with a limited accuracy (Haustein 1992). The magnitude of the error suggests at least a partial compensation for ocular counterroll (error only 3.8°) rather than a pure retino-centric judgement (error 13.2°), which implicates that their judgement was not solely based on retinal information.

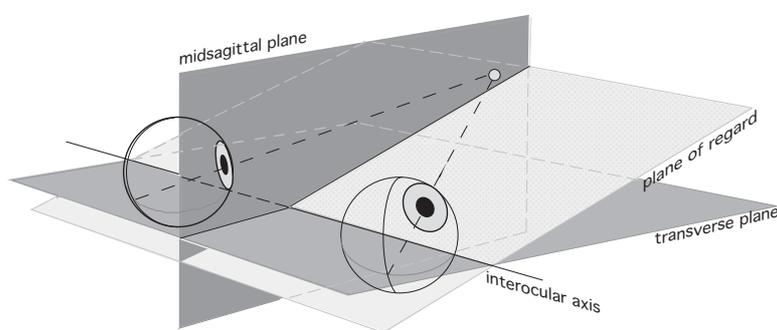


Figure 1. Plane of regard, midsagittal plane and transverse plane. The fixation point and the rotation centers of the eyes define the plane of regard. This plane contains the interocular axis about which the eye can rotate. All points inside the plane have the same elevation. The midsagittal plane is defined as a vertical plane positioned perpendicular to the interocular axis and intersecting that axis half way between the eyes. Orthogonal to the midsagittal plane and containing the interocular axis, lies the transverse plane of the head at eye level.

We wondered if perceptual compensation for torsion occurs also for judgements with respect to the plane of regard, a plane defined by the fixation point and the projection centers of the eyes (Figure 1). Helmholtz torsion is very conveniently defined relative to the plane of regard. It specifies the angle between the plane through the horizontal retinal meridian and the plane of regard. Thus if both eyes have the same Helmholtz torsion, any object in the plane of regard will have the same torsional eccentricity in the two eyes. In this paper we refer by eye torsion to Helmholtz torsion unless explicitly mentioned. Fixating a tertiary position has the consequence that the horizontal meridians of the eyes rotate out of the plane of regard. They do so by an equal amount for the two eyes when targets are at optimal infinity (original Listing's law). This holds also for nearby targets, according to extensions of Listing's law (van Rijn & van den Berg 1993; Minken et al. 1995; Tweed 1997; Hooge & van den Berg 2000), although this may vary across individuals (Bruno & van den Berg 1997). We did not measure eye torsion in our subjects but assumed that their eyes obeyed the extensions of Listing's law for eye vergence. Basically, this means that Helmholtz torsion does not change with respect to viewing at infinity by eye vergence, because the eyes vergence is due to rotation about the eye perpendicular to the plane of regard. Does such eye torsion cause errors of perceived direction of the objects in the plane of regard? We also wondered if binocular vision affects the localization?

In addition, we take the analysis one step further. The plane of regard contains per definition the lines of sight and consequently the fixation point. To

accommodate Listing's law, a displacement of the eye (e.g. a saccade) involves a component of eye torsion that depends both on the initial and the final viewing direction (half-angle rule, Tweed & Vilis 1990). To judge the position of objects relative to a plane that does not pass through the fixation direction, such as the mid-sagittal or the transversal planes of the head, the judgement could rely on the retinal image that these planes would have as seen from reference viewing direction (e.g. eyes straight ahead). A compensation for eye torsion would then be needed that depends on the current and the reference viewing direction. This task would be solved by a system that provides a head centric visual representation for any viewing direction. Our question is then for this task, whether compensation for eye torsion is as accurate as when the plane of regard must be identified? So, our study would be a test between judging positions relative to horizontal and vertical planes that do or do not pass through the fixation point.

Materials and methods

Subjects

Six subjects participated in the study. Four of them took part in all experimental conditions. One subject (EP) was aware of the experimental design and purpose of the study, the rest of the participants were naive. This study has been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. Participation was voluntary and all the subjects gave their informed consent prior to their inclusion into the study.

Apparatus

Experimental stimuli were generated by a Macintosh G4 computer with a Graphics acceleration board (Formac Proformance III) and presented on a computer monitor (Sony 19" FD Trinitron CRT). The subjects were seated at approximately 30 cm in front of the monitor, with their head stabilized by a dental bite-board mounted on the table, in complete darkness. They looked through a red filter with their left eye and a green filter with their right eye. In this way each eye could be stimulated independently, as red and green images were used. Each image was presented as seen from that eye's perspective, which enabled presenting a 3D scene in stereoscopic perspective. A camera-based measurement of the eye's pupil orientation was used to make sure that ocular fixation criteria were met during the experiments (SMI EyeLink-inc Teltow, Germany). Precise location of each subject's eyes relative to the monitor's center was determined by a triangulation procedure (van den Berg, 1996) before the experiment started. The head was oriented straight ahead, the interocular axis was positioned in the horizontal plane, and the eyes had nearly the same distance to the monitor. The exact position and orientation of the plane of regard could be determined using the measured position of the eyes' rotation centers and the position of the fixation point. The fixation points were stereo images presented at the monitor distance and consequently, the images for the left and the right eye had same position on the screen. The probe stimuli were also stereo images of single points presented at the Vieth-Muller circle that passes through the fixation point and the nodal points of the eyes. For points on the Vieth-Muller circle the horizontal disparity is zero. Because the dichoptic image was always

presented on the monitor, a defocus of about 0.2 dioptre would occur. This blur is likely too small to cause any significant localization error. All the dots had a diameter of 0.1° degrees.

Procedure

The experiment was performed in total darkness. The subjects had no visual reference whatsoever during the trials. We explained the concept of the plane of regard to the subjects. All angular measures in the sequel refer to Helmholtz angles, i.e. elevation denotes the rotation about the interocular axis and azimuth rotation about the axis perpendicular to the plane of regard. Subjects judged elevation of flashed probe points relative to their plane of regard while fixating straight ahead, 30° right downward (elevation 30° down, azimuth 30° to the right) or 30° right upward (elevation 30° up, azimuth 30° to the right) relative to their straight ahead. Straight ahead was defined as the direction perpendicular to the interocular axis in the horizontal plane, and intersecting that axis half way between the eyes (i.e. at the cyclopean eye). We used a flat screen so the distance of the fixation point straight ahead and the two eccentric fixations was not the same. Consequently the angles of convergence differed slightly. To give an example, for subject EP the convergence angle was 13° and 9.7° , for the straight-ahead and the eccentric conditions respectively. Each experimental condition, fixating straight ahead, right down or right up, consisted of 175 trials. Probe azimuth ranged from -20° to 20° relative to fixation direction. The probes' elevation varied between 2° under and 2° above the plane of regard. The probe position in any trial was a randomly chosen combination of azimuth (5 positions) and elevation (5 positions). Each combination was repeated seven times. Each trial started with a fixation point, presented for 0.75 seconds. 500 ms after it disappeared, the probe point was flashed (300 ms) on the screen. When the probe disappeared, the subjects indicated whether they had seen the probe above or under their plane of regard. The same fixation direction had to be maintained during the whole trial until the subject's response. Then, the next trial started. When the eye orientation deviated more than 0.5° from that orientation before the fixation point disappeared, the trial was rejected and repeated. A Mathematica program used the Marquardt-Levenberg method to find the best fitting cumulative Gaussian (error function). The horizontal position of the 50% point determined the point of subjective equality, and the SD was derived from the slope of the curve.

Experiment 1. Binocular estimation of the orientation of the plane of regard

The subjects performed the task described above. When they fixated straight ahead, the projection of their plane of regard on the retina was aligned with the horizontal retinal meridian. Therefore, the estimation of the probe position based on retinal representation would lead to the same result as judging the probes relative to the plane of regard, as estimation relative to retinal meridian is the same as estimation relative to the plane of regard in this case. In contrast, when the eyes fixated one of the two eccentric fixations, conjugate eye torsion occurs in accordance with Listing's law, and the orientation of the horizontal meridian varies dependent on the fixation direction (Figure 2). Consequently, if subjects were to identify the plane of regard with their horizontal retinal meridian, systematic errors should occur. If the subject is fixating 30° right up, for instance, the horizontal retinal meridia

rotate 8.9° counterclockwise relative to the plane of regard. A probe point presented on -20° azimuth relative to fixation direction and 1° under the plane of regard would be estimated as “above”, if the judgment is based on retinal representation. A head centric judgment, on the other hand, would lead to a correct localization of target probes.

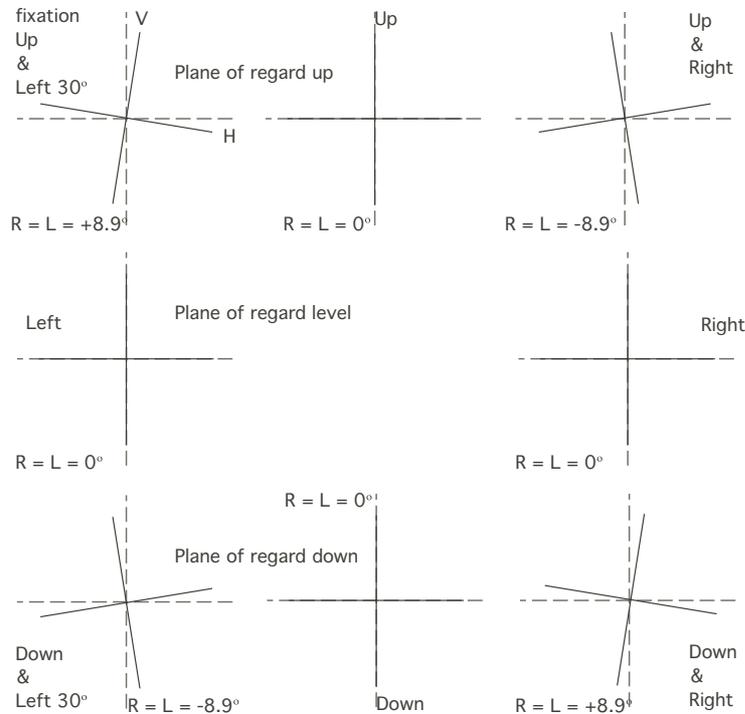


Figure 2. Torsion angles in Helmholtz coordinates at different fixation directions. The orientations of horizontal and vertical retinal meridia associated with different fixation directions. Eye torsion, the rotation of the eyes around the lines of sight, causes the meridia to change orientation. The amount of torsion is dependent on vertical and horizontal eye orientation in the head, and is described by Listing’s law. Eye vergence does not alter Helmholtz torsion according to the extension of Listing’s law to near vision (van Rijn & van den Berg, 1993; Minken, Gielen & van Gisbergen, 1995; Tweed, 1997) because it involves opposite rotations for the two eyes about an axis perpendicular to the plane of regard.

Experiment 2. Binocular estimation of the orientation of the plane of regard with head tilt

In Experiment 1 the subjects were seated upright and looked to the monitor in the frontal plane. Therefore, their plane of regard intersected the image plane of the monitor in such a way that this intersection line was parallel to the external horizon. Although the subjects had no visual reference, we wanted to exclude the possibility that their judgment of the probe position relied on some kind of allocentric representation, like an internal reference of the horizon. We adjusted the experimental setup so that the subject’s head was tilted 20° to the left or 20° to the right. By definition, the plane of regard also changed its orientation, dependent on the condition, 20° to the left or to the right, rotating around straight ahead axis of the cyclopean eye. The stimuli were presented on the same positions relative to the plane of regard as in the first experiment, taking the new orientation of the plane of regard into account. The task the subjects performed was, similar to Experiment 1, to estimate the probe points positions relative to their plane of regard, while fixating, in this case only, straight ahead. When we tilt the head the plane of regard, by definition, follows the changes in head orientation. The head-tilt evokes compensatory eye-torsion. Schworm et al. (2002) showed that the gain of this counterroll, calculated as a ratio between the amplitude of counterroll and the amount of head tilt, ranged between 18% and 27% at 15° head tilt. The magnitude of the compensatory torsion (cyclovergence) ranged between 2.6° and 4.1° at 15° head tilt, and between 5.1° and 6.4° at 30° head tilt. Other studies also show that the compensatory torsion is about 10% of the head tilt (Collewyn et al. 1985), or about 2 deg in our setup.

Experiment 3. Monocular estimation of the orientation of the plane of regard

According to Mayhew and Longuet-Higgins (1982) vertical disparities of non-meridional image points are crucial for the correct computation of the three-dimensional structure of a visual scene. The fixation point and the flashed probe point provide minimal information in this respect, yet, when a stimulus is presented monocularly the disparity information is not available at all. Is binocular presentation essential for correct estimation of probe positions relative to the plane of regard? We repeated conditions of Experiment 1 and Experiment 2, this time presenting stimuli to the left eye only. The position of both eyes was measured before each experiment, in order to determine the orientation of the plane of regard. The subjects were first instructed to estimate the elevation of the flashed probes relative to their plane of regard, while fixating straight ahead, 30° right downward or 30° right upward. Subsequently, they judged the probes' positions with their head tilted 20° to the left or to the right.

Experiment 4. Binocular estimation of the orientation of the midsagittal plane and transverse plane

The plane of regard is not a head-fixed plane, as it can rotate around the interocular axis, and consequently change its orientation relative to the head. It seemed interesting to examine how accurate the subjects would be in estimating the probe position relative to a true head-fixed plane, the task that requires a compensation for torsion to make a correct head centric judgment. We investigated the perception of midsagittal plane, which is defined as a vertical plane positioned perpendicular to the interocular axis and intersecting that axis half way between the eyes (Figure 1). First, comparable to Experiment 1, we instructed the subjects to estimate the remembered position of the flashed probes relative to their midsagittal plane, while fixating straight ahead, 30° right downward or 30° right upward. The two eccentric fixation directions were of particular interest. Here, the actual eye torsion of the fixation directions that follows from Listing's law is not the same as the torsion associated with the eye oriented in the direction of the midsagittal plane. If the relation between the gaze and the amount of torsion is fixed, as Listing's law states, then provided that the motor system yields the correct gaze direction, the ocular torsion may also be deduced from the gaze direction commands (Haustein & Mittelstaedt 1990). Eye torsion may be accessible for a given fixation direction (actual torsion) but no such account for associated torsion change may be available until an eye displacement is made. Thus we wondered if the visual system can compensate for the torsion associated with the change in eye orientation (torsion coupled to a planned eye orientation)? Probe elevation ranged from -20° downwards to 20° upwards relative to straight-ahead direction. For the most eccentric probes this would mean that the retinally based judgment would lead to estimation errors in the range of 2° . The probes' azimuth varied between 4° left and 4° right relative to the midsagittal plane. In addition, the relative position of the flashed probes was judged with the head tilted 20° to the left or to the right, similar to Experiment 2, in this case only for the fixation straight ahead.

In a separate experiment we repeated the same procedure used for midsagittal plane, this time instructing the subjects to estimate the position of probes relative to the second true head-fixed plane examined, their transverse plane of the head, which

is defined as a horizontal plane containing the interocular axis (Figure 1). Probe azimuth ranged from -20° to 20° relative to straight-ahead direction. The probes' elevation varied between 4° under and 4° above the horizontal plane.

Results

Experiment 1. Binocular estimation of the orientation of the plane of regard

Subjects estimated the elevation of flashed probes relative to the plane of regard while fixating straight ahead, right down, or right up. We investigated if judgment is biased towards the location of the horizontal retinal meridian. For instance, for the conditions 30° right downward or 30° right upward, the expected bias would be about 2° , for azimuth 20° , if the judgment of probe position is based on the horizontal retinal meridian. Figure 3 shows the average performance across six subjects for the three experimental conditions. Statistical analysis (ANOVA) revealed no significant effect of the fixation direction ($p=0.85$; $F(2,75)=0.17$), nor the probe azimuth ($p=0.69$; $F(4,75)=0.56$). Estimation bias was below 0.5° and did not deviate significantly from zero, irrespective of the probe azimuth relative to fixation direction. Accordingly, the perceived elevation of eccentric probes was not biased towards the location of the horizontal retinal meridian (Figure 3, dashed line). Detailed analysis of individual performance revealed an interaction effect of fixation direction and probe azimuth in one subject (subject AN, Figure 4). Here, we observe that the retinal prediction and the actual perceived orientation of the plane of regard match closely.

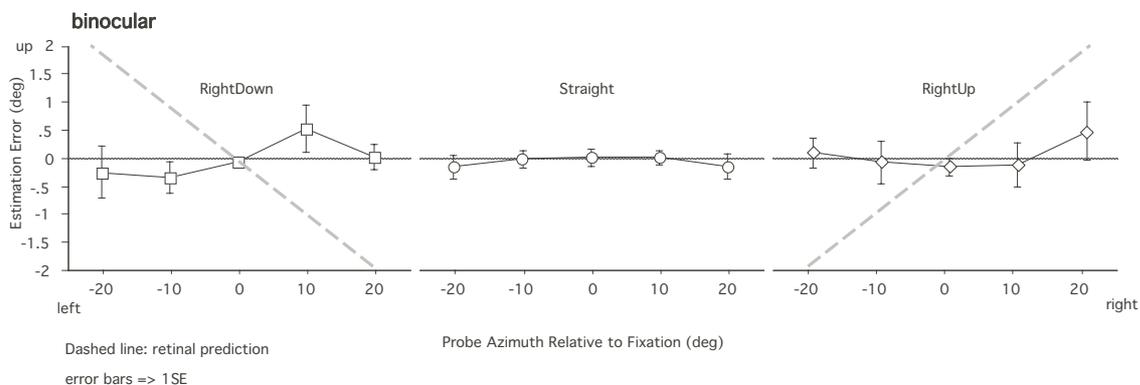


Figure 3. Binocular viewing. Average performance across six subjects does not vary significantly between the three experimental conditions. The estimation of probe position is accurate, the errors ranging below 0.5° . The perceived position was not biased towards the horizontal retinal meridian (dashed lines).

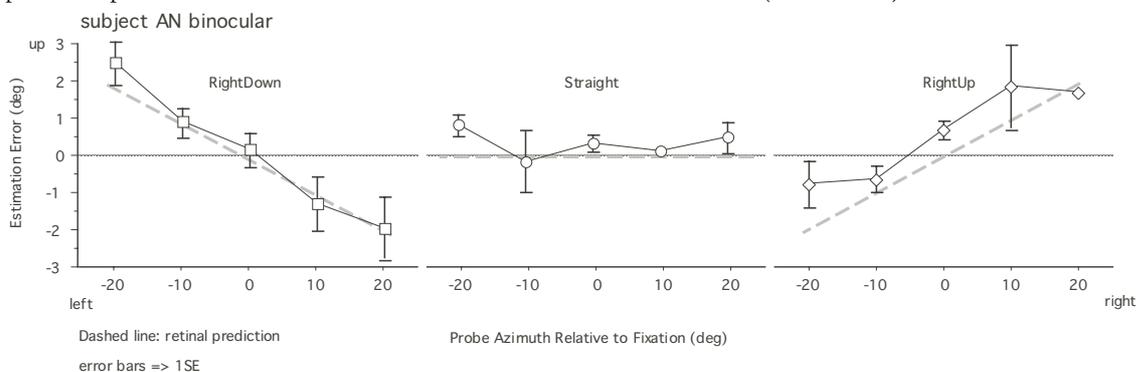


Figure 4. Binocular viewing, subject AN

Clear match between the retinal prediction (dashed lines) and perceived orientation of the plane of regard in subject AN, suggesting the use of a retinal representation of probe position without compensation for torsion.

Experiment 2. Binocular estimation of the orientation of the plane of regard with head tilt

Similar to the Experiment 1, subjects were asked to estimate elevation of flashed targets relative to their plane of regard, while fixating, in this case only, straight ahead. The plane of regard had different orientations in space because of the head tilt. As can be seen in Figure 5, the perceived plane of regard was tilted by as much as the head tilt. ANOVA showed no significant effect of the head tilt ($p=0.74$; $F(1,40)=0.12$) or probe azimuth ($p=0.93$; $F(4,40)=0.22$). Moreover, the estimation pattern is very similar to the condition without head tilt.

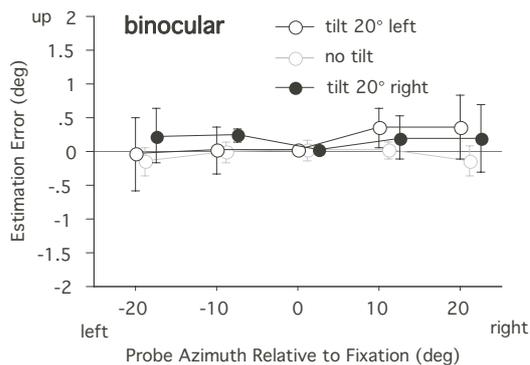


Figure 5. Binocular tilt conditions (compared to right up condition). The perceived plane of regard was tilted by as much as the head tilt. The estimation was as accurate as in the condition without head tilt.

