

# Sensitivity to full-field visual movement compatible with head rotation: Variations with eye-in-head position

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## Abstract

Variations in velocity detection thresholds for full-field visual rotation about various axes are compatible with a simple channel-based system for coding the axis and velocity of the rotation (Harris & Lott, 1995). The present paper looks at the frame of reference for this system. The head-centered, craniotopic reference system and the retinal-based, retinotopic reference systems were separated by using eccentric eye positions. We measured the threshold for detecting full-field visual rotation about a selection of axes in the sagittal plane with the eyes held either  $22\frac{1}{2}$  degs up, straight ahead or  $22\frac{1}{2}$  degs down in the head. The characteristic features of the variation in detection thresholds did not stay stable in craniotopic coordinates but moved with the eyes and were constant in retinotopic coordinates. This suggests that the coding of head rotation by the visual system is in retinotopic coordinates.

**Keywords:** Visual motion, Full-field motion, Visual detection thresholds, Self motion, Channels, Retinotopic coding, Coordinate systems

## Introduction

When the eye moves, either in the head, or as a result of movement of the head, its movement creates a complex pattern of retinal motion. The exact pattern of retinal motion contains potentially useful information about the angular and linear components of the movement that created it (Miles & Wallman, 1993; Harris, 1994). Converging lines of research, investigating oculomotor (e.g. Fetter et al., 1992; Tan et al., 1993), psychophysical (Harris & Lott, 1995), and single cell responses (e.g. Wylie et al., 1993) to full-field visual movement are beginning to suggest that the visual consequences of eye rotation might be extracted from the overall pattern of visual movement by a system comprising a small number of channels each maximally sensitive to the visual consequences of a particular eye rotation.

The threshold velocity for the detection of full-field visual motion varies with the orientation of the axis of rotation in three dimensions (Harris & Lott, 1995). This variation is difficult to account for in terms of the motion sensitivity across the retina. However, it can be convincingly modelled by a three-channel processing system in which each channel responds best to rotation about a particular axis and whose response falls off as the actual rotation axis deviates from this. At least three channels

are needed to code axis orientation because space is three dimensional. The orientation of the axis of rotation can only be recovered by *comparing* the activity of the various channels (see Regan, 1982).

Such a channel-based system for processing full-field visual information is readily compatible with the complementary head-rotation information coming from the vestibular system. Vestibular information is, by virtue of the physical structure of the semicircular canals, encoded in the activity of a small number of channels (the canals). The response from the canals is proportional to the cosine between the axis of rotation and the optimal axis for stimulating that canal (Estes et al., 1975; Blanks et al., 1985; Reisine et al., 1988). The magnitude of the response of any one canal varies with factors other than the orientation of the rotation axis and so the actual orientation of the stimulating axis can only be recovered by comparison of the activity of all of the canals.

Visual information originates in a retinal reference frame whereas vestibular information about head movements originates in a head-centered reference frame. To investigate whether the visual coding system for full-field angular motion is in eye or head coordinates, we measured velocity thresholds for detecting rotation about nine axes in the sagittal plane. We separated eye and head coordinate systems by having our subjects maintain eccentric gaze positions. If the distribution of velocity thresholds reflects the activity of underlying channels, and these channels are in head (or space) coordinates, the variation in threshold for different axis orientations should be unaffected

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by eye position. If, however, this coding is in retinal coordinates, the pattern of velocity thresholds should shift; moving along with the eyes.

## Methods

### Subjects

Four subjects participated in the experiment. Their ages ranged from 20 to 30 years, and each had normal vision with no history of strabismus or other visual disorders. Three subjects were naïve to the experimental hypotheses and were paid for their services; one was one of the authors (LL). All subjects gave their informed consent.

### Apparatus and visual stimulus

The stimulus was a pattern of dots projected by a planetarium projector onto a 57-cm-radius hemispherical screen (see Fig. 1). The dots were generated by shining a single projector bulb through pin holes made with a random distribution in a 10-cm-diameter metal sphere that surrounded it. Each projected dot subtended approximately  $4^\circ \times 3^\circ$  on the screen and had fuzzy edges. The density of the dots was approximately 26 dots/m<sup>2</sup>. The planetarium projector was the only source of light illuminating the screen. When the projector was on, the luminance of the dots and background were 11.56 cd/m<sup>2</sup> and 1.54 cd/m<sup>2</sup>, respectively, which resulted in a Michelson contrast, defined as  $(L_{max} - L_{min}) / (L_{max} + L_{min})$ , of 0.76. The projector could be rotated at velocities of between 0.04 deg/s and 74 deg/s with a resolution of 0.02 deg/s under 12-bit computer control through a Cambridge Electronic Design 1401 interface box. The rotation axis of the projector could be positioned, also under computer control, with  $\pm 0.5^\circ$  accuracy.

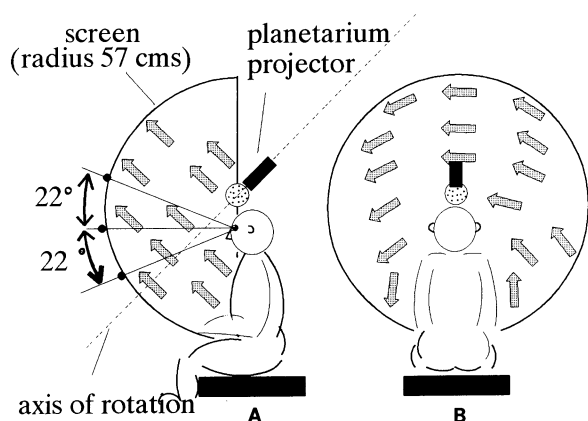
Subjects sat at the center of the dome with their knees and

hands below the screen and not visible. Subjects were positioned by eye with their Frankfurt plane (defined as the plane containing the ear canal and the suborbital bone) approximately horizontal. This is close to the comfortable natural resting position of the head. A chin rest was used to maintain the subject's head position. In this position, the subject's eyes were 12 cm below the geometric center of the screen and the planetarium projector was centered 5 cm above the geometric center (see Fig. 1). Three red LEDs were mounted on the far side of the hemisphere, one at the center, one  $22\frac{1}{2}^\circ$  deg above the center and one  $22\frac{1}{2}^\circ$  deg below. The LEDs, viewed through the translucent material of the screen, served as fixation points in between stimulus presentations.

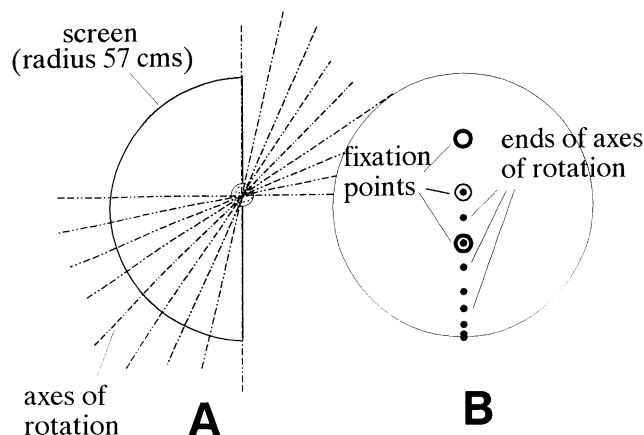
### Procedure

Threshold velocity was measured for the detection of motion about each of nine axes equally spaced in the plane that contains yaw and roll rotation (see Fig. 2). All measures were obtained under binocular viewing conditions. Subjects kept their chin in the chin rest and maintained fixation on an LED whenever it was illuminated. Prior to each trial, the fixation spot disappeared and subjects were instructed to keep looking at that area of the screen throughout the three second trial.

Each trial consisted of two 1-s intervals separated by 1 s. The dot pattern moved continuously at a constant velocity during one period and was stationary in the other. The screen was dark during the interstimulus interval. A two-alternative forced choice (2AFC) with a transformed up-down method was used (Wetherill & Levitt, 1965; Levitt, 1971). Subjects indicated which interval contained movement by pressing one of two buttons on a hand-held box. Two correct responses in a row resulted in a 20% decrease in velocity, and one incorrect response caused velocity to be increased by 20%. The mean of the last four out of eight reversals was taken as threshold. This regime provides



**Fig. 1.** The equipment. The subject sat in a 57-cm-radius hemispherical screen with their eyes 12 cm below the geometric center. A planetarium projector was positioned directly above the subject with its center 5 cm above the geometric center. The projector could rotate around any axis. The grey arrows represent the direction of movement of the projected dots for one particular orientation of the projector when seen from the left side (A) or from behind (B). At the beginning of each trial the subject looked at one of three fixation points, shown as dots in A. Fixation LEDs were positioned on the outside of the dome opposite the geometric center and  $22\frac{1}{2}^\circ$  deg above and below this point.