Experiment 3. Monocular estimation of the orientation of the plane of regard

We repeated conditions of the experiments 1 en 2 presenting the stimuli only to the left eye. First, subjects were asked to estimate the elevation of flashed probes relative to the plane of regard while fixating straight ahead, right down, or right up. Statistical analysis (ANOVA) shows a systematic effect of the azimuth ($p<0.01$; $F(4,45)=8.52$). When we look closely at the fixation directions used (Figure 6), we see that straight ahead condition shows an systematic effect of the probe azimuth ($p<0.01$; $F(4,15)=18.64$) and causes the overall effect, whereas the results for eccentric fixation do not reveal this effect. Figure 6 shows that the retinal prediction (dashed lines) and the subjects' perception of the plane of regard do not correspond in this case, which is true for all subjects.

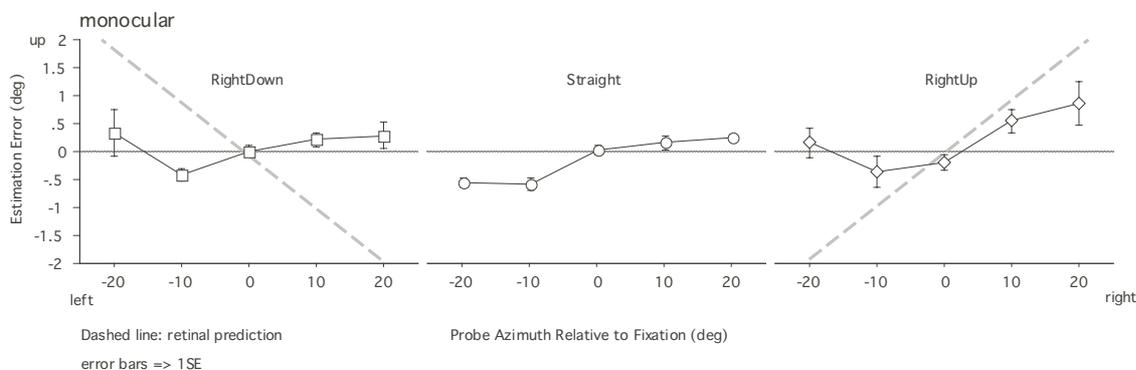


Figure 6. Monocular viewing. The average performance across six subjects in three experimental conditions is shown. In the eccentric conditions there is no correspondence between the retinal prediction (dashed lines) and the actual data. In the straight-ahead condition a significant effect ($p<0.01$; $F(4,15)=18.64$) of the probe position is present.

Subjects also estimated the position of flashed probes monocularly with their head tilted 20° to the left or to the right, while looking only with their left eye. Head tilt had no effect on the performance (ANOVA: $F(1,30)=1.66$; $p=0.21$). Azimuth of the probe relative to the fixation direction, however, appears to have a small effect on performance ($p=0.0027$; $F(4,30)=5.19$), at least for a number of probe positions (Figure 7).

On average, subjects are equally accurate (similar biases) and precise (variance) in their judgment of the plane of regard orientation (Figure 8) in monocular and binocular condition.

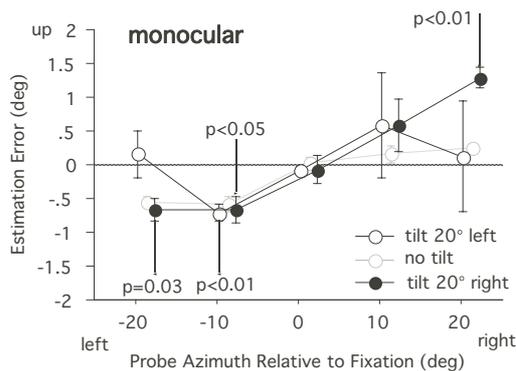
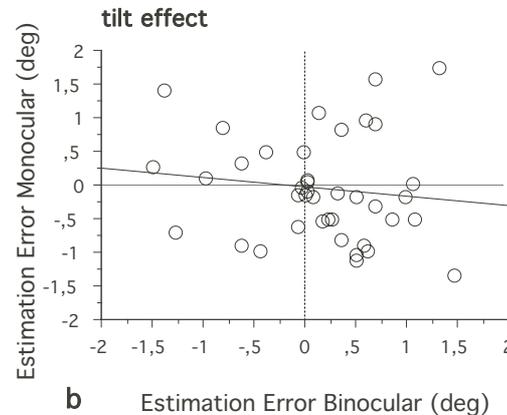
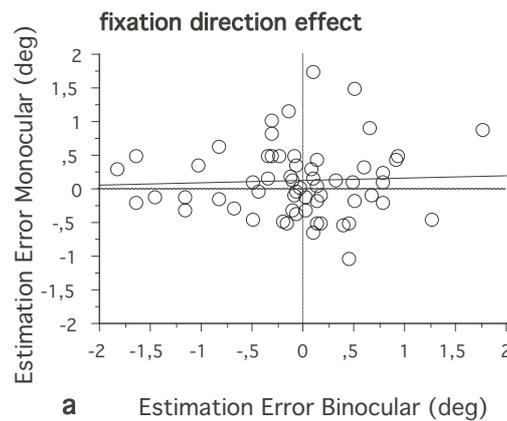


Figure 7. Monocular tilt. Average performance across subjects did not differ between the three conditions. However, for a number of probe positions, probe azimuth relative to fixation direction seemed to affect the performance, so that biases in estimation significantly larger than zero could be observed.

Figure 8. Monocular and binocular stimulation compared. The graphs review the data of binocular and monocular stimuli presentation. Each point represents a mean perceptual bias of one subject for certain combination of (a) fixation direction and probe azimuth or (b) tilt condition and probe azimuth, in monocular and binocular condition. In neither condition there is a correlation between monocular and binocular performance. This relation is retained also if the fixation directions (right-down, straight or right-up) or tilt sides (left or right) are looked at separately.



Experiment 4. Binocular estimation of the orientation of the midsagittal plane and the transverse plane

First, subjects estimated the remembered position of the flashed probes relative to their midsagittal plane, while fixating straight ahead, right down or right up. A significant effect of the fixation direction occurred ($p < 0.01$; $F(2,45)=22.90$), as well as an interaction effect between probe azimuth and fixation ($p < 0.01$; $F(8,45)=7.42$). When fixating straight ahead, subjects estimate the probes very accurately, the estimation bias being smaller than 0.5°. Systematic errors are made when subjects fixate one of our eccentric fixation positions. For the two eccentric fixation directions (Figure 9), the larger the elevation difference between the probe and the fixation, up or down, the larger the estimation bias. The judgment corresponds to the retinal prediction.

Second, the relative position of the flashed probes was judged with the head tilted 20° to the left or to the right, similar to the Experiment 2, for fixation straight ahead. The head tilt alone did not influence the performance of our subjects. As shown in Figure 10, compared to performance when sitting right up and fixating straight ahead without the head tilt, subjects do not make larger errors. ANOVA shows no effect of head tilt ($p=0.97$; $F(8,45)=0.29$).

Finally, subjects estimated the remembered position of the flashed probes relative to their transverse plane, while fixating right down or right up. In Figure 11 the pattern of errors is shown for this task. A significant effect of the fixation direction occurred ($p<0.01$; $F(1,20)=8.3$) and there is also an interaction effect between azimuth and fixation ($p<0.01$; $F(4,20)=3.6$). In one subject (EP) we found the pattern of errors dissimilar to the pattern observed in other subjects, but here too, the fixation direction had a significant effect on the performance, although to a smaller extent. This might be due to a practice-effect, as this subject being the author, tested the setup frequently.

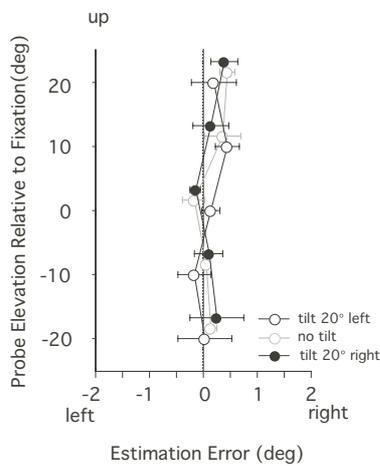
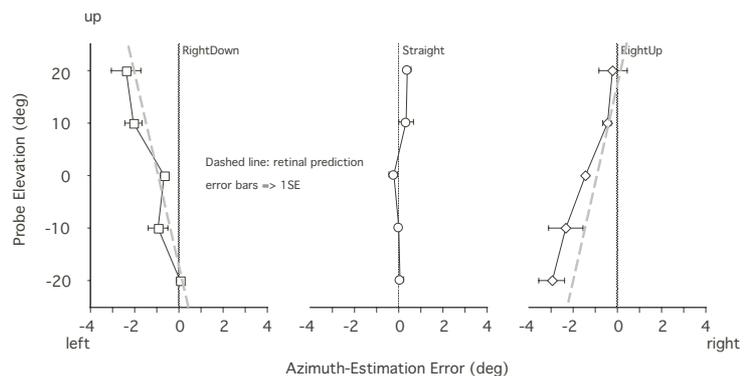


Figure 9. Estimation of the Midsagittal plane: eccentric fixations. The plot shows the average data across six subjects. The estimation of probe position relative to the midsagittal plane was dependent on fixation direction, and inaccurate for eccentric fixations (right down and right up). For both eccentric fixation directions holds that larger elevation difference between the probe and the fixation, up or down, results in a larger estimation bias. The direction of the bias was opposite to the fixation direction. There is a correspondence with the retinal prediction (dashed lines).

Figure 10. Estimation of the Midsagittal plane: head tilt. The tilt conditions of monocular stimulation are very similar to the condition right up. The bias in perceived position of the probes relative to the plane is not significantly different from zero. The average data of six subjects is plotted.



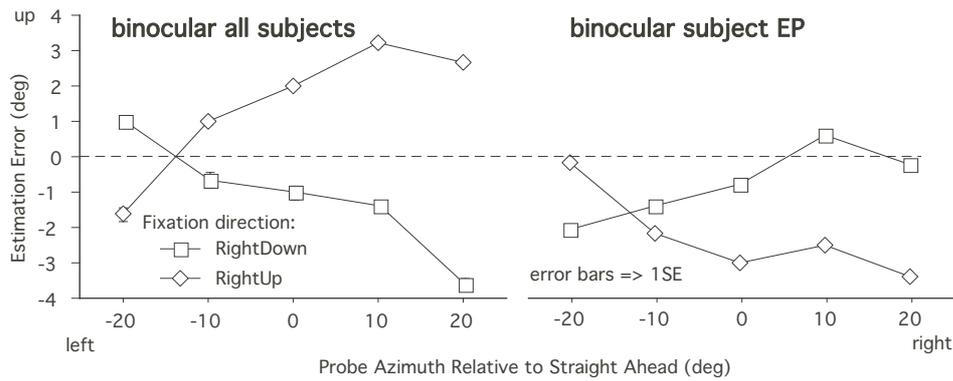


Figure 11. Estimation of the Transverse plane: eccentric fixations. The fixation direction had a significant effect on the performance ($p < 0.01$; $F(1,20) = 8.3$). ANOVA also shows an interaction effect between azimuth and fixation ($p < 0.01$; $F(4,20) = 3.6$). A different pattern was observed in subject EP. The fixation direction had also in this case a significant effect on the performance, but the perceived transverse plane was rotated in the opposite direction compared to the other subjects.

Discussion

When we fixate an object straight ahead, the horizontal meridia of the eyes are aligned and so is the projection of the plane of regard on the retinae. If the eyes change torsional orientation, as when looking in a tertiary eccentric direction, the horizontal meridia rotate out of the plane of regard. We found that ocular torsion did not cause mislocalisation of the plane of regard for binocular or monocular condition. Although eye torsion (Helmholtz) varies by ± 9 degrees across different fixation directions in our experiments, the perceived elevation of eccentric probes is not biased towards the location of the horizontal retinal meridian. This leads us to conclude that the judgment of the probe positions with respect to the plane of regard does not solely rely on the retinal representation as such. Some kind of mechanism is involved that integrates the retinal representation and the eye orientation signal to compensate for the torsion. Similar conclusions come from a number of perceptual (Haustein & Mittelstaedt 1990; Haustein 1992) and motor studies (Bockisch & Miller 1999; Klier & Crawford 1998; Smith & Crawford 2001; Medendorp et al. 2002).

As we move, not only our eyes, but the head also changes orientation constantly. By definition, the plane of regard follows the alterations in head orientation. The head-tilt also evokes compensatory eye-torsion in the direction opposite to the head rotation. Several studies showed that the gain of this counterroll, calculated as a ratio between the amplitude of counterroll and the amount of head tilt, is around 10% (Schworm et al. 2002; Collewijn et al. 1985). If the judgment would be solely based on retinal information, this cycloverision would lead to a bias of the perceived plane of regard position in our head tilt conditions up to 2° , which did not occur. The results of Experiment 2 show that the perceived plane of regard remains veridical. It was tilted by as much as the head tilt which confirms the conclusion that the judgment of head centric visual orientations does not entirely rely on retinal information, but that there is an active mechanism that compensates for eye counterroll (Nakayama & Balliet 1977; Haustein & Mittelstaedt 1990; Haustein 1992; Medendorp et al. 2002).

In the upright position, the horizontal meridia coincide with the visual horizon and the projection of the plane of regard on the retinae. So, one can argue that in this condition the subjects might use the internal representation of the visual horizon, an allocentric representation, to judge the probe positions. The absence of bias in the head tilt conditions rules out that option. Our results support the notion that the subjects report a head centric rather than an allocentric percept.

Under normal circumstances, human subjects are able to localize an object's horizontal location with respect to the median plane with considerable accuracy and precision (Li et al. 2001). The median plane coincides with the sagittal plane when eyes are oriented straight ahead. Eye shift to an eccentric fixation causes the projection of the sagittal plane to change orientation on the retina. Since the midsagittal plane is a true head-fixed plane, estimating the position of probes relative to this plane should not be affected by the eye orientation, if a correct head centric representation is built, and the same applies to our second head-fixed plane, the transverse plane. This is not what we found in our experiment. When subjects fixated 30° right down, the perceived midsagittal plane was slightly rotated in a

counterclockwise direction, from the subject's point of view (Figure 9). For the *same* fixation a *clockwise* bias was found when the subjects had to judge the orientation of the transverse plane (Figure 11).

The opposite occurred when the subjects fixated 30° right up. Now, clockwise bias was found for judgment of the mid-sagittal plane and counterclockwise for judgment of the transverse plane. How could our findings be explained?

It seems reasonable to assume that visual judgment of the midsagittal plane is based on activation of the vertical retinal meridian when the cyclopean eye looks straight ahead. We took for the “torsion” of the cyclopean eye the average Helmholtz torsion of left and right eye while fixating the fixation point right-up or right-down. These torsions are described by the extension of Listing's law to the domain of near vision (van Rijn & van den Berg 1993; Minken et al. 1995; Tweed 1997).

When the eye is positioned in some tertiary position, one could imagine that the brain uses the actual efference copy signals to ‘rotate’ the local sign (as Helmholtz would call it) of the *vertical* retinal meridian and use that rotated vertical meridian as a representation of the judged *mid-sagittal* plane. To relate the horizontal retinal meridian to the judged transverse plane one cannot assume that the *same* transformation was used by the brain, however. This holds because the judged transverse and the judged mid-sagittal planes are *not* perpendicular to one another (Figure 12) as the vertical and the horizontal meridia are, despite the *same* eye fixation. Hence the transformations must have been *different* because of the different judgments.

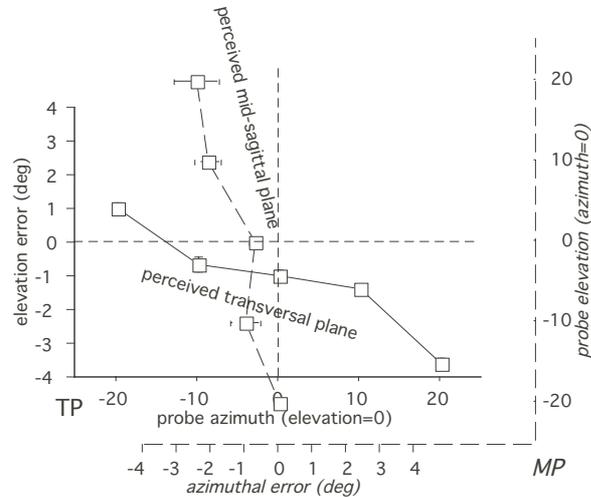


Figure 12. Non-orthogonality of the perceived orientations of the head-fixed planes. For the fixation 30° right and down subjects perceive the mid-sagittal plane (*MP*) as slightly rotated in counterclockwise direction, while in the perceived transversal plane (*TP*) we see a small but significant clockwise rotation. Consequently, the perceived planes are not orthogonal relative to each other. The different error patterns are not consistent with judgments based on single back-rotation towards the primary position, as this would result in errors that are identical for perceived orientation of mid-sagittal and transverse plane, and therefore the perceived planes would be orthogonal relative to each other.

We quantified the difference between the transformations by finding the single rotation that would carry the vertical retinal meridian into the judged mid-sagittal plane and the single rotation that would carry the horizontal meridian into the transverse plane. Figure 13 shows a scatter plot of these rotation axes in a headcentric frame, for 4 subjects, two fixation positions (right-up and right-down) and two judgments (mid-sagittal and transversal).

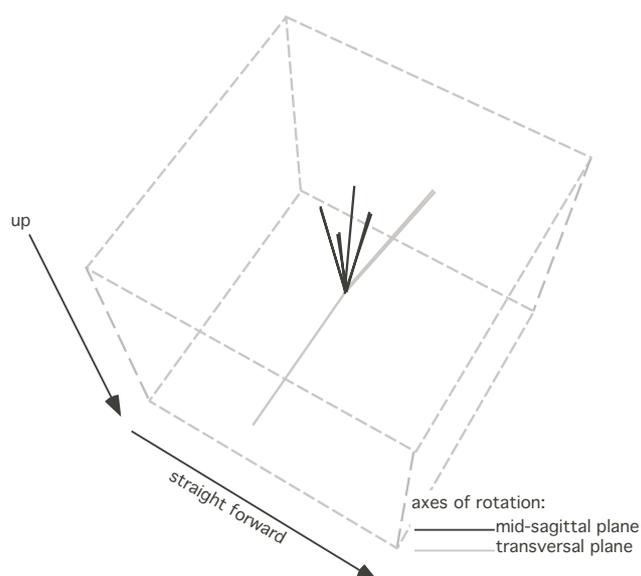


Figure 13. Fits to the data to find the axis of rotation. The rotation axes that would carry the vertical retinal meridian into the mid-sagittal plane and the horizontal retinal meridian into the transversal plane, by a single rotation, have been calculated from the data of four subjects. Figure shows a scatter plot of these rotation axes in a headcentric frame. Axes for two fixation directions (right-up and right-down) and two judgments, mid-sagittal (black lines) and transversal (gray lines) are plotted together. For all mid-sagittal plane judgments, the axes cluster along the head-centric vertical, whereas the transverse plane judgments cluster along the head-centric horizontal axis. Arrows represent the head orientation.

Clearly, for all mid-sagittal plane judgments, the axes cluster along the head-centric vertical, whereas the transverse plane judgments cluster along the head-centric horizontal axis. This result suggests that subjects used a ‘minimal transformation’ strategy to judge the orientations of head-fixed planes. Subjects reduce the transformation to a rotation in one dimension (horizontal or vertical), compared to a pure transformation to head-centric coordinates, that would involve all three components of rotation (head-centric horizontal, vertical and torsional) for right-up and right-down viewing.

Although the data are very close to a head centric judgment, there still seem to be a retinal contribution to the errors. The contribution of the retinal frame of reference is in agreement with the open-loop pointing studies to the remembered straight ahead targets that lie in the midsagittal plane at the same elevation as the eyes (Henriques et al. 1998). The visual targets for pointing are, as those studies reveal, represented in retinocentric frame and dependent on eye orientation. Although the visual judgment of straight ahead targets at the same elevation is accurate (Poljac & van den Berg 2003) and in disagreement with the erroneous pointing data, the misjudgments of targets’ positions in the midsagittal plane that are not at the same elevation as the eyes, as in our tertiary fixation directions, are consistent with the inaccurate pointing.

Of course, a number of other possible sources of errors in our data can be identified, such as random fluctuations of cyclotorsion (Enright 1990), large individual differences, (Bruno & van den Berg 1997), vergence-dependent torsion (Mok et al. 1992; van Rijn & van den Berg 1993; Minken et al. 1995), accommodation inaccuracies (Bruno & van den Berg 1997; Kapoula et al. 1999).

Further, we found that binocular vision is not required to accurately judge the targets in the plane of regard. The subjects were accurate in estimating the probe positions, despite the monocular stimulation and absence of binocular cues. In their model, Mayhew and Longuet-Higgins (1982) propose that the pattern of retinal binocular disparities could be used to determine the three-dimensional structure of space from a retinal image alone, without supplementary information derived from non-visual sources, such as eye movement control and proprioception mechanisms. The horizontal disparities between a pair of retinal images by itself supply

insufficient information, but supplemented by the vertical disparities of non-meridional image points the three-dimensional structure of a visual scene can be computed (Mayhew & Longuet-Higgins 1982).