**Fig. 2.** The stimulus. This diagram uses the same format as Fig. 1 to show the orientation of the nine axes used in this experiment. All of the axes were parallel to the mid-sagittal plane. A: The orientation of the axes of rotation viewed from the side. B: The points where each of the nine axes passed through the screen. Our convention is to refer to the earth-horizontal axis as 0, and the earth vertical axis as 90. These points correspond to the part of the screen where there was purely rotational movement. Also shown (in B) are three open circles corresponding to the three fixation points.

an estimate of the 70.7% correct detection point (Wetherill & Levitt, 1965).

Five rotation axes were tested in each 50-min session. Each axis orientation included both rotation polarities (e.g. rightward and leftward motion in yaw; clockwise and counterclockwise motion in roll, etc.) for a total of ten separate threshold measures per session. For each session, the fixation point was constant at one of the three positions. Three velocity threshold estimates for each rotation axis were obtained for each subject for each eye position. The order of presentation of the axes was randomized.

### Data analysis

The three threshold velocity estimates of each subject, each estimate being the average of the last four reversals of the staircase, were averaged for each axis orientation. The absolute values of the means were computed and the data were subjected to a  $9$  (axis orientation)  $\times 3$  (eye position)  $\times 2$  (rotation polarity), within-subjects analysis of variance (ANOVA). The differences between pairs of means were evaluated using a Fisher test, a correction procedure for multiple pairwise comparisons (Keppel, 1982).

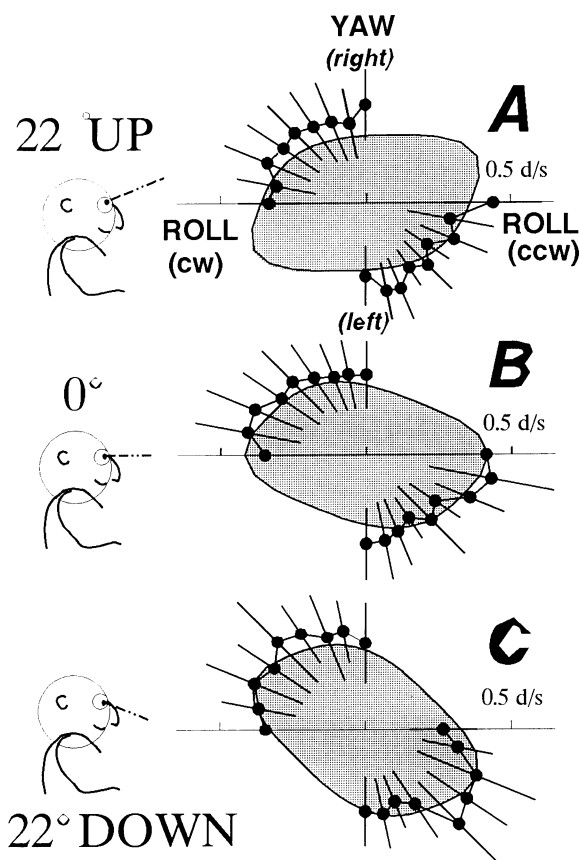
### Results

The velocity detection thresholds for axes between yaw and roll (defined with respect to the head) with the eyes positioned straight ahead,  $22\frac{1}{2}$  deg up or  $22\frac{1}{2}$  deg down are presented in Fig. 3. The results are tabulated in the Appendix with the stimulus axes given in both head and retinal coordinates.

If the distribution reflects the activity of underlying channels and these channels are in head (or space) coordinates, the variations in thresholds should be unaffected by eccentric eye position. A comparison of Figs. 3A–3C shows that this is not the case: the pattern of threshold variations in fact changes with eye position, that is it stays constant in retinal coordinates. Plotted through the data obtained with the eyes centered in the orbit is a shaded area representing the thresholds predicted by the model of Harris and Lott (1995). This curve acts as a convenient reference. When the shaded area is rotated by an amount equal to the displacement of the eyes ( $22\frac{1}{2}$  deg up or down), it can be seen to continue to describe the data well.

Our main result is further illustrated in Fig. 4 which plots the same data in both head coordinates (Fig. 4A) and retinotopic coordinates (Fig. 4B). Clearly, the data neatly overlap when plotted in retinotopic coordinates but show considerable variation when plotted in head coordinates.

The impressions gained by inspection of Figs. 3 and 4 were supported by the ANOVA. This analysis revealed a main effect of axis orientation [ $F(8, 24) = 3.09$ ,  $P < 0.02$ ], reflecting significant differences in threshold for axis orientations collapsed across eye position and rotation polarity. A highly significant eye position  $\times$  axis orientation interaction [ $F(16, 48) = 3.37$ ,  $P < 0.001$ ] was also obtained. The pattern of thresholds for the axis orientations differs for the three eye positions. Finally, a significant interaction of all three factors [ $F(16, 48) = 1.86$ ,  $P < 0.05$ ] suggests that this pattern of results differs for the two rotation polarities. The Fisher test revealed that, when pairs of means in head-centered coordinates were analyzed, significant differences were obtained for eight out of 18 axis orientations

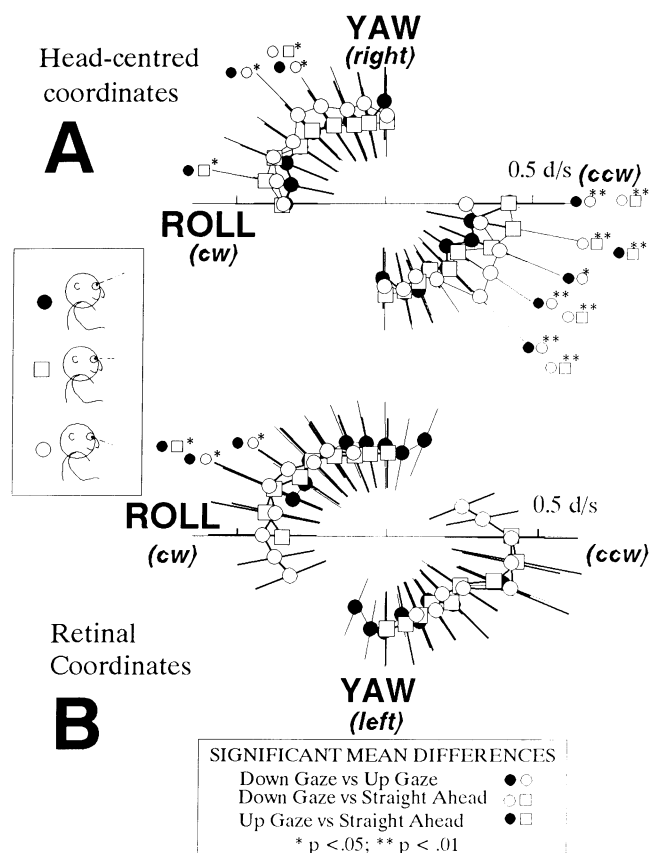


**Fig. 3.** Velocity thresholds for detection of full-field visual rotation as a function of eye position. Each data point represents the mean of three repetitions for each of the four subjects along with the standard deviations. In each graph, the distance of each symbol (filled circle) from the center represents the threshold rotation velocity. The direction of the data point from the center represents the orientation of the axis of rotation. The directions of rotation have been separated using a left-hand rule where the fingers of the left hand curl in the direction of rotation of the stimulus when the left thumb is aligned with the axis. All axes are defined with respect to the head. The data for panel B were obtained with the subjects looking straight ahead. The data shown in panels A and C were obtained with the subjects looking  $22\frac{1}{2}$  deg up and down, respectively. Also plotted in each of the panels is the output expected from a model having three channels for the detection of full-field rotation (shaded zones: see Harris & Lott, 1995). The model's outputs shown in panels A and C are simply that of B tilted up or down by  $22\frac{1}{2}$  deg. No attempt has been made to fit the data shown in panels A and C.

(i.e. nine axes  $\times$  two rotation polarities). These axis orientations along with their associated  $P$  values are indicated on Fig. 4A (see figure legend for details). When comparisons were made in retinal coordinates, only two out of 18 axis orientations showed significant differences (see Fig. 4B).