Banks et al. (2002), in contrast with the Longuet-Higgins' model, suggest that vertical disparity is not always used for representation of space. They found that when stimuli are presented without or with a very small vertical disparity, perceived azimuth relied on the retinal eccentricity of the image and felt eye position. This is consistent with our finding that even in the absence of disparity information, such as in monocular stimulation, subjects are able to judge the position of objects in space relative to the plane of regard. Vertical disparities were not available in our experiment. Eye elevation, an extraretinal cue, could be utilized to estimate the probe position. The perceived drift of after-images in the dark when the subjects make an eye movement testifies to the use of horizontal and vertical eye signals for direction perception. Even when stimuli are viewed monocularly vertical gaze angle is used (Carey et al. 1998) to judge distance, for instance.

So, the position relative to the plane of regard is perceived correctly, irrespective of fixation direction, head orientation or presence of binocular cues. By definition, the plane of regard contains the interocular axis, the axis connecting the two projection centers of the eyes. The change in the eye elevation causes the plane of regard to rotate around that axis, which is the only degree of freedom of this plane. Objects outside the plane have certain offset in elevation with respect to the plane. Binocular localization relative to the plane of regard might be a good starting point to judge other objects' positions relative to the head. If the position of an object is known relative to the plane, then we are only one step away from the head centric representation. That step involves the estimation of the orientation of the plane of regard relative to the head. We already pointed out that the orientation of the plane of regard depends exclusively on eye elevation. To reconstruct the position of the plane of regard, the eye elevation must be known.

In principle, the information about eye elevation is available from extra-retinal sources. To use the gaze angle, orientation of the head relative to the shoulders and the eye orientation in the head, eye elevation, must be known (Gardner & Mon-Williams 2001). Direction of gaze is in general recognized as a very useful source of information, for instance, to estimate distance (Ooi et al. 2001), especially where pictorial cues are impoverished (Mon-Williams et al. 2001). Gardner and Mon-Williams (2001) demonstrated clear evidence that the visual system utilizes vertical gaze angle as a distance cue. They perturbed the vertical gaze angle without affecting the retinal cues to distance to affect judgment. Vertical gaze angle can also be used as a distance cue for the programming of prehension or judging objects' heights (Wraga & Proffitt 2000). Information on vertical gaze angle can be obtained from efference copy and afferent feedback (Mon-Williams & Tresilian 1999; Adams et al. 1996).

Thus, these studies of vertical gaze implicate that the information about eye elevation is available. Similarly, slant studies also demonstrate the use of vertical eye position information that is coming from extra-retinal sources such as the sensed eye position (James et al. 2001) to make judgments.

In summary, we found that people perceive the elevation of objects relative to the plane of regard correctly irrespective of eye or head orientation, which is an indication of a compensation for eye torsion associated with the current eye

orientation (actual torsion). However, the position of probes relative to the midsagittal or the transverse plane, both true head-fixed planes, was misjudged. The subjects seemed unable to compensate for eye torsion when judging position of objects that do not contain the lines of sight. With regard to the plane of regard we conclude that this plane is a good starting point to represent the position of visual stimuli in head centric coordinates.

Reference

Adams W, Frisby JP, Buckley D, Gårding J, Hippisley-Cox SD, Porrill J (1996) Pooling of vertical disparities by human visual system *Perception* 25: 165-176

Banks MS, Backus BT, Banks RS (2002) Is vertical disparity used to determine azimuth? *Vision Research* 42: 801-807

van den Berg AV (1996) Judgments of heading *Vision Research* 36(15): 2337-2350

Bockisch JC, Miller JM (1999) Different motor systems use similar damped extraretinal eye position information. *Vision Research* 39: 1025-1038

Bremmer F, Schlack A, Shah NJ, Zafiris O, Kubischik M, Hoffmann K, Zilles K, Fink GR (2001) Polymodal motion processing in posterior parietal and premotor cortex: a human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron* 29(1): 287-96

Bruno P, van den Berg AV (1997) Relative orientation of primary positions of the two eyes. *Vision Research* 37(7): 935-947

Carey DP, Dijkerman HC, Milner AD (1998) Perception and action in depth. *Consciousness and Cognition* 7: 438-453

Collewijn H, van der Steen J, Ferman L, Jansen TC (1985) Human ocular counterroll: assessment of static and dynamic properties from electromagnetic scleral coil recordings. *Experimental Brain Research* 59: 185-196

Crawford JD, Guitton D (1997) Visual-motor transformations required for accurate and kinematically correct saccades. *Journal of Neurophysiology* 78: 1447-1467

Duhamel JR, Bremmer F, BenHamed S, Graf W (1997) Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature* 389(6653): 845-848

Enright JT (1990) Stereopsis, cyclotorsional "noise" and the apparent vertical. *Vision Research* 30: 1487-1497

Fetter M, Haslwanter T, Misslisch H, Tweed D (1997) Three-dimensional kinematics of eye, head and limb movements. Amsterdam: Harwood Academic Publishers

Flanders M, Tillery SI, Soechting JF (1992) Early stages in a sensorimotor transformation. *Behavioral and Brain Sciences* 15: 309-362

Gardner PL, Mon-Williams M (2001) Vertical gaze angle: absolute height-in-scene information for the programming of prehension. *Experimental Brain Research* 136: 379-385

Haustein W (1992) Head-centric visual localization with lateral body tilt. *Vision Research* 32: 669-673

- Haustein W, Mittelstaedt H (1990) Evaluation of retinal orientation and gaze direction in the perception of the vertical. *Vision Research* 30: 255-262
- von Helmholtz, H (1910) *Physiological Optics* (Translation by JPC Southall from the 3rd German edition of *Handbuch der Physiologischen Optik* Voss, Hamburg) Dover, New York
- Henriques DYP, Klier ME, Smith MA, Lowy D, & Crawford JD (1998) Gaze centered remapping of remembered visual space in an open-loop pointing task. *Journal of Neuroscience* 18: 1583-1594
- Hooge IThC, van den Berg AV (2000) Visually evoked cyclovergence and extended Listing's law. *Journal of Neurophysiology* 83: 2757-2775
- James FMK, Whitehead S, Humphrey GK, Banks MS, Vilis T (2001) Eye position sense contributes to the judgment of slant. *Vision Research* 41: 3447-3454
- Kapoula Z, Bernotas M, Haslwanter T (1999) Listing's plane rotation with convergence: role of disparity, accommodation, and depth perception. *Experimental Brain Research* 126: 175-186
- Klier EM Crawford JD (1998) Human oculomotor system accounts for 3-D eye orientation in the visual-motor transformation for saccades. *Journal of Neurophysiology* 80: 2274-2294
- Li W, Dallar N, Marin L (2001) Influences of visual pitch and visual yaw on visually perceived eye level (VPEL) and straight ahead (VPSA) for erect and rolled-to-horizontal observers. *Vision Research* 41: 2873-2894
- Mayhew JEW, Longuet-Higgins HC (1982) A computational model of binocular depth perception. *Nature* 297: 376-378
- Medendorp WP, Smith MA, Tweed DB, Crawford JD (2002) Rotational remapping in human spatial memory during eye and head motion. *The Journal of Neuroscience* 22: RC196
- Minken AWH, Gielen CCAM, van Gisbergen JAM (1995) An alternative three-dimensional interpretation of Hering's equal-innervation law for version and vergence eye movements. *Vision Research* 35: 93-102
- Mon-Williams M, McIntosh RD, Milner AD (2001) Vertical gaze angle as a distance cue for programming reaching: insights from visual agnosia II (of III). *Experimental Brain Research* 139: 137-142
- Mon-Williams M, Tresilian JR (1999) Some recent studies on the extraretinal contribution to distance perception. *Perception* 28(2): 167-181
- Mok D, Ro A, Cadera W, Crawford JD, Vilis T (1992) Rotation of Listing's plane during vergence. *Vision Research* 32: 2055-2064
- Nakayama K, Balliet R (1977) Listing's law, eye position sense, and the perception of the vertical. *Vision Research* 17: 453-457
- Ooi TL, Wu B, He ZJ (2001) Distance determined by the angular declination below the horizon. *Nature* 414: 197-200
- Poljac E, van den Berg AV (2003) Representation of heading direction in far and near-head space. *Experimental Brain Research* 151: 501-513
- van Rijn LJ, van den Berg AV (1993) Binocular eye orientation during fixation: Listing's law extended to include eye vergence. *Vision Research* 33(5/6): 691-708
- Schworm HD, Ygge J, Pansell T, Lennerstrand G (2002) Assessment of ocular counterroll during head

tilt using binocular video oculography. *Investigative Ophthalmology & Visual Science* 43(3): 662-667

Smith MA, Crawford JD (2001) Implications of ocular kinematics for the internal updating of visual space. *Journal of Neurophysiology* 86: 2112-2117

Tweed D (1997) Visual-motor optimization in binocular control. *Vision Research* 37: 1939-1951

Tweed D, Vilis T (1990) Geometric relations of eye position and velocity vectors during saccades. *Vision Research* 30: 111-127

Wraga M, Proffitt DR (2000) Mapping the zone of eye-height utility for seated and standing observers. *Perception* 29: 1361-1383

Localization of the plane of regard in space¹



¹ *adapted from:* Poljac E, van den Berg, AV (2004) Localization of the plane of regard in space, *in press*

Abstract

When we fixate an object in space, the rotation centers of the eyes together with the object, define a plane of regard. People perceive the elevation of objects relative to this plane accurately, irrespective of eye or head orientation (Poljac et al. 2004). Yet, to create a correct representation of objects in space, the orientation of the plane of regard in space is required. Subjects pointed along an eccentric vertical line on the touch screen to the location where their plane of regard intersected the touch screen positioned on their right. The distance of the vertical line to the subject's eyes varied from 10 to 40 cm. Subjects were sitting upright and fixating one of the nine randomly presented directions ranging from 20° left down to 20° right up relative to their straight ahead. The eccentricity of fixations relative to the pointing location varied up to 40°. Subjects underestimated the elevation of their plane of regard (on average 3.69 cm, SD=1.44 cm), regardless of the fixation direction or pointing distance. However, when the targets were shown on a display mounted in a table, to provide support of the subject's hand throughout the trial, subjects pointed accurately (average error 0.3 cm, SD=0.8 cm). In addition, head tilt 20° to the left or right did not cause a change in accuracy. The bias observed in the first task could be caused by maintained tonus in arm muscles when arm is raised, that might interfere with the transformation from visual to motor signal needed to perform the pointing movement. We conclude that the plane of regard is correctly localized in space. This may be a good starting point to represent objects in head-centric coordinates.

Introduction

From several recent studies we know that the extraretinal signals about eye orientation in the head are available. Orientation of the head relative to the shoulders and the eye orientation in the head, eye elevation, combined provide the vertical gaze angle (Gardner & Mon-Williams 2001), commonly recognized as a very useful source of information to estimate distance (Ooi et al. 2001). Gardner and Mon-Williams (2001) varied the vertical gaze angle without affecting the retinal cues to distance to affect judgment and demonstrated clear evidence that the visual system utilizes vertical gaze angle as a distance cue. Efference copy and afferent feedback can be the source of information on vertical gaze (Mon-Williams & Tresilian 1999; Adams et al. 1996) and in their model, Mon-Williams and Tresilian (1998) describe the possible way of how these extra-retinal signals might be utilized by the visual system for a more accurate perceptual judgment.

Thus, the studies of vertical gaze suggest that the information about eye elevation is available. By definition, the plane of regard contains the interocular axis, the axis connecting the two projection centers of the eyes, and the lines of sight. The change in the eye elevation causes the plane of regard to rotate around that axis, which is the only degree of freedom of this plane. Hence, the vertical angle of the plane of regard is the only information needed to define its location relative to the head. To define the plane of regard relative to space, head orientation should also be taken into account. In this study we investigate if people can point to their plane of regard accurately, with the head upright and tilted.

Objects outside the plane have a certain offset in elevation with respect to the plane. In their recent study, Poljac et al. (2004) found that people perceive the elevation of objects relative to the plane of regard accurately, irrespective of eye or head orientation. The authors concluded that the localisation relative to the plane of regard is a good starting point to judge other objects' positions relative to the head. The only information needed to be able to create a head-centric representation of objects is the accurate estimation of the plane's orientation relative to the head.

Building a head-centric representation in this way is in accordance with one broadly accepted view that such a representation arises from a retinal representation, taking the eye orientation relative to the head into account. The first step, binocular perception of an object relative to the plane of regard, could be based on the pattern of binocular disparities. Vertical disparity (is zero for objects inside the plane of regard, and) varies when objects' vertical position relative to the plane changes. According to Mayhew and Longuet-Higgins (1982) the pattern of binocular disparities could be used to determine the three-dimensional structure of space from a retinal image alone, without supplementary information derived from extra-retinal sources, such as eye movement control and proprioception mechanisms. To extract disparity information that is used for a three-dimensional percept, first, correspondence is established between the projections of images onto the retinae of the two eyes (Gårding 1995). From the horizontal disparities between a pair of retinal images, supplemented by the vertical disparities of non-meridional images, the three-dimensional structure of a visual scene can be created (Mayhew & Longuet-Higgins 1982).

However, even if patterns of binocular disparities were used as in Mayhew and Longuet-Higgins' analysis, at least the vertical orientation of the eyes in the head is required to build the representation of an object's position relative to the head. This holds because different positions of the object with respect to the head can give rise to the same pattern of vertical disparities (Figure 1). So in absence of eye elevation signals, vertical disparities cannot provide sufficient information to build a completely unambiguous head-centric representation. Removal of the remaining ambiguity of the retinal images by eye elevation signals is the second important step towards a head-centric representation. To be able to do that, the position of the eyes in the orbit must be available and combined with the retinal coordinates of the object.

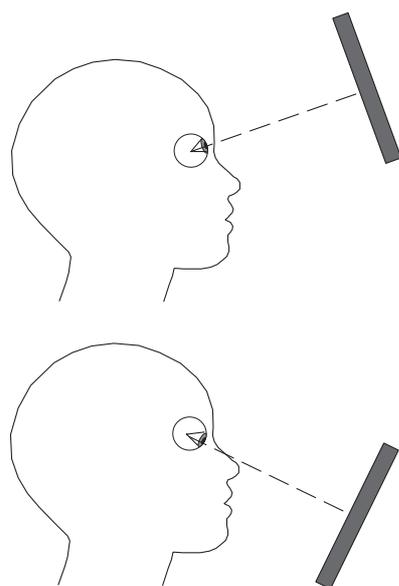


Figure 1. Same retinal images for different eye orientations. The image projected on the retina is identical in the two depicted conditions. To estimate the object's position relative to the head, eye orientation in the head must be known.

Judging the location relative to the head is useful to protect the head from collisions with potentially harmful objects, for example. Utilizing a head-centric representation of object's location would be a rather straightforward way to estimate where the object is positioned relative to the head. Strong evidence that such head-centric representations exist is coming from the high proportion of neuronal responses to stimuli near and approaching the face (Cooke et al. 2003) and neurophysiological studies that have identified brain areas in the monkey containing cells with head-centric receptive fields (Duhamel et al. 1997). These receptive fields have the same spatial location relative to the head, irrespective of eye orientation. Areas with similar properties may exist also in the human brain (Bremmer et al. 2001).

Materials and methods

Subjects

Six subjects participated in the experiment. Two of them were left-handed. One subject (EP) was aware of the design and purpose of the experiments, the rest of the subjects were naïve. This study has been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. Participation was voluntary and all the subjects gave their informed consent prior to their inclusion into the study.

Apparatus

Subjects were seated in complete darkness and looked at a monitor (Sony 19" FD Trinitron CRT), on which the stimuli generated by a Macintosh G4 computer with a Graphics acceleration board (Formac Proformance III) were presented. To record the right-index finger position in our pointing paradigm, a transparent touch screen (21" IntelliTouch) was used. The subject's head was stabilized by a dental bite-board mounted on the table. Looking through a red filter with their left eye and a green filter with their right eye, each eye could be stimulated independently, as red and green images were used. Each image was presented as seen from that eye's perspective, which enabled presenting a 3D scene in stereoscopic perspective. A camera-based measurement of the eye's pupil orientation (accuracy $\approx 0.25^\circ$) was used to make sure that ocular fixation criteria were met throughout the trials (SMI EyeLink-inc Teltow, Germany). Before the experiment started, the precise location of each subject's eyes relative to the monitor's center was determined by a triangulation procedure (van den Berg 1996). Two vertical and one horizontal calibration line were positioned at a distance of 15 cm in front of the screen, in the subject's frontal plane parallel to the screen. The subjects were asked to align a pointer on the screen, with either calibration line in turn. This allows construction of three gaze lines for each eye. The intersection of the three gaze lines allows for a precise localization of each eye's center of rotation relative to the monitor.

In each experiment the face was oriented parallel to the monitor, and the eyes had nearly the same distance to the monitor. The exact position and orientation of the plane of regard could be determined using the measured position of the eyes' rotation centers and the position of the fixation point. Two laser pointers (custom made) with adjustable rotation centers were placed carefully (average error ± 0.2 mm) at the position of the rotation centers of the eyes. They enabled us to determine where the plane of regard intersected the touch screen, for each fixation direction. The fixation point was a stereo image of a single point at a simulated cyclopean distance of approximately 40 cm.

Procedure

The experiments were performed in total darkness. Consequently, the subjects had no visual reference during the trials. The concept of the plane of regard was explained to the subjects prior to the experiment. All angular measures in the sequel refer to Helmholtz angles, i.e. elevation denotes the rotation about the interocular axis and azimuth rotation about the axis perpendicular to the plane of regard.

Subjects were asked to point to their plane of regard, at the place where the plane of regard intersected the touch screen, while maintaining fixation. Nine fixation directions ranging from 20° left and down to 20° right and up relative to their straight ahead were used. Straight ahead was defined as the direction perpendicular to the interocular axis in the horizontal plane, and intersecting that axis half way between the eyes. The fixation point was presented for 0.75 seconds. Its disappearance indicated that an arm movement could be initiated. A stick, positioned vertically in front of the touch screen, restricted the movement of the subject's finger in azimuth direction, so the subjects only had to judge the elevation (Figure 2). The same fixation direction had to be maintained during the whole trial until the subject's response, which ended the trial and started a new one. When the eye orientation deviated more than 0.5° from the orientation before the fixation point disappeared, the trial was rejected. For each fixation direction ten repeats were collected. Pointing errors that we report later, are computed as the pointing position relative to the corresponding pointed position during calibration.

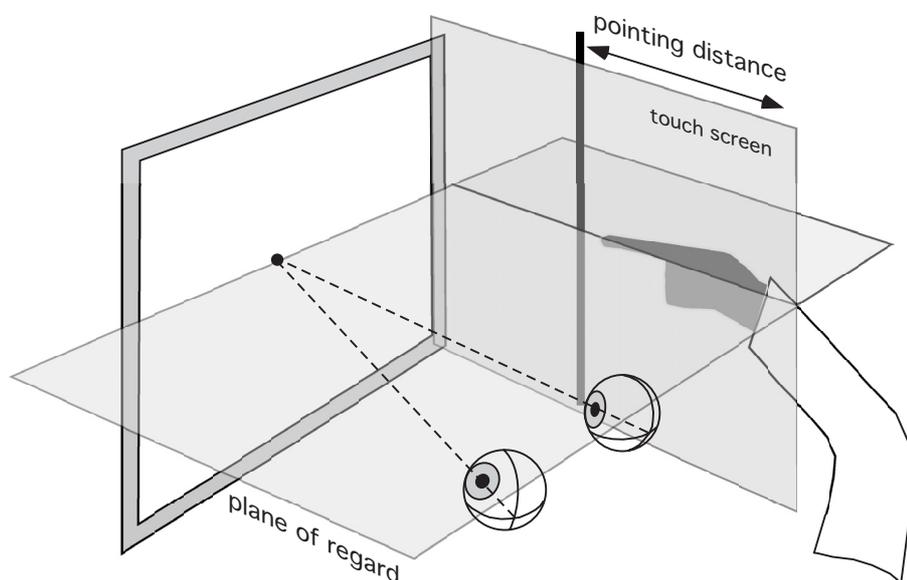


Figure 2. Experimental setup for the pointing paradigm. In Experiment 1 the touch screen was positioned on the right. In this way, the azimuthal eccentricity of fixations relative to the pointing location could vary up to 40° . Dependent on the elevation of fixation, the plane of regard intersects the touch screen at a certain position along the stick placed vertically in front of the touch screen. Pointing distance was adjusted by placing the vertical stick at a different location along the touch screen.

Experiment 1. Pointing to the plane of regard, head upright

Subjects were seated in an upright position while performing the task described above. The touch screen was positioned on their right side as depicted in Figure 2. Consequently, the eccentricity of fixations relative to the pointing location varied up to 40° . The subjects could easily reach every position on the touch screen with their right index finger. They repeated the task in blocks for four different positions of the stick, representing four pointing depths, the closest being approximately 10 cm in front of the eye's position and the most distant 40 cm in front of the eyes, which was roughly at the monitor's distance. The sequence in which the stick position was changed was varied for different subjects to avoid a possible order-effect. After the experiment was completed, the two laser pointers were positioned exactly at the same place as the subjects' eyes during the experiment by repeating the triangulation procedure until the laser positions matched eye position. In this way we could reproduce the orientation of their plane of regard for each fixation direction and in addition also where the plane of regard intersected the touch screen. In this calibration procedure subjects pointed to the place of this

intersection, which was used as a calibration value and off-line compared with the pointing positions during the experiment.

Experiment 2. Pointing to the plane of regard, with head slant and arm support

To make a pointing movement in Experiment 1, subjects had to lift their arm, hand and finger to the height of the perceived plane of regard position. The maintained tonus in arm muscles when the arm is raised might interfere with the transformation from visual to motor signal, needed to perform the movement that guides the finger to the right location. We adjusted the experimental setup in order to eliminate this possibly interfering signal. Subjects were again seated in complete darkness and looked at a monitor (Sony 19" FD Trinitron CRT) mounted in the table with a slanted surface (5° relative to the floor). Just in front of the monitor, the touch screen was placed (Figure 3). The surface of the touch screen and the table were even. The face was, just as in upright condition, positioned parallel to the monitor. Data analysis and the calibration procedure were as in Experiment 1. The table provided support to the subject's hand throughout the trial. The experiment was done for two pointing distances, approximately 20 cm and 40 cm relative to the subject's eyes.

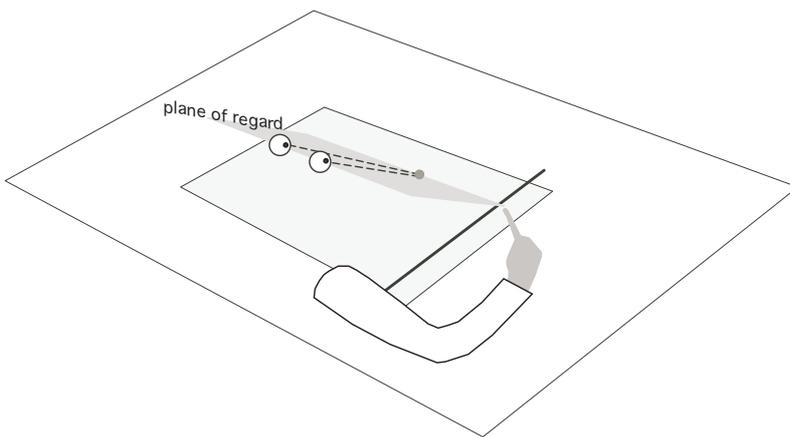


Figure 3. The setup for experiments with head tilt and arm support. The experimental setup was adjusted to provide support to the subjects' hand. A computer monitor was mounted in the table and just on top of it the touch screen was placed.

Experiment 3. Pointing to the plane of regard with head slant and head tilt

In Experiment 2 the subjects looked to the monitor in the frontal plane. Therefore, their plane of regard intersected the image plane of the monitor in such a way that this intersection line was parallel to the horizontal edge of the monitor and table edge. Although the subjects had no visual reference, we wanted to exclude the possibility that their judgment of the plane of regard position relied on some kind of allocentric representation, like an internal reference of the horizon. Hence, Experiment 2 was repeated while the subject's head was tilted 20° to the left or 20° to the right shoulder and accordingly the orientation of the plane of regard was changed. Due to restrictions put by our experimental setup it was not possible to present the fixation points for upward direction in case of the left head tilt, and for downward fixation direction in case of the right head tilt. Data analysis and the calibration procedure were as in Experiment 1.

Results

Experiment 1. Pointing to the plane of regard, head upright

Subjects pointed to the location where their plane of regard intersected the touch screen, while sitting upright and fixating in one of the nine fixation directions. Figure 4 shows the performance of our six subjects. ANOVA shows no effect of the fixation azimuth ($F(2,180)=0.32$, $p=0.73$).

Therefore, we combined all data collected at one elevation in the figures. Example of data (subject JB, Experiment 2) for all fixation directions is shown in Figure 5b. In general, the subjects pointed inaccurately towards their plane of regard, underestimating the elevation for almost all points measured (average error 3.69 cm, $SD=1.44$). All subjects pointed below the actual position of their plane of regard with nearly the same magnitude irrespective of the pointing distance which did not have a significant effect on the pointing error ($F(3,180)=0.95$, $p=0.42$).

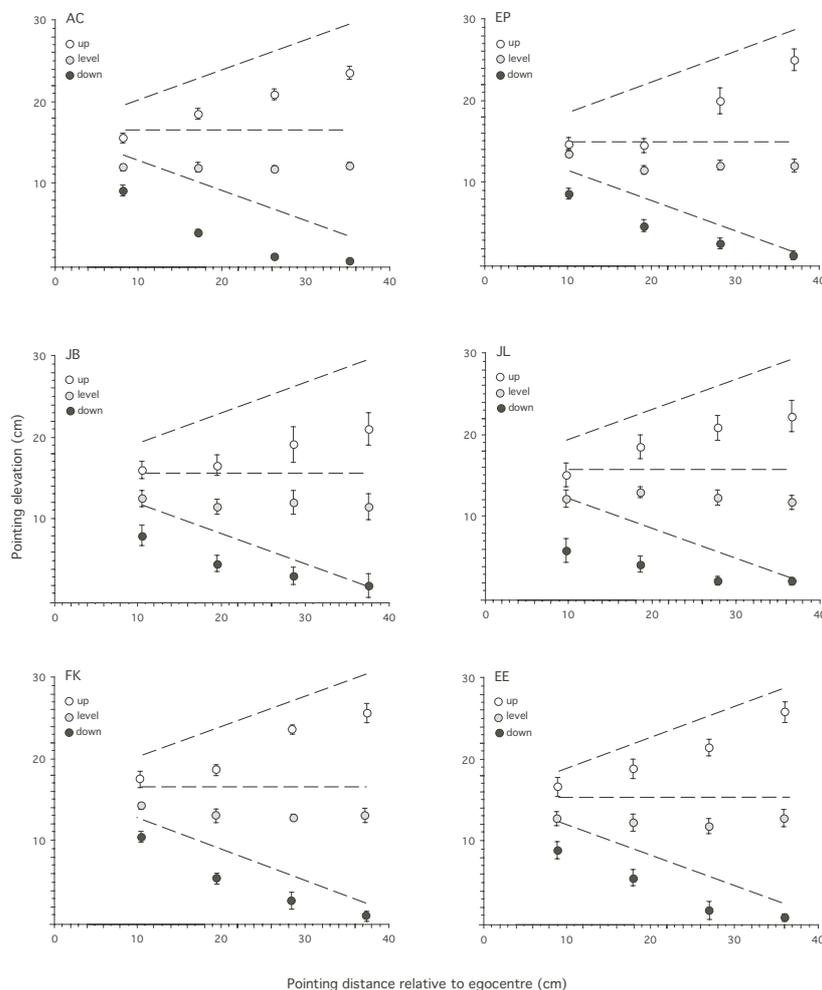


Figure 4. Pointing to the plane of regard, head upright. The performance of our four subjects in Experiment 1. The dotted lines represent the actual orientation of the plane of regard. It was derived from the calibration procedure. The subjects could not point accurately towards their plane of regard. They underestimated the elevation a magnitude that was independent of the pointing distance for almost all points measured. Each point is an average of ten repeats. The error bars denote 1SD.

However, the errors for upward fixation directions are somewhat larger (average difference of 0.9 cm) than for the other two fixation directions and consequently, ANOVA shows an effect of elevation ($F(2,180)=6.52$, $p=0.013$). We did not observe any interaction effects. Worth mentioning is a rather small error appearing at 40 cm depth, in downward fixation condition (1.6 cm). Here, the subjects could not point much lower without going outside the touch screen, which we think is the explanation for a moderate error. Note also that the distance varies

slightly between subjects because we could not exactly position the ego-centre at the same location relative to the screen for different subjects.

Experiment 2. Pointing to the plane of regard, with arm support

Subjects were once again asked to point to their plane of regard while looking to the monitor, now mounted in the table (Figure 3). In this way they could rest their arms on the table throughout the trials. As can be seen from Figure 5 the performance improved considerably compared to Experiment 1. The subjects were very accurate in pointing to the place where their plane of regard intersected with the touch screen. In the statistical analysis we used absolute values of the pointing deviations relative to the expected values, regardless of the direction of error. This means that, across subjects, pointing values could not average out.

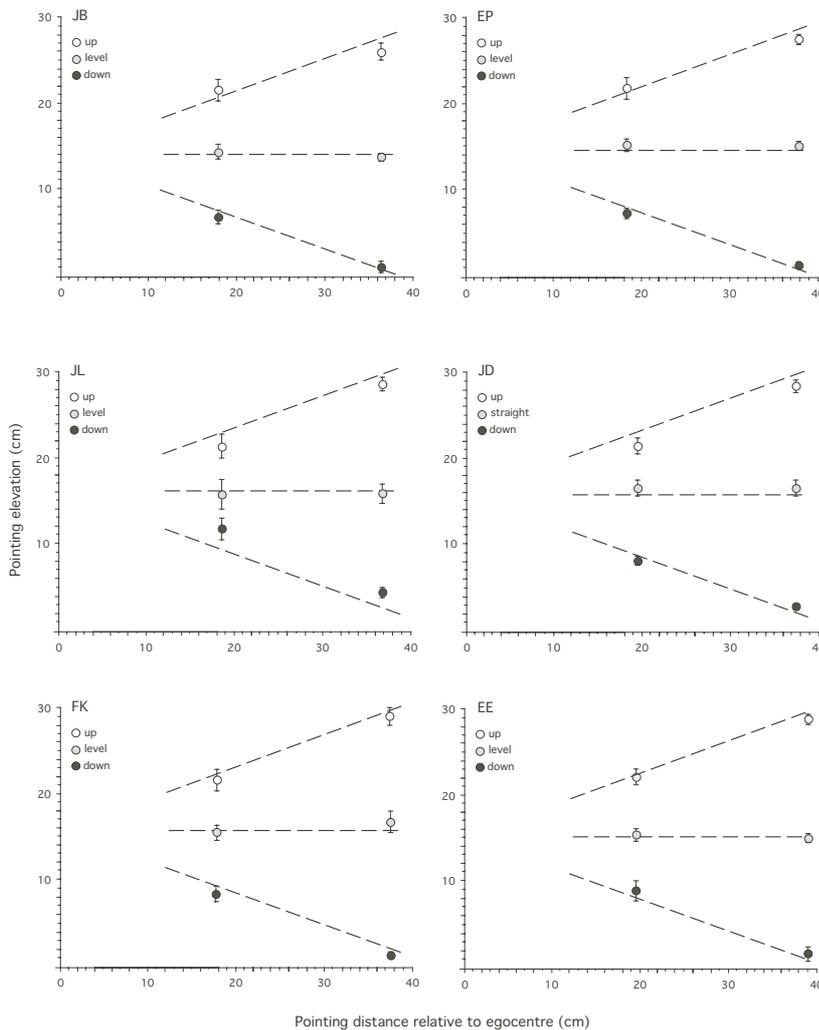


Figure 5a. Pointing to the plane of regard with arm support. The individual pointing performance is plotted, compared with calibration measurement of the position of the plane of regard (dotted lines). In comparison to the Experiment 1, the subjects significantly improved their pointing accuracy. This is true for all of the subjects. In one subject (JL) there is a slight underestimation of the elevation of the plane of regard in the up condition and an overestimation in the down condition. This could be interpreted as a forward shift in the perceived ego-centre. Each point is an average of ten repeats. The error bars denote 1SD.

The average (absolute) difference with the expected pointing positions based on calibration values was 0.8 cm (SD=0.5cm), which is about 1.1° at 40 cm distance. In one subject (JL) we observe a slight underestimation of the elevation of the plane of regard in the up condition and an overestimation in the down condition, which resembles an ego centre slightly shifted forward. ANOVA shows that error magnitude is not affected by pointing distance ($F(1,90)=0.018$, $p=0.89$), fixation azimuth ($F(2,90)=0.05$, $p=0.95$) or elevation ($F(2,90)=3.06$, $p=0.06$) and that there are no interaction effects. The absolute errors for straight-ahead fixation direction

were on the average 0.38 cm smaller than for the two other fixation directions, but just not significant ($p=0.04$). Average signed error across six subjects does not differ from zero ($p=0.69$).

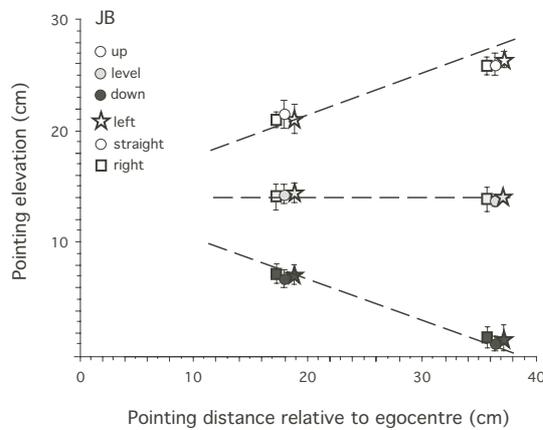


Figure 5b. Pointing to the plane of regard with arm support, example of all fixation directions, subject JB. Pointing performance of subject JB is plotted for the nine fixation directions. We see that different fixation azimuths do not differ from each other, within each elevation. The icons representing the left and right fixation azimuths are shifted slightly relative to the straight-ahead fixations to make the figure clearer. The error bars denote 1SD.

Experiment 3. Pointing to the plane of regard with head tilt

Subjects pointed to their plane of regard with their head tilted 20° to the left or to the right. The head orientation did not have an effect on the performance ($F(1,26)=0.62$, $p=0.44$). Subjects were very accurate with an average (absolute) error relative to the calibration positions of 0.85 cm ($SD=0.84$ cm) for the head tilt towards the left shoulder (Figure 6a), and an error of 0.64 cm ($SD=0.67$ cm) for the right head tilt (Figure 6b). ANOVA did not reveal any effects of pointing distance ($F(1,26)=0.41$, $p=0.53$). However, the subjects were more accurate when fixating straight-ahead, and ANOVA showed significantly smaller error (average difference of 0.6 cm) than for upward or downward fixation ($F(2,26)=5.62$, $p=0.012$). Again, here we used absolute values of the pointing errors. If the analysis is done on signed errors, we observe that the average across our six subjects does not significantly differ from zero ($p=0.63$).

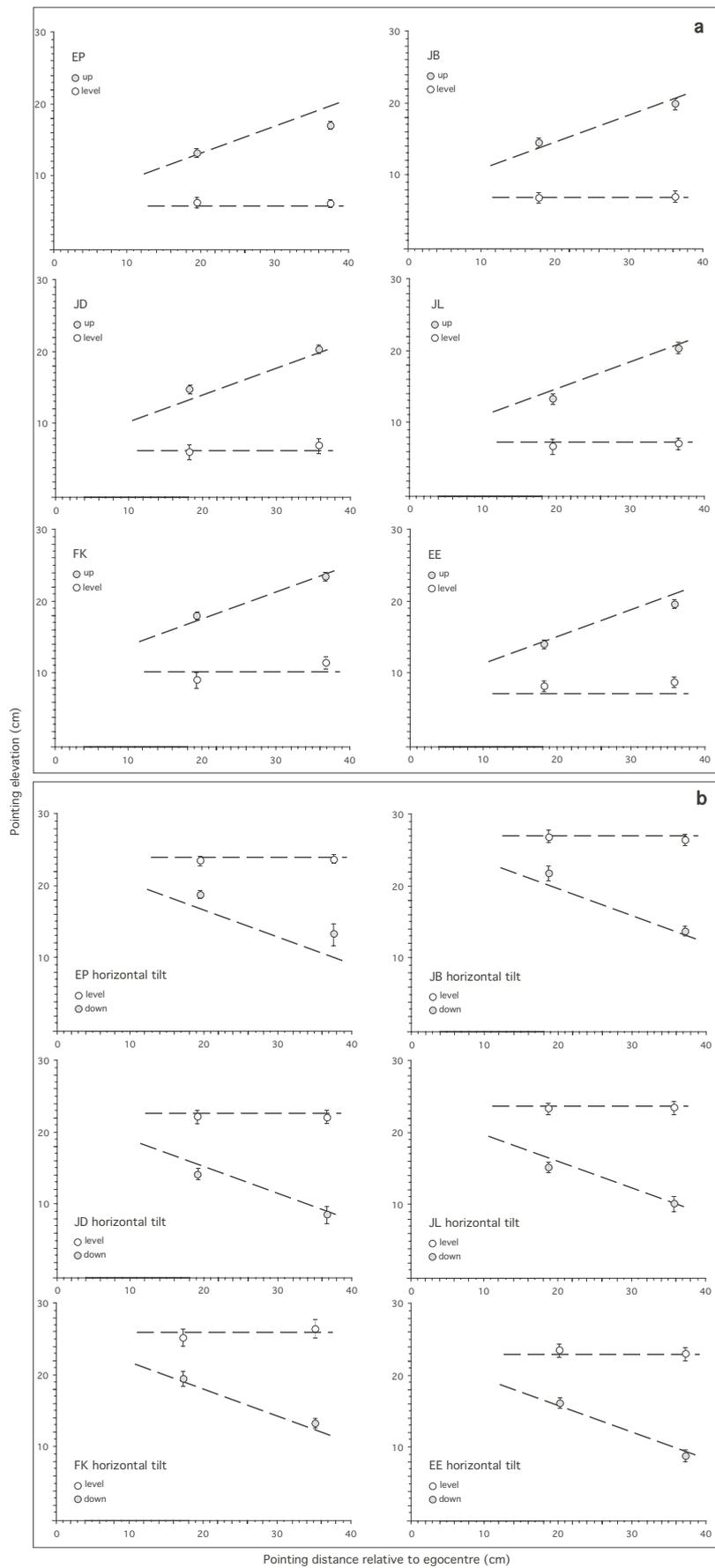


Figure 6. Pointing to the plane of regard with head tilt. Figures represent the pointing performance for the head tilt condition, 20° to the right (**a**) or 20° to the left (**b**). The performance was not affected by the change in the head orientation. A significantly larger pointing error for the upward fixation of the rightward head tilt than for the level fixation is caused by the relatively large pointing error for the upward condition at 40 cm distance of one subject (EP). Each point is an average of ten repeats. The error bars denote 1SD.

Discussion

Mayhew and Longuet-Higgins (1982) proposed that the pattern of retinal binocular disparities could be used to determine the three-dimensional structure of space from a retinal image alone, without supplementary information derived from non-visual sources. Although their model is plausible for the representation in an oculocentric reference frame, it is not sufficient to achieve a representation in a head or body centric frames since the same pattern of vertical disparities can occur for different levels of eye elevation (Figure 1). Vertical orientation of the eyes in the head is required to build a completely unambiguous head-centric representation. Our study demonstrates that the plane of regard, which is exclusively defined by eye elevation, can be localized accurately relative to the body and the head. This implicates the availability of the eye elevation signals and an accurate transformation of visual signals into the motor command for a pointing movement.

In general, to bring the hand to an object at a certain position in space, the visually perceived position of the object must be translated into an appropriate motor command for the hand-movement. What exactly is encoded is a matter of debate. The required displacement of the hand to reach the target from a starting position might be coded, for example (Desmurget et al. 1998; Rosetti et al. 1995), the starting position of the hand being determined through visual and proprioceptive information (van Beers et al. 1999; Graziano 1999). Alternatively, the target position might be coded in an egocentric (McIntyre et al. 1997; Carrozzo et al. 1999), head-, body- or a hand-centred frame of reference (Graziano, 1994). So, by combining a retinal signal and extra-retinal signals such as efference copy of the eye orientation in the head (Desmurget et al. 1998), the position of the target can be encoded in a frame of reference suitable for the planning of the hand movement.

When vision of the hand is absent, as in our paradigm, the required movement planning relies on the proprioception from the hand, and if the eyes are directed towards the remembered target position also on a copy of the efferent signal from the oculomotor system (Perenin et al. 1977; Lewis et al. 1998) and efference of the eye orientation in the head (Gauthier et al. 1990). These extraretinal eye signals are strong cues used to point to the correct position even when visual information about the target is distorted by illusions or prisms and conflicting with extraretinal signals (Rine and Skavenski 1997). Open loop pointing studies show an accurate performance for remembered targets, when the eyes are aimed toward that same position (Bock 1986; Henriques 1998, 2000; Poljac & van den Berg 2003). Thus, in this case the gaze direction and target position coincide.

In our paradigm, pointing direction and gaze direction did not correspond. Based on target location, the plane of regard was reconstructed from non-visual signals. Irrespective of the azimuth direction (up to 40°) of pointing relative to the fixation direction, the pointing performance was equal. This is in accordance with our earlier finding that the position of stimuli relative to the plane of regard is estimated with a similar accuracy irrespective of the fixation eccentricity relative to the estimated probe position (Poljac et al. 2004). Other pointing studies showed systematic errors associated with the horizontal fixation eccentricity. A central target's eccentricity is overestimated in the azimuth direction (Bock 1986; Enright 1995; Henriques et al. 1998; Poljac & van den Berg 2003). Henriques et al. (2000)

also investigated vertical gaze directions and found a similar pattern of errors. Interestingly, the target's vertical position was not overestimated, rather underestimated, for oblique eccentric downward fixations and for the fixations on the eye level it was slightly underestimated (up to about 2°). Although much smaller, the same effect is present in Enright's (1995) study. This is in accordance with the errors we found in our first experiment where subjects underestimate their plane of regard with the same magnitude of errors in the downward direction, irrespective of the fixation direction. Since it takes longer than a simple pointing movement toward a target, to adjust the finger position in the vertical direction to correspond with the location of the plane of regard, one explanation for our findings might be a gradually altered (not perceived) signal of the sensed vertical hand position, due to the gravitation force. Additional weight or fatigued muscles are known to cause proprioceptive deficits (Ledin et al. 2004; Björklund et al. 2000). The bias observed in the first task could be also caused by maintained tonus in arm muscles when the arm is raised, that might interfere with the transformation from visual to motor signal, needed to perform the pointing movement. Indeed, when we eliminated this factor by allowing subjects to support their hand on the table, the vertical bias disappeared (Experiment 2).