### Discussion

The visual and vestibular systems both contribute to the processing of head-rotation information. Visual and vestibular signals originate in different coordinate systems: visual input is in retinal coordinates whereas vestibular information concerning



**Fig. 4.** Same data as for Fig. 3 plotted in head-centered coordinates (A) and retinal coordinates (B). Data from all three eye positions have been superimposed. To convert the data into retinal coordinates, the eye's position has been subtracted from the orientation of the axis described with respect to the head. Thus, the head-centered axis called 0, becomes the eye centered axis called  $-22\frac{1}{2}$  when the eyes are looking downwards and  $22\frac{1}{2}$  when the eyes are looking up. Additional symbols at the ends of some of the error bars indicate significant differences between pairs of means at these axis orientations. There are many significant differences if the data are compared in head coordinates, but only two if they are compared in retinal coordinates.

head rotation originates in the canals which are embedded in the skull and thus give information in coordinates fixed with respect to the head. When the eyes are looking straight ahead these reference frames are aligned, but during eccentric eye positions the two reference systems are separated. This study shows that the characteristic variations in the detection thresholds for full-field visual rotation move with the eyes indicating that the coding system uses a retinal reference frame.

#### *The contribution of compensatory eye movements*

Full-field visual movement, even for the brief duration (1 s) and low velocities (less than 0.5 deg/s) used in this study, evokes a compensatory oculomotor response which tends to cancel out any slippage of the retinal movement (Honrubia et al., 1968). Thus, the anisotropies we observe in threshold velocities among axes could be influenced by anisotropies in the oculomotor

response to these stimuli: more efficiently compensated retinal movement might be more difficult to detect. This is unlikely, however, since torsional visual movement (rotating about the line of sight) is associated with the highest thresholds (see Figs. 3 and 4) but evokes the weakest compensatory eye-movement response (Collewijn et al., 1985). Subjects could perhaps be detecting the stimulus movement not directly, but by monitoring their response to the visual stimulus (either oculomotor or anything else). If that monitored response showed anisotropies, they might then be reflected as variations in the velocity detection threshold. By whatever means subjects performed the task, the results were constant in retinal coordinates. Thus, we can conclude that the visual response, in the most general sense including perceptual and oculomotor elements, is in retinal coordinates.

#### *A common reference system?*

We thus have two systems involved in processing information to do with head movement that appear to be working with different reference frames. Is one transformed into the reference frame of the other to generate a common reference frame? The present study does not directly address this question. We can conclude that the initial visual coding of full-field movement by the brain is in retinotopic coordinates. The movements with the eyes of the characteristic pattern of variations in the motion detection thresholds betrays the retinotopic nature of the initial visual coding. But processes that happen at later stages in the system would not shift these retinotopic features. To reveal the frame of reference of such *additional* processes, we would have to measure the output of such transforms; for example, the perceived orientation in space of the axis of visual rotation with eccentric eye position. These experiments are underway at present.

Similarly, looking at the neurophysiological data, although it is *implied* there is a common reference system shared by visual and vestibular contributions to the head-movement processing system, there has been no actual demonstration of this. Vestibular nucleus neurones are responsive to both visual and vestibular information (Henn et al., 1974; Robinson, 1977; Waespe & Henn, 1977a,b, 1978, 1979; Keller & Precht, 1979; Bauer, 1980; Horn et al., 1983). The visual response properties of vestibular nucleus cells have never been reported in greater detail than comparing the response in opposite directions (e.g. Waespe & Henn, 1979), although it is *implied* that the visual and vestibular information that converge at this site are compatible, that is they are both in channel-based systems and they are both using the same reference frame. The reported visual response properties of the various nuclei of the accessory optic system (Simpson, 1984; Simpson et al., 1988; Soodak & Simpson, 1988; Wylie & Frost, 1990) and cells in the inferior olive (Barmack & Hess, 1980; Takeda & Maekawa, 1980; Simpson et al., 1981; Harris & Isaacs, 1982; Leonard et al., 1988) and cerebellum (Waespe et al., 1981; Waespe & Henn, 1981; Graf et al., 1988; Wylie et al., 1993; Wylie & Frost, 1993; Van der Steen et al., 1994), which have been demonstrated to be involved in relaying visual information to the vestibular nucleus (Simpson, 1984), are likewise in essentially unknown reference frames.

Information from the vestibular complex is used to generate both movements of the head and movements of the eyes as well as providing perceptual information about head rotation.