To be able to point accurately towards their plane of regard subjects had to create a representation of the plane based on eye elevation signals. Accurate pointing performance with the head tilted toward the shoulder implicates that subjects take head orientation into account also. In other words, subjects are capable of making a transformation to a body centred reference frame. Van Beuzenkom and colleges (2001) found that subjects can correctly indicate the amount of the head tilt (for small angles also the amount of body tilt) and concluded that people have a good percept of head orientation in space. This would implicate that, once the orientation of the plane of regard in relation to the head is known and combined with the correct representation of the object's position relative to the plane of regard (Poljac et al. 2004), the transformation to a space centric reference frame is possible.

In conclusion, we found evidence that the plane of regard is correctly localized relative to the head. This may be a good starting point to represent objects in head-centric coordinates. The significance of the plane of regard for the representation of visual objects in space might not be limited to stationary objects, but also extend to representing objects moving towards the head.

Reference

- Adams W, Frisby JP, Buckley D, Gårding J, Hippisley-Cox SD, Porrill J (1996) Pooling of vertical disparities by human visual system. *Perception* 25: 165-176
- Backus BT, Banks MS, van Ee R, Crowell JA (1999) Horizontal and vertical disparity, eye position, and stereoscopic slant perception. *Vision Research* 39: 1143-1170
- van Beers RJ, Sittig AC, Denier van der Gon JJ (1999) Localization of a seen finger is based exclusively on proprioception and on vision of the finger. *Experimental Brain Research* 125(1): 43-9
- van Beuzenkom AD, Medendorp WP, van Gisbergen JAM (2001) The subjective vertical and the sense of self orientation during active body tilt. *Vision Research* 41: 3229-3242

van den Berg AV (1996) Judgments of heading. *Vision Research* 36(15): 2337-2350

Björklund M, Crenshaw AG, Djupsjöbacka M, Johansson H (2000) Position sense acuity is diminished following repetitive low-intensity work to fatigue in a simulated occupational setting. *European Journal of Applied Physiology* 81(5): 361-367

Bock O (1986) Contribution of retinal versus extraretinal signals towards visual localisation in goal-directed movements. *Experimental Brain Research* 64: 476-482

Bremmer F, Schlack A, Shah NJ, Zafiris O, Kubischik M, Hoffmann K, Zilles K, Fink GR (2001) Polymodal motion processing in posterior parietal and premotor cortex: a human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron* 29(1): 287-96

Carrozzo M, McIntyre J, Zago M, Lacquaniti (1999) Viewer-centered and body-centered frames of reference in direct visuomotor transformations. *Experimental Brain Research* 129: 201-210

Cooke DF, Taylor CSR, Moore T, Graziano MSA (2003) Complex movements evoked by microstimulation of the ventral intraparietal area. *Proceedings of the National Academy of the Sciences of the United States of America* 100(10): 6163-8

Desmurget M, Pelisson D, Rosetti Y, Prablanc C (1998) From eye to hand: Planning goal-directed movements. *Neuroscience and Biobehavioral Reviews* 22(6): 761-788

Duhamel JR, Bremmer F, BenHamed S, Graf W (1997) Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature* 389(6653): 845-848

Enright JT (1995) The non-visual impact of eye orientation on eye-hand coordination. *Vision Research* 35(11): 1611-1618

Gårding J, Porrill J, Mayhew JEW, Frisby JP (1995) Stereopsis, vertical disparity and relief transformations. *Vision Research* 35(5): 703-722

Gardner PL, Mon-Williams M (2001) Vertical gaze angle: absolute height-in-scene information for the programming of prehension. *Experimental Brain Research* 136: 379-385

Gauthier GM, Nommay, D, Vercher JL (1990) The role of ocular muscle proprioception in visual localization of targets. *Science* 249(4964): 58-61

Graziano, MS (1999) Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position. *Proceedings of the National Academy of the Sciences of the United States of America* 96(18): 10418-21

Graziano MS, Yap GS, Gross CG (1994) Coding of visual space by premotor neurons. *Science* 266(5187): 1054-7

Henriques DYP, Klier ME, Smith MA, Lowy D, Crawford JD (1998) Gaze centered remapping of remembered visual space in an open-loop pointing task. *Journal of Neuroscience* 18: 1583-1594

Henriques DYP, Crawford JD (2000) Direction-dependent distortions of retinotopic space in the visuomotor transformation for pointing. *Experimental Brain Research* 132: 179-194

Howard IP (2002) *Seeing in depth*. Thornhill, Ontario: I Porteous

Ledin T, Fransson PA, Magnusson M (2004) Effects of postural disturbances with fatigued triceps surae muscles or with 20% additional body weight. *Gait Posture* 19(2): 184-93

- Lewis RF, Gaymard, BM, Tamargo RJ (1998) Efference copy provides the eye position information required for visually guided reaching. *Journal of Neurophysiology* 80(3): 1605-8
- Mayhew JEW, Longuet-Higgins HC (1982) A computational model of binocular depth perception. *Nature* 297: 376-378
- McIntyre J, Stratta F, Lacquaniti F (1997) A viewer-centered reference frame for pointing to memorized targets in three-dimensional space. *Journal of Neurophysiology* 78: 1601-1618
- Mon-Williams M, Tresilian JR (1998) A framework for considering the role of afference and efference in the control and perception of ocular position. *Biological Cybernetics* 79: 175-189
- Mon-Williams M, Tresilian JR (1999) Some recent studies on the extraretinal contribution to distance perception. *Perception* 28(2): 167-181
- Ogle KN (1950) *Researches in binocular vision*. Philadelphia, PA: WB Saunders
- Ooi TL, Wu B, He ZJ (2001) Distance determined by the angular declination below the horizon. *Nature* 414: 197-200
- Perenin MT, Jeannerod, M, Prablanc, C (1977) Spatial localization with paralyzed eye muscles. *Ophthalmologica* 175(4): 206-14
- Poljac E, van den Berg AV (2003). Representation of heading direction in far and near-head space. *Experimental Brain Research* 151: 501-513
- Poljac E, Lankheet M, van den Berg AV (2004) Perceptual compensation for eye torsion. *Vision Research* DOI: 10.1016/j.visres.2004.09.009
- Rine R, Skavenski AA (1997) Extraretinal eye position signals determine perceived target location when they conflict with visual cues. *Vision Research* 37(6): 775-787
- Rosetti Y, Desmurget M, Prablanc C (1995) Vectorial coding of movement: vision, proprioception or both? *Journal of Neurophysiology* 74: 457-463

Collision judgment of objects approaching the head¹



¹ *adapted from:* Poljac E, Neggers SF, van den Berg, AV (2004) Collision judgment of objects approaching the head, *in press*

Abstract

This study investigated the accuracy of stereoscopic motion-in-depth perception. Subjects estimated the point of impact of an object approaching the head from a distance of 30 or 60 cm, while fixating straight ahead. Simulated object's motion was presented only for the first 10 cm. Consequently, subjects had to extrapolate the remainder of its trajectory to be able to estimate the point of impact. Trajectory start and end positions were varied in the vertical plane. Half of the trajectories intersected the plane of regard.

Subjects were first asked to indicate if the object is going to hit below or above a reference point on the face (perceptual judgment). We manipulated the strength of the reference point's representation by additional tactile information; subjects held their finger or a stick on the location of a reference point. Tactile and proprioceptive information about the reference point significantly improved accuracy. Bias was virtually absent for all conditions. Second, when subjects pointed with their index finger to the perceived location of impact points on their face (visuo-motor judgment) they slightly overestimated (1.9 cm) the *horizontal* eccentricity of the locations of impact (pointing task). The vertical bias, however, was virtually absent.

Interestingly, when trajectories intersected the plane of regard a lower variability of the responses was observed in the perceptual task. However, neither bias nor accuracy in the pointing task depended on the trajectories' intersections with the plane of regard. When asked to point to the location where an trajectory intersected the plane of regard, subjects overestimated the depth component of this intersection location by about 3 cm.

Our observations indicate perception of trajectories relative to the head with much higher precision and accuracy than has been reported previously.

Introduction

It is amazing how effortlessly, confidently and precise we avoid collision with objects in our environment. To perform this task accurately we have to estimate the direction of ego-motion relative to objects or, when objects move toward us, the direction of objects' motion in depth, and make a correct and appropriate representation of the object relative to a relevant body part. An object that is approaching can be represented in various reference frames (Gross and Graziano 1995; Colby et al. 1991) depending on the behavioral response. The most convenient representation is then used for the response (Brenner and Cornelissen 2000). If one, for example, needs to catch an approaching object, an arm centric representation would be appropriate. If, on the other hand, the estimation has to be made whether the object is going to hit the head, utilizing a head centric representation would be convenient.

Moving through the environment without getting our head injured provides a strong suggestion that people are able to make these (head-centric) judgments accurately. It is not surprising then that neurophysiological studies have found cell populations that are associated with head centric representations (Zhang et al. 2004; Cooke et al. 2002; Bremmer et al. 2001). Moreover, these studies show that not only the locations of objects (near the head) but also the motion trajectories of objects moving towards the face (in area VIP; Duhamel et al. 1997) are represented relative to the head, independent of eye orientation. This type of neurons, called trajectory neurons, respond to stimuli moving towards a certain location of the face. The anticipated point of contact is more important for the cell response than the absolute direction of the stimulus in space (Colby and Duhamel 1996).

A number of studies have investigated the ability to estimate motion in depth (Portfors-Yeomans and Regan 1996; Peper et al. 1994; Cumming and Parker 1994; Regan and Kaushal 1993; Todd 1981; Cynader and Regan 1978; Beverley and Regan 1975). Most of those studies were mainly concerned with two issues: First, the kind of cues that are used to estimate motion in depth, such as disparity cues, ratios of velocities of the object's left and right retinal image and other binocular cues (Portfors-Yeomans & Regan 1996), or monocular cues such as velocities of object's edges or looming (Regan & Vincent 1995; Regan & Hamstra 1993). Second, behavioral studies have in general concentrated on *precision* of motion in depth estimation (Regan and Kaushal 1994; Beverley and Regan 1975). Subjects usually performed a discrimination task in which they estimated whether the trajectory of an approaching object had smaller or larger angle relative the observer than the previous one (object's trajectory). These studies found thresholds for differences in motion direction in depth down to 0.1° (Regan and Kaushal 1994).

On the other hand, *accuracy* (of absolute direction) of motion in depth perception was not studied until very recently. Harris and Dean (2003) conducted a behavioral study to investigate accuracy of *horizontal* 3D motion perception. They asked subjects to judge the trajectories of objects moving in the horizontal depth plane towards the head and found, just as earlier studies, high precision, as subjects consistently were choosing similar angles. However, their subjects largely overestimated the (absolute) trajectory angle, which implicated low accuracy. This is a surprising result, as it suggests that subjects perceive many objects that would hit

the head as missing it (not very helpful from the evolutionary point of view). Judging an object's trajectory in space does not necessarily involve the egocentric reference frame. However, for judging collisions with the head an egocentric representation seems most convenient. The main focus of the present study is such estimation of objects' trajectories, *horizontal and vertical*, relative to the head, and in particular human ability to estimate the point of impact on the face.

The study by Cooke (2002) mentioned above, revealed not only the existence of cell populations that are associated with head centric representations, but also that tactile stimulation of the location of impact on the face is coded by the same groups of (multimodal) neurons. Multisensory information processing is also seen in midbrain structures such as superior colliculus (e.g. Burnett et al. 2004; Stein et al. 2001). Signals that come from distinct sensory systems but are related to the same physical object are combined in order to integrate into a more robust percept with a more precise representation (Ernst and Bühlhoff 2004). Multisensory integration involves various neural structures and multiple reference frames. Often, merging of the sensory inputs coming from different senses, but originating from the same object provides a more accurate representation than what one might expect based on combination of independent representations. Different sensory representations lead to an enhanced, more robust and precise representation. For instance, spatial and temporal relationships of the multisensory stimuli (auditory information combined with visual) strongly influence target localization, as Wallace et al. (2004) observed. That study showed that when the two signals are perceived as spatially unified, the judgment variability decreased. Multisensory facilitation occurs not only for static, but for moving stimuli as well, as in natural situations information about object's motion is provided by two or more modalities simultaneously (Kitigawa & Ichihara 2002). In the current study we combine information from different sensory systems to investigate whether the visual estimation of motion in depth is facilitated by additional tactile and proprioceptive information about a potential end-position of the trajectory. An accurate estimation of end-position of the target's trajectory is crucial when judging collisions. Multisensory information of this end position may improve its judgment. This is the second question of the present study.

In our recent studies we found that people estimate the elevation of objects relative to the plane of regard, a plane defined by the two rotation centers of the eyes and a fixation point, correctly (Poljac et al. 2004), and also that the orientation of this plane is estimated accurately relative to the head (Poljac & van den Berg 2004). Our conclusion was that the plane of regard might play an important role in building a head-centric representation of *static* visual objects. The involvement of the plane of regard might also extend to creating head-centric representations of objects *moving* in depth, approaching the observer. The motion in depth might be judged more accurately when the trajectory intersects the plane of regard in front of the subject than when it is not. As the third goal, our present study tested whether the plane of regard contributes to a more accurate percept of visual stimuli moving towards the head.

Materials and methods

Subjects

Six subjects participated in the study. One subject (EP) was aware of the experimental design and purpose of the study, the rest of the participants were naive. This study has been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. Participation was voluntary and all the subjects gave their informed consent prior to their inclusion into the study.

Apparatus

Experimental stimuli were generated by a PC with Graphics acceleration board and presented on a computer monitor with a refresh rate of 120 Hz. Stereogoggles (CrystalEyes liquid crystal shutters) synchronized to the monitor refresh rate (120 Hz) were used to stimulate each eye independently. Each image provided a view on a simulated 3D scene as seen from that eye's perspective. The subjects were seated at approximately 30 cm in front of the monitor, with their head stabilized by a dental bite-board mounted on the table, in complete darkness. The head was oriented straight ahead, the interocular axis was positioned in the horizontal plane, and the eyes had nearly the same distance to the monitor. A camera-based measurement of the eye's pupil orientation was used to verify that ocular fixation criteria were met during the experiments (SMI EyeLink-inc Teltow, Germany). Precise location of each subject's eyes relative to the monitor's center was determined by a triangulation procedure (van den Berg, 1996), using reference lines 15 cm in front of the monitor, before the experiment started. MiniBIRD, a magnetic field based system (Acension Technologies) was used to measure 3D position (x,y,z) coordinates of the subjects' index finger in pointing tasks. It consists of an electronic unit, a transmitter and a receiver that is held by the subject. The changes in DC magnetic field generated by the transmitter induce a current in the receiver, which depend on the orientation and the distance of the receiver relative to the transmitter. The electronic unit decodes the current in terms of position and orientation (about 1mm precision).

Calibration

To translate the values from MiniBIRD to the same coordinate system that we use for the description of eye position and to define the movement of the stimuli in depth (space coordinates), a calibration procedure was performed prior to each experiment. A wooden cube, with sides of 28 cm length, was positioned so that the center of the cube's surface parallel to the monitor coincided with the monitor's center. This means that the center of the cube is positioned 14 cm in front of the monitor and at zero elevation and azimuth relative to the monitor's center. The eight positions of the cube were calculated in stimulus or space coordinates. Using MiniBIRD receiver the position of each corner of the cube was recorded. An affine transformation (Jacobian matrix J) was computed to transform MiniBIRD values in cube coordinates (in the remainder of this paper referred to as "cube space coordinates", which is the same coordinate system as used to define the stimuli). To do this, a point based registration procedure was used, minimizing the error between the cube's space coordinates and measured MiniBIRD coordinates such that

$$M_{\text{MiniBird}} = J * M_{\text{cube}} + E^1$$

where $\sum |E|$ is minimal (see Neggers et al. 2004). After this calibration procedure, all measured MiniBIRD data could be transformed to cube space coordinates in real time.

Precise location of each subject's eye relative to the monitor's center was determined by a triangulation procedure mentioned above (van den Berg 1996). Two vertical and one horizontal calibration line were positioned at a distance of 15 cm in front of the monitor, in the subject's frontal plane parallel to the monitor. The subjects had to align a pointer on the screen, with either calibration line in turn. This allows construction of three gaze planes (2 vertical and 1 horizontal) for each eye. The intersection of the three gaze planes coincides with a precise location of each eye's center of rotation relative to the center of the screen.

Stimuli

Each stimulus consisted of stereo motion of one textured sphere (simulated diameter 1 cm). Binocular cues to depth such as disparity, as well as monocular cues like looming and texture contributed to a very strong stereo percept. Simulated motion extended for 10 cm toward the subjects with constant speed of motion (8 cm/sec) in space and thus had a fixed duration of 1.25 s. This means that the trajectory towards the face was not completed at the moment of stimulus' disappearance and that the subjects had to extrapolate the remainder of the trajectory and the collision location. So, in this way, the ability to extrapolate the trajectories of objects moving in depth towards the head was examined. Beside the moving object, a stereoscopic fixation point was shown at the monitor distance and consequently, its image for the left and the right eye had same position on the screen. The fixation point had a diameter of 0.5° degrees.

Procedure

The experiment was performed in total darkness. The subjects had no visual reference whatsoever during the trials. The subjects were instructed to judge whether the object moving toward their face is going to hit the face above or below a reference point on the face. A trial was started by the subject through a key press, at which time the fixation point appeared for 0.5 s. The fixation point disappeared and after 100 ms the target appeared and moved toward the subject's head. The same fixation direction had to be maintained during the whole trial until the subject's response, which concluded the trial and initiated the next one. When the eye orientation deviated more than 0.5° from that orientation the trial was rejected and repeated. Subjects indicated at the end of the motion whether the object would hit above or below a reference point on their face by pressing a key, while keeping gaze fixed at the location of the now absent fixation point. The Marquardt-Levenberg method was used to find the best fitting cumulative Gaussian (error function) to the "higher"-response probability as a function of the elevation of the simulated point of impact. The elevation at which 50% of the responses was higher determined the point of subjective equality, and the SD was derived from the slope of the curve.

¹ E denotes the remaining errors that should be minimized by choosing the proper transformation matrix

Experiment 1. Binocular estimation of the motion towards the head (two alternatives forced choice paradigm)

The subjects performed the task described above, while fixating one of the three directions. These three conditions were investigated in blocks of 75 trials: straight ahead (the direction perpendicular to the interocular axis in the horizontal plane, and intersecting that axis half way between the eyes), 20° down or 20° up relative to the straight ahead. For each viewing condition, the stimulus moved from the starting position simulated at the depth of 5 cm behind the screen and 20° below or 20° above the fixation level, towards a position on the face that could vary randomly from 2 cm below to 2 cm (in steps of 1 cm) above a reference position. The reference position on the face was measured by MiniBIRD prior to the beginning of the experiment and was used for simulation of the trajectory of the approaching sphere. This reference position could be on the subject's chin or forehead. This implicates that trajectories did or did not intersect the plane of regard, depending on the combination of starting and end positions (Figure 1).

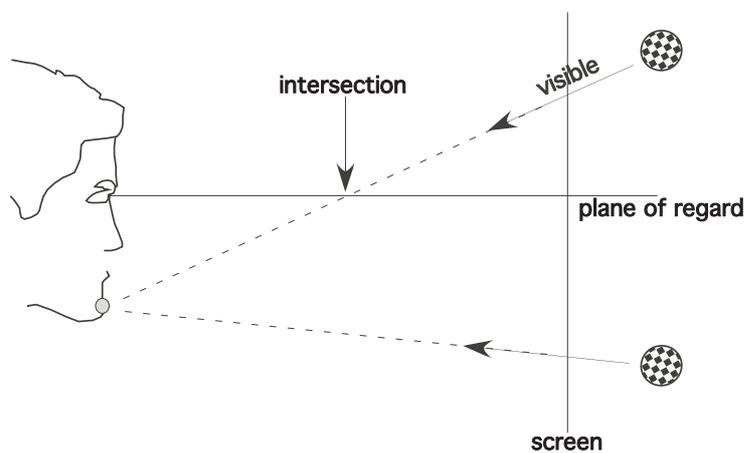


Figure 1. Targets moving towards the reference point on the chin. The stimulus started to move from a simulated position at approximately 35 cm of depth, 5 cm behind the screen, 20° below or 20° above the fixation level. The visible trajectories of the objects extended for 10 cm from starting point towards the reference position on the subject's chin or forehead. Subjects had to extrapolate the remainder of the trajectory. Some of the trajectories intersected the plane of regard, depending on the combination of start- and end-positions.

The intersecting and non-intersecting trajectories were similar in all respects (retinal eccentricity, velocity, direction and the length of the movement of retinal image) except for the direction of motion in space coordinates and the direction of motion of the retinal image with respect to the fovea. Intersecting trajectories had a retinal image whose vertical component moved foveopetal, while the non-intersecting moved away from the fovea. The trajectory extended for 10 cm from the starting position. Due to a flat screen, the fixation distance for straight-ahead and for the two eccentric fixations was not the same. The angles of convergence differed slightly. For instance, for subject EP the convergence angle was 12.9° and 11.6°, for the straight-ahead and the eccentric conditions, respectively.

We repeated the experiment with subjects sitting 60 cm in front of the screen in order to investigate the distance effect. In addition, the experiment was repeated with the instruction to pursue with the eyes the object during its approach toward the subject and again to judge whether it would hit below or above the reference position. During the choice period of this task fixation was free.

Experiment 2. Binocular estimation of the motion towards the head with proprioceptive and tactile information

The judgment of a location in space becomes more accurate when it is represented in more than one modality (Wallace et al. 2004). To investigate if additional tactile or proprioceptive information about the reference point location leads to a more precise judgment we repeated the task from Experiment 1 and all its variants and asked the subjects to press the end-point of a stick (length 20 cm) or the top of their left index finger at the location of the reference point on chin or forehead. Holding a stick provides some proprioceptive information, (the spatial relationship between the finger and the stick is more or less invariant), holding a finger on the reference point is a more direct and natural way to use the proprioceptive information. For clarity we will refer to our three conditions as visual (V), tactile-congruent proprioception (T_c) and tactile-incongruent proprioception (T_i), respectively. To prevent adaptation, the subjects were allowed to move their fingertip or the stick between the trials, but only when they became uncertain about the reference position. Their arm was supported throughout the trial to prevent a possible interference from the maintained tonus in arm muscles when the arm is raised.

Experiment 3. Pointing to the location of impact

Judging the location of objects relative to our head is not only required when objects are approaching the observer, but also in an active task of bringing an object to some location on the face, when eating for example. Such activity requires a stable head-centric representation of the location on the face to where the object must be brought, and preferably the object's representation in the same frame of reference (and with respect to the body after taking the head position relative to the body into account). We introduced a pointing task to investigate such forms of localization. Subjects were again asked to look at the fixation point, and to maintain the same direction when it disappeared and targets were presented. Similar to Experiment 1, the target could start at the location 20° above, 20° below, or at the eye-level, on an approximate distance of 35 cm from subject's eyes. The target moved for 10 cm in depth towards the subject, starting on a simulated distance of 5 cm behind the screen, as in Experiment 1.

Different locations on the face do not necessarily have to be equally well represented in the brain, as far as their location is concerned. The mouth is represented more accurately and in more detail than some location on the forehead (Colby & Goldberg 1999). To obtain targets that are in this respect similar in different subjects, the positions of four points of impact on the face, the locations that specified the targets' end positions on the face, would the target complete the movement along the whole trajectory, were determined in the following fashion. First, we indicated the four end-locations, two on the forehead and one on each cheek, in one (standard) subject, using MiniBIRD marker. We called these "the standard targets" (T_{standard}). Second, to find the corresponding targets on the face of other subjects, that would match the standard targets, we used a mapping procedure. We recorded eight anatomical landmarks (the crest of helix of the left and right ear, medial and temporal commissure of the left and right eye, the bridge of the nose and the chin, see Figure 2) in each subject using the MiniBIRD marker, and mapped

them to cube space coordinates (which is the same as stimulus space). Then, we mapped these eight positions from the cube space to the standard face by determining an affine co-registration matrix J for each subject, established by point-based registration ($M_{\text{standard}}=J*M_{\text{subject}}+E$, where $\sum |E|$ is minimal). We then used the inverse matrix of J (J^{-1}) to calculate the four target positions for each subject ($J^{-1}*T_{\text{standard}} = T_{\text{subject}}$). These individual target positions were used as the end points for the simulated motion trajectories. For the detailed description of the mapping algorithms and the acquisition of anatomical landmarks see Neggers et al. (2004).

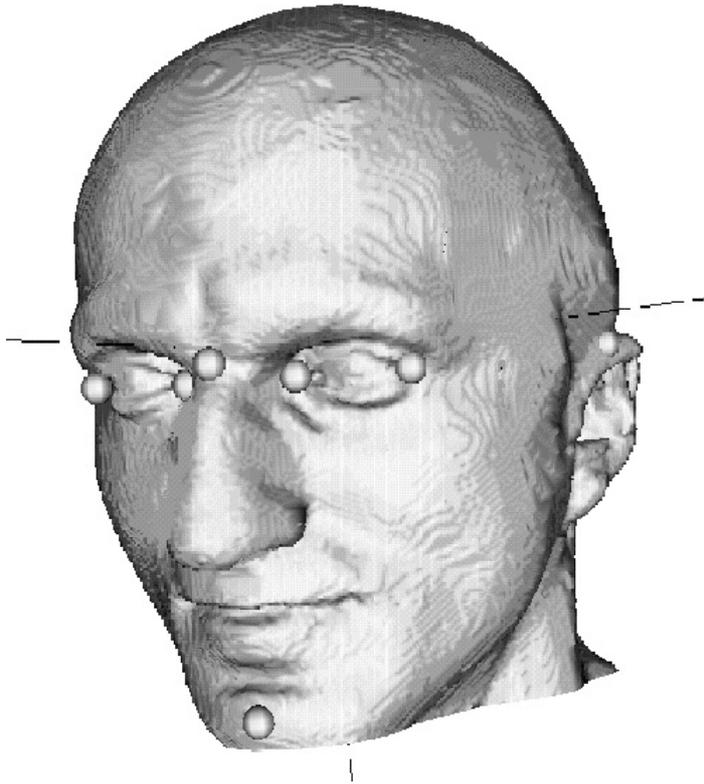


Figure 2. Recorded anatomical positions. Eight locations used to find a transformation matrix for the conversion of coordinates from MiniBIRD space to cube-space to standard-head space.

Subjects were now asked to point with their index finger to the location where they estimated the stimulus would hit their head. These MiniBIRD data (judged hit-points on the face) for each subject were transformed off-line to the standard head, using the (straight) affine transformation matrix J as described above. To determine the end of each pointing movement (hit-point) we took that point in time where the velocity dropped off below the threshold (1mm/s).

Experiment 4. Pointing to the intersection of target trajectories with the plane of regard

When targets move towards the head, they may cross the plane of regard. This depends on start position, end position and orientation of the plane of regard. If a subject is fixating straight ahead and the target moves from above the eye level toward a position on the chin, at a certain point the trajectory will intersect the plane of regard. The subjects could see only the first 1.25 s of the trajectory, which corresponds to 10 cm, at which time the target did not intersect the plane of regard yet, and consequently the subjects had to extrapolate the rest of the trajectory (Figure 3). If the orientation of the plane of regard is perceived correctly (Poljac & van den Berg 2004) as well as the location of the target relative to the plane of regard (Poljac et al. 2004), then pointing to the location where the targets trajectory

intersects this plane should also be possible. Subjects performed this task sitting in total darkness, pointing with their index finger. In addition, the same task was done with a small reference point (about 4 mm) fairly glowing, on top of the index finger. In this way visual feedback about the index-finger position was provided. Simulation procedures and analysis of pointing data was comparable to those for Experiment 3.

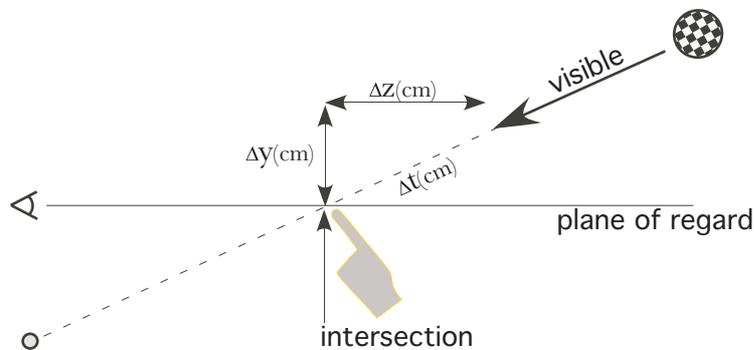


Figure 3. Point of intersection with the plane of regard. When a target starts to move from above the eye level towards a position below, its path intersects the plane of regard. To point to that intersection, subjects have to extrapolate the trajectory, as it is only partly visible.

Results

Experiment 1. Binocular estimation of the motion towards the head (two alternatives forced choice paradigm)

Subjects were asked to estimate whether a stimulus moving toward a reference position on the head is going to hit below or above that reference point. The trajectories of the stimuli were chosen so that they either did or did not intersect the plane of regard (Figure 1). ANOVA shows that the responses were significantly affected by trajectories ($F(3,68)=4.6$; $p=0.006$). The means did not differ significantly, irrespective of the condition. The average vertical bias of the perceived impact position was 0.14 cm below the actual position for intersect conditions and 0.2 cm for non-intersect conditions. However, the variance of the responses where a trajectory intersects the plane of regard was significantly smaller (about 19%), which indicates a more confident response (Figure 4). This was true irrespective of the start position. Another argument supporting the facilitating effect of intersection with the plane of regard is the fact that the trajectories intersecting the plane of regard were longer compared to non-intersecting trajectories.

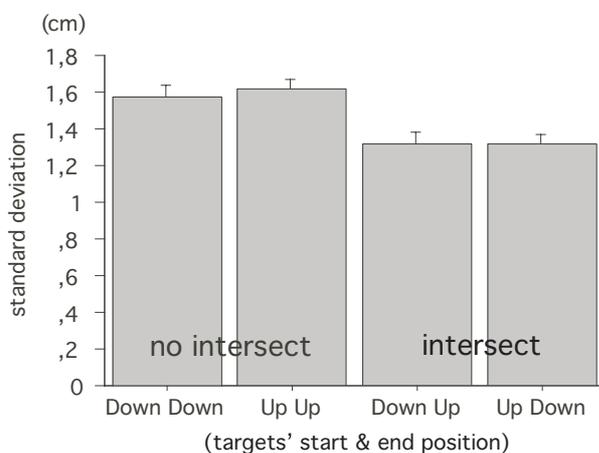


Figure 4. The effect of the plane of regard on variance. Standard deviation is plotted for the experimental conditions. The responses were significantly affected by trajectories, as their variance was significantly smaller (about 19%) when a trajectory intersects the plane of regard, irrespective of the start position.

This means that the same angular error of the trajectory direction during its visible part (10 cm) would result in a larger pointing error (mm displacement) of the estimated end point for the longer trajectories, which is the opposite to our finding.

In addition, the direction in which the subjects fixated (elevation) had no effect on the response bias or variance ($F(2,68)=0.27$; $p=0.77$), nor did the distance of the start positions to subject's eyes ($p=0.22$). Although the subjects reported that pursuit eye movement facilitated the task, this effect was not present in their responses, as the variance or the bias were not significantly different in the two tasks (t-test: $p=0.62$). This finding is consistent with the study by Welchman and Harris (2004) and might implicate the use of different cues for motion in depth in the two conditions. The subjects might be more used to utilize the cues that accompany eye pursuit of the target (such as vergence change or eye orientation change), which evoked the impression that the task was easier to do. However, the cues used in case of fixation (a combination of looming and binocular disparity change) turn out to be at least as effective.

Experiment 2. Binocular estimation of the motion towards the head with proprioceptive and tactile information

We manipulated the amount of information about reference point location by additional tactile or proprioceptive information to see whether the judgment would change in accuracy. Subjects were asked to hold their left index finger or a stick at the location of the reference point on their chin or forehead and to estimate whether the target is going to hit the face above or below this reference point. ANOVA revealed a significant contribution of both tactile congruent (T_c , finger) and tactile incongruent (T_i , stick) proprioceptive information. It manifests itself in reduced variance (Figure 5) of responses compared to the condition involving exclusively visual stimulation ($F(2,68)=6.8$, $p<0.002$). The lowest variance can be observed when the finger is used (T_c), although the difference between this condition and the stick-condition (T_i) is just not significant ($p=0.09$). It was also interesting to examine whether the effect of the plane of regard was still present in this paradigm, as also in these new conditions some trajectories did and other did not intersect the plane of regard. We again performed ANOVA and tested if intersecting the plane of regard was a factor of significance. When target intersected the plane of regard on its path toward a reference point on the face, the subjects responded with more confidence (Figure 5), revealed by a smaller variance compared to conditions in which targets did not intersect the plane of regard ($F(1,58)=14.32$; $p=0.0004$). However, when we did a separate analysis, it was clear that this was not true for the condition where the subjects held their finger (T_c) on the reference point ($F(1,18)=0.99$; $p=0.33$). In that case the variance had approximately the same low value as for intersecting trajectories in visual (V) and tactile-incongruent (T_i) conditions. The vertical bias of the estimated point of impact did not differ across the three conditions (average estimation was 0.17 cm below the reference point).

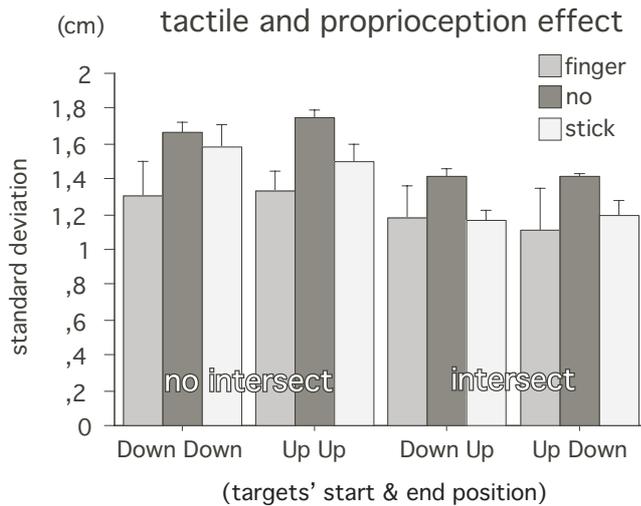


Figure 5. The effect of additional tactile and proprioceptive information on variance. Figure shows that the variance of the responses is significantly lower when tactile-congruent-proprioceptive (stick, T_i) and tactile-incongruent-proprioceptive (finger, T_c) information is present. The tactile-congruent (T_i) and tactile-incongruent (T_c) conditions, however, are not significantly different from each other. When target intersected the plane of regard on its path toward a reference point on the face, the subjects responded with more confidence, which we see as smaller variance bars in those conditions.

Experiment 3. Pointing to the location of impact

Subjects pointed toward the location on their face where they estimated that the approaching target would hit their head. This location we called the point of impact.

First, we calculated the accuracy and precision of pointing performance in following fashion. We started with an analysis of our data in cube space coordinates (i.e. after transformation of all subjects' data to the standard head), calculating the magnitude of vector-error relative to the target. The average pointing error was 1.9 cm, which was significantly deviating from actual target position (t-test, $p < 0.0001$). The largest contribution to this error comes from the error in the horizontal direction (1.7 cm), as the subjects largely overestimated the eccentricity of the target in this direction (Figure 6)¹.

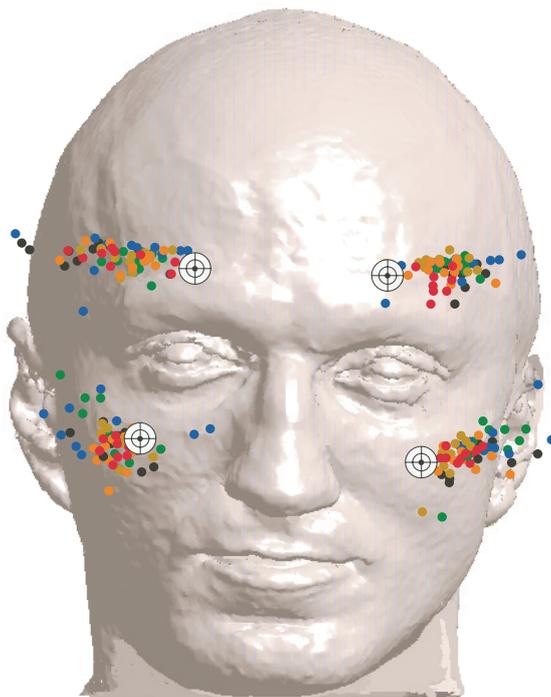


Figure 6. Standard face and pointed positions. All the data points (transformed to standard head) of one experiment are plotted (6 subjects in different color) relative to the four targets on the standard head. The size of the spheres is the actual size relative to the standard head.

¹ The head in Figure 5 originates from a T3 structural MRI scan made during another study in which this subject took part (Neggert et al. *in press*).

The average vertical bias was 0.36 cm above the reference position. ANOVA shows that the start position of the target (20° below or above the eye-level) is not affecting the judgment of perceived target location (point of impact; $F(1,476)=1.37$; $p=0.24$). The variance of responses, however, was invariable across different conditions ($F(1,68)=0.16$; $p=0.86$).

The above analysis uses the spatial reference frame of the trajectories. We wondered whether analysis of the errors in the local reference frame of the simulated point of impact would reveal any further effects. Again, we started by a transformation of the pointing data to the standard head. We fitted a plane through the pointing data, separately for each subject and each target. A reference frame was set up for each fitted plane, with the X-axis positioned in the mid-sagittal plane and Y-axis perpendicular to that X-axis. Each data point position was transformed to that reference frame. All data was then rotated about the axis orthogonal to the plane to find the best fitting pair of orthogonal cumulative Gaussians. The quality of the fit created in this way was evaluated with Kolmogorov-Smirnov test, and was very high (for all fits $\underline{D}(KS)$ smaller than 0.35, meaning that the difference between fit and data is coincidental with $p>0.96 \pm 0.04$). Figure 7 shows the pointing performance of our six subjects. Each ellipse represents the variability ($\pm 1SD$) of the responses. The mean pointing position relative to the target corresponds to the centre of the ellipse. The average mean pointing error across subjects was about 1.4 cm and did not differ significantly between the subjects. In each condition we observed a lateral overestimation of the targets' end positions. This is in accordance with Harris' (2003; also Welchman et al. 2004) findings, although the magnitude of overestimation is very different (see also Discussion).

Finally, we investigated if the intersection with the plane of regard affected the pointing performance. The first analysis in spatial coordinates shows a significantly smaller error in conditions where the target's trajectory passes through the plane of regard ($F(1,476)=28.2$; $p<0.0001$). The mean pointing error in the second analysis is slightly smaller when trajectories toward the head are intersecting the plane of regard (solid-line ellipses, Figure 7). Yet, the difference with non-intersecting (dotted-line ellipses) conditions is just not significant ($F(1,40)=4.35$; $p=0.08$). The same holds for the response variance ($F(1,40)=2.02$; $p=0.16$), unlike our first two experiments in which the latter showed a more confident response for trajectories that crossed the plane of regard.

Experiment 4. Pointing to the intersection of target trajectories with the plane of regard

Brief trajectories that intersect the plane of regard were presented and subjects were asked to point to the locations of the intersection with the plane of regard by extrapolation of the perceived path. Figure 8 shows all subjects' performance for the four targets. Each ellipse is located in the plane of regard of the standard head and stands for the variance of responses of one subject for one target. The centre of ellipse represents the mean pointing location relative to the true intersection point, just as in the Experiment 3. Mean error is about 2.7 cm (± 1.05 cm), but the depth component contributes the most (73%) to this error. Subjects overestimate the distance of intersection location relative to the head. There is also a small lateral overestimation (0.9 cm). This is in line with the observed overestimation of the trajectories' angle in the preceding experiments. The subjects were accurate in

the vertical direction (average error of 0.23 cm), pointing correctly in the plane of regard. We neither observed significant differences in response variability nor bias in different conditions.

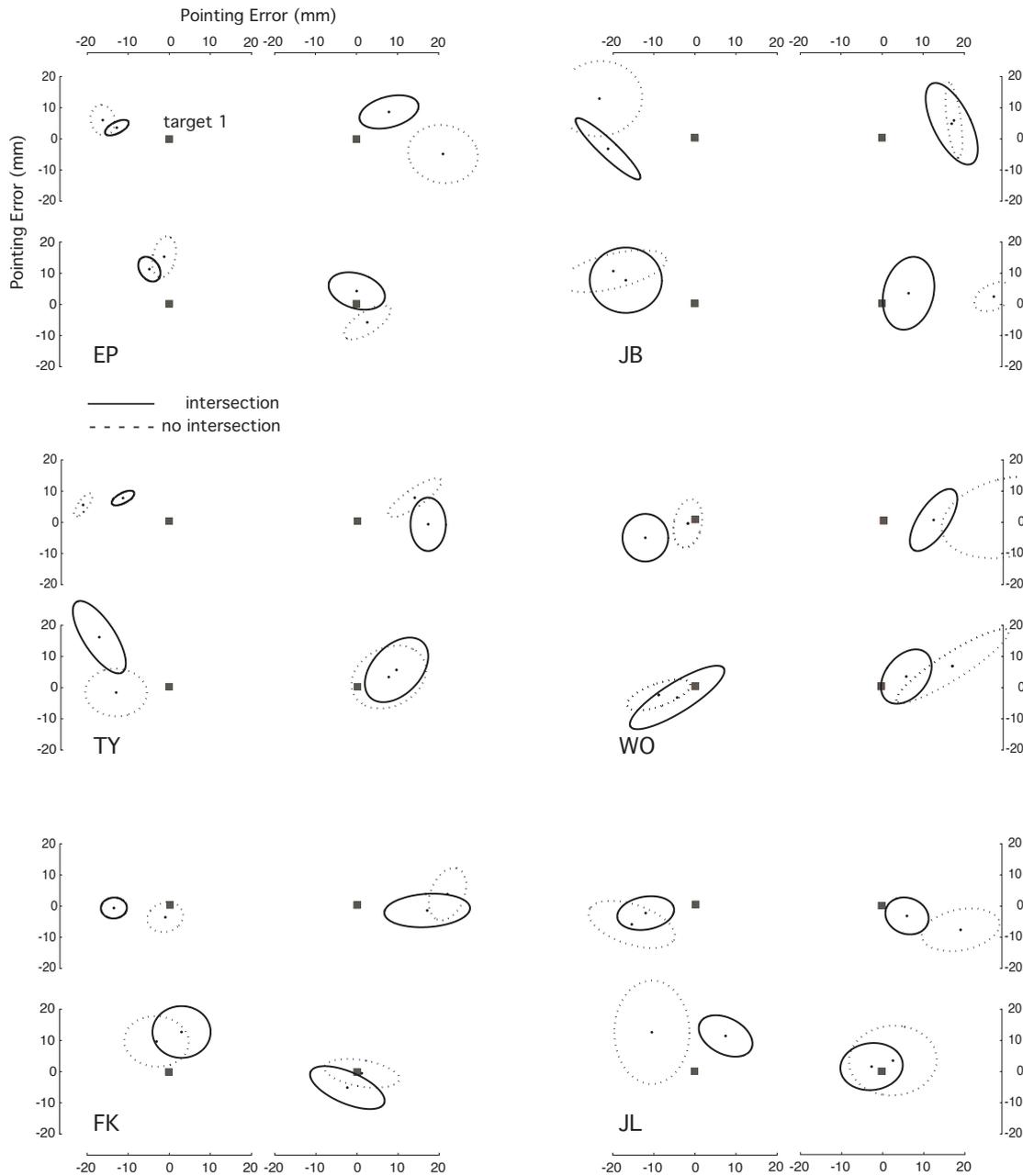


Figure 7. Pointing towards the location of impact. The pointing performance of our six subjects. Each ellipse represents the variability ($\pm 1SD$) of the responses with the mean pointing position relative to the target in the centre of the ellipse. The average error across subjects was about 1.4 cm and did not differ significantly between the subjects. A lateral overestimation of the targets' end positions can be observed. The trajectories toward the head that are intersecting the plane of regard (solid-line ellipses) and with non-intersecting (dotted-line ellipses) trajectories are just not significantly different from each other and neither is the response variance (ellipses' surfaces).

The additional task with visual feedback about the index-finger position resulted in pointing performance that differed from the condition without feedback. Contrary to our expectations, the visual feedback did not lead to an improvement of the pointing performance. Quite the reverse, the subjects made significantly larger errors. On the average, the pointing errors were 0.9 cm larger, but there was no change in variance (paired t-test).

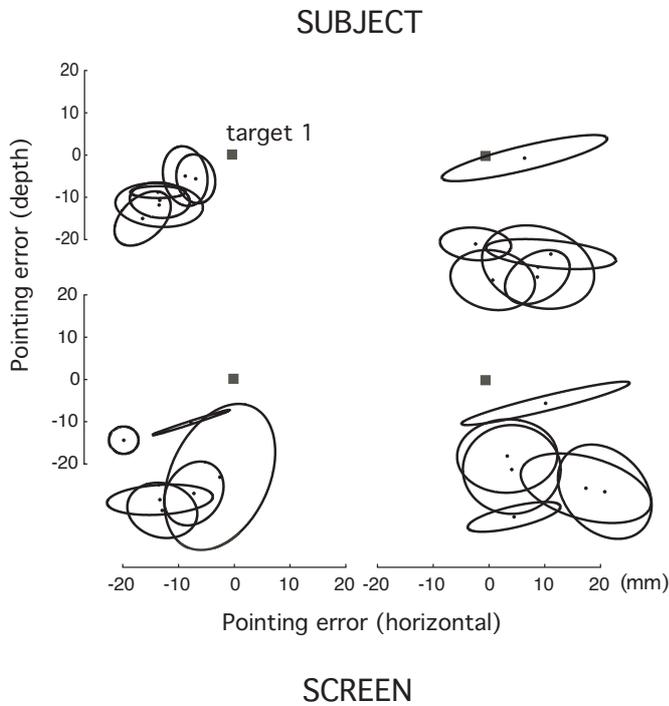


Figure 8. Pointing toward the intersection location. The performance of all subjects is plotted in X-Z plane. Response variability is represented by ellipses' size (\pm SD), with the centre of each ellipse standing for the mean pointing position (mm) relative to the target. Most of the subjects overestimate the horizontal eccentricity of the intersection location, although this error is much smaller than the pointing error that the subjects make in depth (Z) direction.

Discussion

In this study we have investigated the human ability to estimate the location of impact of an approaching object on the face. We found that, in general, people are able to perform this task with a much better accuracy than expected on the basis of a previous study. Subjects do overestimate the azimuthal eccentricity of the presented trajectories, in agreement with the recent study conducted by Harris and Dean (2003). They observed a large overestimation of the horizontal angle of approach for stereoscopic objects moving at a small angle with respect to the mid-sagittal plane. However, the pointing bias in our study is *much* smaller (average of 1.4 cm, which corresponds to 2.3°) compared to Harris' study (up to 16°). We discuss several possible reasons for this difference.

First, we used much "richer" visual stimuli, containing multiple depth cues besides stereo cues, such as looming and texture. In a recent study, Welchman et al. (2004) extended Harris' study for multiple depth cues, to investigate if these supplementary cues would improve the motion in depth judgment. They observed a judging bias that was consistent with the previous findings by Harris and Dean (2003) for objects moving at a small angle ($<30^\circ$) relative to the mid-sagittal plane. The bias varied with the angle of approach. For angles greater than 30° - 40° there was an *underestimation* of the perceived approach-angle. Additionally, they also investigated a real object moving in depth. They found that the performance was

virtually identical with the simulated-stimulus condition. Thus, the discrepancy can be only partially explained by the stimulus differences.

Another, perhaps more appropriate explanation is the task difference. Different instructions and tasks can for example lead to an altered judgment of simulated (self)motion (van den Berg 1996; Royden & Conti 2003) on the basis of looming stimuli. Harris' subjects were asked to reproduce the object's trajectory by adjusting an arrow in front of them or drawing the perceived trajectory as seen from above. In our task the subject judged the point of impact on the head, which likely evokes egocentric judgment to a larger extent than the task in Harris' study (an allocentric task). Therefore, different neuronal structures might be addressed due to these task dissimilarities.

Monkey studies showed that the motion trajectories of objects moving towards the face (the task in Harris' study) are represented in area VIP (Duhamel et al. 1997) and that a different type of neurons in the same area, called trajectory neurons, respond to stimuli moving towards a certain location on the face (that had to be specified in our task). These latter neurons encode the anticipated point of contact rather than the absolute direction of the stimulus in space (Colby and Duhamel 1996), and hence might be involved in our present task, but not in Harris' study.

Further, although the stimulus was visible until approximately 25 cm from the eyes, the remainder of its path had to be predicted to estimate its end position on the face. Pointing to that location on the head and the fact that the estimation is required for the locations in near space, might involve more head-centric mechanisms, since a head centric representation might be advantageous to respond to objects in close proximity of the head. Target distance is known to affect visual responsiveness in several classes of parietal cells (Colby and Goldberg 1999). Hence, the transformation to a head-centric representation might be also distance dependent. Utilizing a head-centric representation here might result in a more accurate judgment.

Another possible issue concerns multiple representations. A visual input can be transformed to different representations, dependent on the action this information will be engaged in. We already have learned that the representation of object's position for motor action and perceptual judgment share the same source to a large extent, but do not necessarily have to be the same (Bridgeman et al. 2000). Two representations of visual space, a cognitive that drives perception, and a sensorimotor that controls visually guided behavior can be built and exist as two separate representations. These representations may also not be equally accurate. Sometimes, the representation for motor action can "outperform" the representation built for visual judgment only (Rine 1997), but on the other hand the visual (perceptual) judgment can in certain situations be far more accurate than estimation which involves motor action (pointing, for example; Ashida 2004; Poljac & van den Berg 2003). Likely, our pointing task has led to an action related representation of the motion trajectory. Our data suggest this representation is much more accurate than that of spatial trajectories, as in Harris' study.

Multisensory facilitation

We found that tactile and proprioceptive information facilitated the judgment of the motion trajectories of approaching objects, manifesting itself in reduced variance of responses.

A natural stimulus is usually represented in different modalities (for example visual, tactile, auditory) that, by themselves, might be ambiguous and imprecise, but combined together can be localized correctly. This is true for static stimuli, but also for objects moving in depth (Kitigawa & Ichihara 2002). Different sensory modalities originating from the same object enhance the representation. For example, the location of impact on the face is coded by the same groups of (multimodal) neurons that code for visual information about approaching stimulus (Cooke, 2002). The visual and tactile receptive fields are corresponding with regard to the size and location of the stimuli, and might strengthen their representation.

We find that that tactile and proprioceptive information combines with visual information about the point of impact on the face. Consistence between proprioceptive and simultaneously presented visual and tactile signals does not significantly improve the confidence of the judgment relative to the condition where proprioception is not consistent. Apparently, tactile information already creates a reference that makes vision accurate enough to make a confident judgment.

Could this mean that the stick has become part of the body schema? Numerous studies have demonstrated that the body representation can change (Iriki et al. 1996; Berti & Frassinetti 2000; Maravita & Iriki 2004; Gentilucci et al 2004). Iriki et al. (1996) reported changes in body representation of macaques following the use of simple tools. Neuronal activity recordings from intraparietal cortex showed the expansion of the receptive fields of some bimodal neurons (responsive to somatosensory stimulation at the hand, and visual stimuli near the hand) to include the entire length of the tool. We use many different tools to extend our action space and consequently it might be possible that the stick used in our tactile condition (T_c) became incorporated in the body representation and in this way contained also proprioceptive information. Although such an extension of the body schema cannot be excluded, we believe it is unlikely. Visual feedback is essential to initiate the changes in receptive field properties of the neurons associated with the representation of the hand and its extension to the used tools (Iriki et al. 1996). Moreover, passive holding of the tool did not bring about a change in the representation of the hand (Iriki et al. 1996). Hence, the extension of the hand representation to include the stick likely does not occur when a stick is used.

Remarkably, plane of regard intersection does not improve the judgment when finger is held on the reference point (T_i). The variance for both intersecting and non-intersecting trajectories equals the lower variance that we found in visual and tactile intersecting conditions. This could be due to the use of different, more precise representation, this time originating from proprioceptive information.

Plane of regard

Studies dealing with human ability to estimate motion in depth mainly concentrated on measuring discrimination threshold, or just noticeable difference in direction of motion. From an evolutionary perspective, far more important is the question whether an approaching object is going to hit the head or not. Using binocular disparities may help to determine the direction of motion in depth (Welchman et al. 2004; Cumming & DeAngelis, 2001; Regan & Gray 2000; Mayhew & Longuet-Higgins 1982), but does so only relative to the retina, and therefore fails to provide the information about the direction of motion relative to the head. To enable the visual system to judge the motion in depth relative to the head, the vertical orientation of the eyes in the head must also be known. The plane of regard might be just that reference needed to make head-centric estimations, as it contains information about eyes' vertical orientation. In the present study we find some indications that the plane of regard enables a more accurate representation (relative to the head) of visual stimuli *moving in depth*. To clarify the possible role of the plane of regard we might need to look separately to vertical and horizontal judgment errors.

When subjects are asked to point to a location of impact of an approaching sphere they slightly overestimate mainly the lateral component. This is in accordance with Harris' findings, although the magnitude of pointing errors is very different (we already discussed some possible causes for this difference, see above). For the horizontal judgment of motion in depth the pattern of disparities might be sufficient. However, for the vertical component of motion other mechanism might be engaged. The bias in the vertical direction was very similar in the first three experiments, showing consistence between the psychophysical and the pointing techniques. For the pointing experiment (Exp 3) mean error in the vertical direction was about five times smaller than in the horizontal direction. Together, this indicates that horizontal error (within the plane of regard) depends on different perceptual mechanisms than vertical error (perpendicular to the plane of regard). Although there was no difference in mean vertical error in our first two experiments, we observed a more confident judgment of objects' trajectories towards the head when they intersected the plane of regard, as variance was significantly smaller. That could mean that judgment of objects' paths relative to the plane of regard is easier to make when the object is intersecting the plane as opposed to trajectories that are not passing through the plane.

Another interesting finding concerns pointing to the intersections with the plane of regard. Subjects performed reasonably well when pointing to the location of trajectories' intersections with the plane of regard. Beside a small, but consistent lateral error (overestimation of azimuthal eccentricity), the main component of the pointing error was in depth direction. Subjects overestimate the egocentric distance of the point of intersection of the motion trajectory with the plane of regard. This overestimation in depth-direction is consistent with earlier findings that in near space there is an overestimation of distance of reaching/pointing targets (Medendorp et al. 1999; Foley 1980). It is also in agreement with the study of Brenner et al. (1996) that showed an underestimation of perceived velocity and an overestimation of the final position of approaching motion in depth. When subjects were asked to adjust final positions of objects moving in depth towards the observer

to the lateral motion they saw earlier in the same trail, they consistently overestimated the final position relative to them selves. In their condition with rich-cue stimulus, the magnitude of the position estimation error resembles that of our study (about 4 cm and 3 cm respectively).

We wondered if the overestimation is consistent with the so-called mutual repulsion between two moving visual targets (Marshak & Sekuler 1979). The difference in directions of two oblique motions is exaggerated, as much as by 20° in this illusion. The existence of this effect might be explained in terms of enhancement of discrimination of direction. If this effect would be present in our stimuli, the consequence would be that a starting position is perceived further away, and the end position as closer than simulated. In other words, the perceived motion in depth would be faster. This, in turn, might lead to a misperceived intersection located closer to the observer, which is an effect opposite to our finding.

Erroneous pointing to intersections (overestimation of depth and lateral component) is also in accordance with overestimation of pointing to the head found in the present study. If we assume that the trajectory towards the face is calculated based on the trajectory's angle relative to the plane of regard and the location of intersection with the plane of regard, then the (depth) error is consistent, at least qualitatively, with the error of the estimated point of impact on the head (also an overestimation of eccentricity).

In summary, there are three main findings of the present study. First, human subjects are inaccurate in pointing to the location of impact of an object approaching the head, as they overestimate the object's eccentricity. However, our study revealed a far better response than previous studies of accuracy of motion in depth. Second, additional proprioceptive and tactile information facilitated visual judgments of objects' trajectories toward the head. Combining different sources of sensory information leads to a more accurate judgment. Finally, we observed that objects with the trajectories that are intersecting the plane of regard are perceived more accurately than non-intersecting trajectories.

Reference

- Ashida H (2004) Action-specific extrapolation of target motion in human visual system. *Neuropsychologia* 42: 1515-1524
- van den Berg AV (1996) Judgments of heading. *Vision Research* 36(15): 2337-2350
- Berti A, Frassinetti F (2000) When far becomes near: Remapping of space by tool use. *Journal of Cognitive Neuroscience* 12(3): 415-420
- Beverley KI, Regan D (1975) The relation between discrimination and sensitivity in the perception of motion in depth. *Journal of Physiology* 249(2): 387-398
- Bremmer, F., Schlack, A., Shah, N.J., Zafiris, O., Kubischik, M., Hoffmann, K., Zilles, K., & Fink, G.R. (2001). Polymodal motion processing in posterior parietal and premotor cortex: a human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron* 29(1), 287-96
- Brenner E, van den Berg AV, van Damme WJ (1996) Perceived motion in depth. *Vision Research* 36(5): 699-706
- Brenner, E., Cornelissen, F.W. (2000). Separate simultaneous processing of egocentric and relative

positions. *Vision Research* 40, 2557-2563

Bridgeman B, Gemmer A, Forsman T, Huemer V (2000) Processing spatial information in the sensorimotor branch of the visual system. *Vision Research* 40: 3539-3552

Burnett LR, Stein BE, Chaponis D, Wallace MT (2004) Superior colliculus lesions preferentially disrupt multisensory orientation. *Neuroscience* 124(3): 535-47

Colby CL, Duhamel JR, Goldberg ME (1991) Heterogeneity of extrastriate visual areas and multiple parietal areas in the macaque monkey. *Neuropsychologia* 29 517-537

Colby CL, Duhamel JR (1996) Spatial representations for action in parietal cortex. *Cognitive Brain Research* (5) 105-115

Colby LC, Goldberg ME (1999) Space and attention in parietal cortex. *Annu Rev Neurosci* 22:319-49

Cooke DF, Taylor CSR, Moore T, Graziano MSA (2003) Complex movements evoked by microstimulation of the ventral intraparietal area. *Proceedings of the National Academy of the Sciences of the United States of America* 100(10), 6163-6168

Cumming BG, DeAngelis GC (2001) The physiology of stereopsis. *Annual Review of Neuroscience* 24: 203-38

Cumming BG, Parker AJ (1994) Binocular mechanisms for detecting motion-in-depth. *Vision Research* 34(4): 483-95

Cynader M, Regan (1978) Neurons in catparastriate cortex sensitive to the direction of motion in three-dimensional space. *Journal of Physiology* 274: 549-69

Duhamel JR, Bremmer F, BenHamed S, Graf W (1997) Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature* 389(6653), 845-848

Ernst MO, Bühlhoff HH (2004) Merging the senses into a robust percept. *Trends in cognitive sciences* 8(4): 162-169

Foley JM (1980) Binocular distance perception. *Psychological Review* 87: 411-434

Gentilucci M, Roy AC, Stefanini S (2004) Grasping an object naturally or with a tool: are these tasks guided by a common motor representation? *Experimental Brain Research* 157: 496-506

Gross CG and Graziano MSA (1995) Multiple representations in space in the brain, *Neuroscientist*, 1 43-50

Harris JM, Dean PJA (2003) Accuracy and precision of binocular 3-D motion perception. *Journal of Experimental Psychology: Human Perception and Performance* 29(5): 869-881

Iriki A, Tanaka M, Iwamura Y (1996) Coding of modified body schema during tool use by macaque postcentral neurons. *Neuroreport* 7(14): 2325-30

Kitigawa N, Ichihara S (2002) Hearing visual motion in depth. *Nature* 416: 172-174

Lewis CF McBeath MK (2004) Bias to experience approaching motion in a three-dimensional virtual environment. *Perception* 33: 259-276

Maravita A, Iriki A (2004) Tools for the body schema. *Trends in Cognitive Sciences* 8(2): 79-86

Marshak W, Sekuler R (1979) Mutual repulsion between moving visual targets. *Science* 205(4413): 1399-401

Mayhew JEW, Longuet-Higgins HC (1982) A computational model of binocular depth perception

Nature 297: 376-378

Medendorp WP, van Asselt S, Gielen CCAM (1999) Pointing to remembered targets after active one-step self-displacements within reaching space. *Experimental Brain Research* 125: 50-60

Neggers SFW, Langerak TR, Schutter DJLG, Mandl RCW, Ramsey NF, Lemmens PJJ, Postma A (2004) A stereotactic method for image-guided transcranial magnetic stimulation validated with fMRI and motor-evoked potentials. *NeuroImage* 21: 1805-1817

Peper L, Bootsma RJ, Mestre DR, Bakker FC (1994) Catching balls: how to get the hand to the right place at the right time. *Journal of Experimental Psychology: Human Perception and Performance* 20(3): 591-612

Poljac E, van den Berg AV (2003). Representation of heading direction in far and near-head space. *Experimental Brain Research* 151: 501-513

Poljac E, van den Berg, AV (2004) Localization of the plane of regard in space, *in press*

Poljac E, Lankheet M, van den Berg AV (2004) Perceptual compensation for eye torsion. *Vision Research* DOI: 10.1016/j.visres.2004.09.009

Portfors-Yeomans CV, Regan D (1996). Cyclopean discrimination thresholds for the direction and speed of motion in depth. *Vision Research* 36(20): 3265-3279

Raymond JE (1994) Directional anisotropy of motion sensitivity across the visual field. *Vision Research* 34(8): 1029-1037

Regan D, Gray R (2000) Visually guided collision avoidance and collision achievement. *Trends in Cognitive Sciences* 4(3): 99-107

Regan D, Hamstra SJ (1993) Dissociation of discrimination thresholds for time to contact and for rate of angular expansion. *Vision Research* 33(4): 447-462

Regan D, Kaushal S (1994) Monocular discrimination of the direction of motion in depth. *Vision Research* 34(2): 163-177

Regan D, Vincent A (1995) Visual processing of looming and time to contact throughout the visual field. *Vision Research* 35: 1845-1857

Rine R, Skavenski AA (1997) Extraretinal eye position signals determine perceived target location when they conflict with visual cues. *Vision Research* 37(6):775-787

Royden CS, Conti DM (2003) A model using MT-like motion-opponent operators explains an illusory transformation in the optic flow field. *Vision Research* 43(26): 2811-2826

Stein BE, Jiang W, Wallace MT, Stanford TR (2001) Nonvisual influences on visual information processing in the superior colliculus. *Prog Brain Research* 134: 143-56

Todd JT (1981) Visual information about moving objects. *Journal of Experimental Psychology: Human Perception and Performance* 7(4): 975-810

Wallace MT, Roberson GE, Hairston WD, Stein BE, Vaughan JW, Schirillo JA (2004) Unifying multisensory signals across time and space. *Experimental Brain Research*, 158: 252-258

Welchman AE, Tuck VL, Harris JM (2004) Human observers are biased in judging the angular approach of a projectile. *Vision Research* 44: 2027-2042

Zhang T, Heuer HW, Britten KH (2004) Parietal area VIP neuronal responses to heading stimuli are encoded in head-centered coordinates. *Neuron* 42: 993-1001

Summary and conclusions

6

Manipulating objects in near head-space requires a stable representation of their location relative to the head. Objects can have multiple such representations existing simultaneously in the brain, using several different perceptual modalities of the same object. Which definition of an object is used for a particular task is largely dependent on the planned action. In this thesis we deal with the question whether a head-centric representation of objects is used in the space near the head.

In an attempt to answer that question we first addressed the human ability to judge locations of static visual objects in space near the head and in far-space. The capacity to estimate the remembered location of an object was investigated for different static eye orientations and also after an eye movement was performed. In our first study, described in *Chapter 2*, subjects had to point towards a remembered position of a distant object after they made a saccadic eye-movement. The purpose of this design was to clarify the mechanism behind the creation of an object's representation and to identify the frame of reference in which an object's location is described. If the estimation accuracy of the object's location is not dependent on eye orientation and if it does not change after an eye movement has been made, then the representation of that remembered object is at least head centric. Recent neurophysiological studies showed that in near-head space a retino-centric representation of objects is transformed into a representation relative to the head. For that reason we also conducted the experiment in near personal space. In addition, we investigated the competence to estimate heading direction. When moving forward, a radial expanding pattern occurs on the retina. The center of that pattern is the direction in which we are moving. Although visual structure may be absent at this center, people can estimate its location accurately, inferring it from the whole pattern. Similar to the representation of objects, we investigated in which frame of reference the center of expansion is defined in the brain in far and near-head space. According to previous research, when eye-movements are involved, the representation of objects for goal-directed arm movement in far-space relies on retinal updating (Henriques 1998). Similarly, we too found that the pointing errors reflected a bias in the visuo-motor transformation which was dependent on gaze displacement. This was true for both a single object and the centre of an expanding motion pattern. Our conclusion was that a representation of the remembered visual direction is updated in a retinal frame and that this mechanism is utilized in far and near-space alike.

As a sequel to our first study we wondered what consequences do eye rotations have for the representation of object's location. Fixating an eccentric object changes the eye's horizontal and vertical orientation. Additionally, the eyes also rotate around the lines of sight in accordance with Listing's law (Fetter, Haslwanter, Misslisch & Tweed 1997). To create a correct representation of an object's position relative to the head, the brain must compensate for these eye rotations. We investigated the capacity to compensate for torsion asking subjects to

estimate the location of flashed point-targets relative to their binocular plane of regard (defined by the rotation centers of the eyes and the fixated object), and to make such estimates relative to two true head-centric planes: the mid-sagittal and the transverse plane of the head. In this way we looked at the accuracy of the perception of object's location relative to these planes and whether the visual system compensates for torsion when making such judgments. To evoke eye-torsion according to Listing's law, subjects fixated straight ahead, right upward, or right downward. Although torsion varied by ± 9 degrees across these different conditions, subjects perceived the location of flashed targets accurately relative to their plane of regard, irrespective of eccentric viewing, head-tilt, and monocular or binocular vision. However, they misjudged position of probes relative to the mid-sagittal or the transverse plane. These errors were consistent with opposite torsional compensation errors. Because only the judgement was altered (the horizontal or the vertical plane of the head) the error does not have its basis in the compensation for the actual eye torsion. This led us to conclude that judgment of the orientation of the plane of regard is correct, indicating accurate compensation for actual eye torsion. Yet, judgements of head-centric planes that are offset with respect to the line of sight are not perceived correctly, because compensation for torsion in combination with another (horizontal and/or vertical) rotation is apparently not performed correctly. This study is presented in *Chapter 3*.

Subsequently, in our study described in *Chapter 4*, we examined the perception of the plane of regard in space. For a correct representation of objects in head-centric coordinates that relies on object's location relative to the plane of regard, beside a correct representation of their elevation relative to the plane of regard (Chapter 3), the orientation of this plane relative to the head is required. To do this correctly, eye-in-head signals must be available to the visual system. We asked the subjects to indicate the orientation of their plane of regard, while fixating one of the nine randomly presented directions ranging from 20° left down to 20° right up relative to their straight ahead. When subjects were sitting upright while pointing to their plane of regard we observed a constant bias directed below the actual position of the plane of regard. The bias was apparently caused by maintained tonus in arm muscles when the arm is raised. For, when the targets were shown on a display mounted in a table, to provide support of the subject's arm and hand throughout the trial, subjects pointed accurately, regardless of the fixation direction or pointing distance. In addition, head tilt did not cause a change in accuracy. We concluded that the plane of regard is correctly localized in space and might be a good reference for defining objects relative to the head. The analysis of horizontal and vertical binocular disparities to determine the layout of the environment, as proposed by Mayhew and Longuet-Higgins (1982), combined with the information about the plane of regard's orientation would enable the visual system to describe the direction and distance of objects with respect to the head. Yet, as indicated by our results in Chapters 2 and 3, we have no evidence that such a transformation occurs free of systematic errors.

Finally, we extended our exploration of the brain's representations of locations to objects that are moving in depth. Estimating the direction of object's motion in depth is an important action in a natural situation, as it is necessary to avoid collision with objects as we are moving through the surroundings. Apparently, people are very good at this. Collision avoidance as well as collision achievement (bringing objects to a certain location on the face, for instance) are everyday tasks. The question has arisen, how accurate people are at these tasks? A baseball player cannot catch a ball approaching with a high speed, if he misjudge the trajectory by even a few millimeters. On the other hand, preventing to bump into a door-post might not necessarily require a very precise knowledge of its location. We just might choose keeping away from it by employing a safe distance-margin while passing through the door. It seemed interesting to investigate the absolute accuracy of stereoscopic motion-in-depth perception. Most previous studies concentrated on precision, that is perception of discrimination thresholds for motion in depth. In our study presented in *Chapter 5*, subjects estimated the point of impact of an object approaching the head while fixating straight ahead. Because the simulated motion of the approaching sphere was presented only partially, subjects had to extrapolate the remainder of it's trajectory towards the face. In two separate series of experiments we investigated a perceptual judgment and the capability to point to the location of impact on the face (a motor task). We found an overestimation of the horizontal eccentricity of the perceived point of impact on the head in the motor task. The vertical error, however, was insignificant. The confidence of the judgment in the perceptual task was considerably improved by additional tactile and proprioceptive information about the point of impact, as the variance of their responses was lower. A lower variance in the perceptual task was also observed when trajectories intersected the plane of regard. These observations show much higher accuracy for the perception of trajectories relative to the head than reported by previous studies.

Samenvatting

Manipulatie van objecten rond ons hoofd vereist een stabiele representatie van hun locatie ten opzichte van het hoofd. Objecten kunnen tegelijkertijd meerdere representaties hebben, waarbij de informatie kan worden gebruikt afkomstig van verschillende sensorische modaliteiten van hetzelfde object. Welke representatie uiteindelijk gebruikt wordt om een taak uit te voeren hangt grotendeels af van de geplande actie. In dit proefschrift behandelen we de vraag of een hoofdcintrische representatie van objecten bestaat in de ruimte nabij het hoofd.

Om die vraag te beantwoorden onderzochten wij eerst het vermogen om locaties van visuele statische objecten te schatten in de ruimte nabij het hoofd en op een grotere afstand. De waarneming van een herinnerde positie werd getest voor verscheidene statische oog-orientaties. Ook onderzochten we de localisatie van herinnerde objecten nadat een oogbeweging is uitgevoerd. In onze eerste reeks experimenten, beschreven in Hoofdstuk 2, werden de proefpersonen gevraagd om te wijzen in de richting van de herinnerde positie van een ver gelegen object nadat ze een saccadische oog-beweging hebben gemaakt. Hiermee trachtten we het mechanisme te doorgronden dat verantwoordelijk is voor de object-representatie. De opzet van deze experimenten stelde ons ook in staat om het referentie frame te identificeren waarin de locatie van een object is beschreven: als de fout in de waargenomen locatie van een object onafhankelijk is van oog-orientatie en onveranderd blijft nadat een oogbeweging is gemaakt, dan kunnen we zeggen dat de representatie op z'n minst hoofdcintrisch is. Recent neurofysiologisch onderzoek liet zien dat in de ruimte nabij het hoofd een retinocintrische representatie getransformeerd wordt naar een representatie ten opzichte van het hoofd. Om die reden hebben we hetzelfde experiment uitgevoerd op een kleinere afstand, in de ruimte nabij het hoofd.

Verder onderzochten wij met gebruik van dezelfde taak het vermogen om de richting van bewegen, de heading richting, aan te wijzen. Wanneer men naar voren beweegt, ontstaat een radiaal expanderend patroon op de retina. Het centrum van dit patroon komt overeen met de richting waarin we bewegen. Hoewel visuele structuur soms niet aanwezig is in dit centrum, hebben proefpersonen geen moeite om het centrum aan te wijzen. De positie van het centrum wordt bepaald uit het hele patroon. Analooq aan representatie van objecten, onderzochten we ook in welke referentie frame dit centrum is gerepresenteerd in de hersenen, voor de ruimte ver weg en nabij het hoofd. Volgens eerder onderzoek, wanneer het om oog bewegingen gaat, berust de representatie van objecten voor doel-gerichte arm bewegingen in ver weg ruimte op retinale actualisatie (retinal update) van de ruimtelijke kaarten (Henriques 1998). Ook wij vonden dat wijsfouten een afwijking in de visuo-motor transformatie weerspiegelden, die afhankelijk is van de verplaatsing van het oog. Dit geldt voor zowel de richting van enkel object als voor het centrum van een expanderend bewegingspatroon. We concludeerden dat de representatie van een herinnerde visuele richting bewaard wordt in een retinale referentie frame, maar dat het voor elke oog-beweging geactualiseerd wordt om voor die oog-rotatie te compenseren. Dit mechanisme wordt gebruikt zowel in de ruimte nabij het hoofd als op grotere afstanden ten opzichte van het hoofd.

Als we een eccentric object fixeren, verandert de orientatie van het oog in de horizontale en de verticale richting. Daarnaast draaien de ogen ook om de kijkassen volgens de wet van Listing (Fetter, Haslwanter, Misslisch & Tweed 1997). In ons volgende onderzoek vroegen we ons af wat de consequenties van zulke oogrotaties zouden zijn voor de representaties objecten. Om een correcte representatie van de positie van een object tot stand te kunnen brengen, moet het brein ook voor deze rotaties compenseren. We onderzochten het vermogen om te compenseren voor torsie door de proefpersonen te vragen om de locatie van geflitste doelen te schatten ten opzichte van het binoculaire vlak der kijk-lijnen (het vlak waarin kijk-lijnen liggen; gedefinieerd door twee rotatie-centra van de twee ogen en het fixatie-punt; in de rest van de tekst gerefereerd als PR). Daarnaast probeerden we ook inzicht te krijgen in de waarneming van posities van objecten ten opzichte van twee echte hoofdcentrische vlakken: het mid-sagittale en het transversale vlak van het hoofd. Hier stond de vraag centraal of het visueel systeem volledig compenseert voor torsie ook in geval van deze twee vlakken. Om torsie die de wet van Listing volgt op te roepen, fixeerden de proefpersonen recht-voort, rechts-boven of rechts-onder. Hoewel de torsie sterk varieerde tussen de verschillende condities ($\pm 9^\circ$) localiseerden de proefpersonen geflitste targets even nauwkeurig ten opzichte van hun PR, onafhankelijk van de fixatie richting, monoculaire of binoculaire waarneming, of hoofd-kanteling. De localisatie van geflitste punt-doelen ten opzichte van de mid-sagittaal of transversaal vlak liet wel systematische fouten zien.

We concludeerden dan ook dat de waarneming van de orientatie van het PR correct is. Kennelijk wordt gecompenseerd voor actuele torsie. De waarneming van de hoofdcentrische vlakken, aan de andere kant, is niet juist. Wellicht is hier een compensatie voor torsie nodig die gecombineerd moet worden met compensatie van een andere (horizontale en/of verticale) rotatie. Deze studie is beschreven in Hoofdstuk 3.

In onze studie beschreven in Hoofdstuk 4 onderzochten we de perceptie van het PR in de ruimte. Voor een nauwkeurige representatie van objecten in hoofdcentrische coördinaten, is naast representatie van de elevatie van objecten ten opzichte van het PR, ook de oriëntatie van het plane of regard zelf (Hoofdstuk 3) noodzakelijk (in relatie tot het hoofd). Het visueel systeem moet daarom over de signalen van de verticale oog-orientatie in het hoofd beschikken. De proefpersonen werden gevraagd om de orientatie van het plane of regard aan te wijzen, terwijl ze een van de negen willekeurig gepresenteerde richtingen fixeerden, variërend van 20° links-onder tot 20° recht-boven ten opzichte van hun recht-voort. In het eerste experiment vonden we een systematische fout in de neerwaartse richting, beneden de werkelijke positie van het PR. Omdat de proefpersonen rechtop zaten tijdens dit experiment, vermoedden we dat de geobserveerde afwijking wellicht was veroorzaakt door de tonus in de arm spieren die ontstaat als de arm opgetild wordt. Om dit vermoeden te testen werden de doelen op een scherm gepresenteerd dat in een tafelblad was gemonteerd en dus in het horizontale vlak lag waarop de arm rustte. Genoemde afwijking was afwezig ongeacht de fixatie-richting wanneer de arm ondersteund werd gedurende het experiment. Hoofd-kanteling in de richting van een van de schouders veroorzaakte geen verandering in de nauwkeurigheid van het

wijzen.

We concludeerden dat het PR correct kan worden gelocaliseerd ten opzicht van het hoofd en het lichaam en dat het daarom een goede referentie zou kunnen zijn om de positie van objecten ten opzichte van het hoofd te definiëren. Mayhew en Longuet-Higgins (1982) beschrijven een analyse van horizontale en verticale binoculaire dispariteiten met behulp waarvan de structuur van het visueel veld te bepalen is. Dit kan, gecombineerd met de informatie over de oriëntatie van het PR, het visueel systeem in staat stellen om de richting én de afstand van objecten te beschrijven in hoofdcintrische coördinaten. Echter, onze resultaten in Hoofdstuk 2 en 3 geven aan dat deze transformatie naar een hoofdcintrische frame niet fout-vrij verloopt.

Tenslotte hebben we onze exploratie van representaties die door het brein worden gecreëerd uitgebreid met objecten die bewegen in diepte. In een natuurlijke situatie is het vermogen om de positie van objecten die om ons heen bewegen te schatten van groot belang. Vaak moeten we objecten kunnen vermijden, als ze bijvoorbeeld bedreigend zijn. Soms is het juist nodig om iets naar een bepaalde plaats op ons lichaam of het gezicht te brengen, zoals wanneer we eten. Kennelijk zijn mensen heel goed in deze taak. Een honkbal speler kan zich niet veroorloven om een snel naderende bal verkeerd in te schatten. Aan de andere kant hoeft men wellicht niet altijd naderende objecten met een hoge nauwkeurigheid te kunnen schatten, zoals wanneer we door een deur gaan. In dit geval kunnen we een veilige marge aannemen van enkele centimeters om niet tegen de deurpost aan te lopen. Het leek ons daarom interessant om de absolute nauwkeurigheid te onderzoeken waarmee stereoscopische beweging in diepte wordt waargenomen. De meeste voorgaande studies concentreerden zich op precisie van beweging. Ze onderzochten de perceptuele discriminatie-drempels voor de beweging in diepte. Dat zegt helaas niet veel over de nauwkeurigheid waarmee het gebeurt. In onze studie gepresenteerd in Hoofdstuk 5, beoordelen de proefpersonen de locatie van naderende objecten. Ze werden gevraagd om de plaats aan te wijzen op hun gezicht waar gesimuleerde bolvormige objecten naartoe bewogen, terwijl ze rechtvooruit fixeerden. Omdat de gesimuleerde beweging van de naderende bol maar gedeeltelijk werd getoond, moesten onze proefpersonen de rest van het traject extrapoleren. In twee series van experimenten onderzochten we het vermogen om het punt van inslag op het gezicht aan te wijzen. Wat we vonden was een overschatting van de horizontale eccentriciteit van de waargenomen inslag in onze motor-taak. De verticale fout was daarentegen niet significant. De variabele fout van de beoordeling in de perceptuele taak nam aanzienlijk af door toevoeging van tactiele en proprioceptieve informatie over het inslagpunt. Dezelfde lagere variantie in de perceptuele taak observeerden wij voor de trajecten die het PR doorsneden. Onze bevindingen laten een veel hogere nauwkeurigheid van waarneming zien van de trajecten naar het hoofd dan wat eerdere studies op dit gebied rapporteerden.

Curriculum vitae

Ervin Poljac werd geboren op 25 juni 1972 in Derventa, Bosnië-Herzegovina, waar hij in 1991 het VWO diploma behaalde. Na een korte periode in Sarajevo waar hij begon met de studie Geneeskunde, verhuisde hij naar Nijmegen. Daar studeerde hij in de periode 1994-1999 psychologie, afstudeerrichting Neuro- en Revalidatie-psychologie. Zijn wetenschappelijke avontuur begon in 2000 op de toenmalige afdeling Fysiologie (Neurowetenschappen) van de Erasmus Universiteit in Rotterdam. Daar kreeg hij de gelegenheid om zijn promotie-onderzoek te doen onder begeleiding van Bert van den Berg. Na één jaar werd dat onderzoek voortgezet op de afdeling Functionele Neurobiologie van de Universiteit Utrecht. Dit proefschrift is daarvan het resultaat. Ervin is momenteel hard bezig met het oprichten van een onderzoeksgroep op de afdeling Psychologie van de Universiteit in Sarajevo.

List of publications

Poljac E, van den Berg AV (2003). Representation of heading direction in far and near-head space. *Experimental Brain Research* 151:501-513

Poljac E, Lankheet M, van den Berg AV (2004) Perceptual compensation for eye torsion. *Vision Research* 45(4): 485-96

Poljac E, van den Berg AV (2005) Localization of the plane of regard in space. *Experimental Brain Research*, *in press*

Poljac E, Neggers SF, van den Berg AV (2005) Collision judgment of objects approaching the head. *Experimental Brain Research*, *in press*

Dankwoord

Vanaf deze plek wil ik iedereen hartelijk bedanken voor hun positieve bijdrage aan de totstandkoming van dit proefschrift. Ten eerste ben ik veel dank verschuldigd aan mijn promotor, Bert van den Berg. Bedankt voor alle wetenschappelijke ideeën die verwerkt zijn in dit proefschrift, jouw opbouwende kritiek en het gevoel dat je me gaf dat ik altijd bij je kon binnenlopen voor een probleem of een discussie. Dat heb ik zeer gewaardeerd.

De leden van de leescommissie, Prof. Stan Gielen, Prof. Edward de Haan en Prof. Casper Erkelens, wil ik bedanken voor de tijd en energie die ze hebben gestopt in het lezen van dit proefschrift.

Een aantal mensen leverde een directe bijdrage aan het onderzoek in dit proefschrift. De samenwerking met Martin Lankheet en Bas Neggers resulteerde in twee goede wetenschappelijke publicaties.

John, Editha, Jeroen, bedankt voor de goede sfeer in Rotterdam. Jaap, Jan, jullie waren geweldige kamergenoten. Ildikó, bedankt voor een warm gevoel. Een Miriam is onmisbaar op elke afdeling, hartelijk dank. Gerard en Ed, ben ik dankbaar voor snelle en technisch perfecte oplossingen. Mijn andere collega's wil ik ook bedanken voor alle hulp en gezelligheid op de afdeling: Andre, Erik, Florence, Frank, Jacob, János, Jeannette, Lonneke, Michiel, Miriam, Richard, Robben (alle drie), Roger, Wim, allen bedankt voor een leuke tijd.

Harold en Edward wil ik nog bedanken voor hun positieve instelling betreffende mijn plannen omtrent Sarajevo.

Een speciaal woord van dank aan mijn vrienden uit Nijmegen, Rotterdam, Amsterdam en Arnhem, die zorgden voor de ontspanning buiten het werk om.

Uiteraard wil ik ook mijn twee paranimfen bedanken. Samir, vooral voor je hulp in moeilijke tijden. Kuan, al sinds onze studietijd werkt jouw interesse en enthousiasme zeer motiverend.

In het bijzonder wil ik mijn zus en mijn ouders bedanken voor al hun begrip, steun en geduld.

Ervin



ISBN 90-393-0075-5