For all of these, a head-centered reference system would seem to be most appropriate. Even for eye-movement control, the appropriate signals are in head-centered coordinates since muscular pulls are converted into eye-centered coordinates by the physical arrangement of the eye muscles and insertions on the globe (Simpson & Graf, 1981; Miller & Robins, 1987). Thus, we might expect the visual signal to be converted to head-based coordinates rather than the vestibular signal to be converted to retinal-based coordinates.

Another possibility is that in fact no coordinate transform occurs at all. It would be possible to operate on the assumption that the eyes were roughly centered in the orbits at all times under which conditions the retinal and head-centered coordinates are interchangeable. This assumption seems to be employed, for example, with minimal behavioral consequences by the cat's and to a lesser extent the monkey's superior colliculus where the visual (retinal coordinates) and auditory (head coordinates) spatial maps are allowed to become misaligned in at least some cells whenever the eyes are displaced (cat: Harris et al., 1980; monkey: Jay & Sparks, 1984).

# Possible solutions

The potential problems and ambiguities of having two coordinate systems could be largely overcome if visual information were to be transformed in accordance with eye position in such a way as to redirect the visual input to the appropriate vestibularly driven cells. Eye-position information could be obtained from efference copy or from the huge extraocular proprioceptive input to the vestibular complex (Buisseret-Delmas et al., 1990). Only eye eccentricities that threatened the axes alignment would be relevant: eye movements with the goal of stabilizing a visual stimulus tend to be around the same axis as the stimulus motion and would therefore pose no threat to the interpretation of the orientation of the axis of rotation in space.

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## Appendix

These are the thresholds for each of the nine tested axes (tilted from 0 to 90 deg), in each direction (+ve and -ve) for each of the four subjects (AV, SM, LM, and LL) and for each of the three eye eccentricities (22½ deg down/straight ahead/22½ deg up). Each value is the mean of the last four reversals and each axis was repeated three times for each subject and for each eye eccentricity ( $n = 12$ ). The first column on the left shows the orientation of the axis in eye coordinates (0 means axis aligned to line of sight), and the second column shows the orientation of the axis in head coordinates (0 means axis parallel to earth-horizontal). The columns on the right show the mean and standard deviations of all data averaged across subjects.

Orientation of axis								Overall STD
Eye	Head	AV	SM	LM	LL	Overall		
Eyes looking down 22.5								
-22.5	0	0.14	0.31	0.27	0.32	0.26		0.11
-11	11	0.28	0.32	0.36	0.32	0.32		0.12
0	22.5	0.31	0.64	0.37	0.31	0.41		0.21
11	34	0.40	0.53	0.45	0.29	0.42		0.16
22.5	45	0.40	0.64	0.44	0.33	0.45		0.20
34	56	0.27	0.40	0.32	0.22	0.30		0.13
45	67.5	0.20	0.29	0.29	0.26	0.26		0.09
56	79	0.25	0.30	0.31	0.28	0.29		0.12
67.5	90	0.27	0.36	0.27	0.20	0.27		0.11
-22.5	0	-0.23	-0.46	-0.33	-0.33	-0.34		0.12
-11	11	-0.32	-0.44	-0.31	-0.40	-0.37		0.13
0	22.5	-0.22	-0.57	-0.39	-0.44	-0.41		0.17
11	34	-0.23	-0.50	-0.31	-0.45	-0.37		0.15
22.5	45	-0.25	-0.50	-0.41	-0.54	-0.42		0.20
34	56	-0.27	-0.45	-0.45	-0.40	-0.39		0.12
45	67.5	-0.26	-0.45	-0.42	-0.23	-0.34		0.16
56	79	-0.31	-0.35	-0.44	-0.24	-0.34		0.11
67.5	90	-0.22	-0.41	-0.33	-0.21	-0.29		0.14
Eyes looking up 22.5								
22.5	0	0.28	0.55	0.43	0.49	0.44		0.16
34	11	0.21	0.42	0.22	0.32	0.29		0.15
45	22.5	0.27	0.45	0.27	0.33	0.33		0.12
56	34	0.26	0.29	0.19	0.27	0.25		0.09
67.5	45	0.25	0.26	0.44	0.26	0.30		0.11
79	56	0.26	0.27	0.31	0.22	0.27		0.07
90	67.5	0.30	0.32	0.41	0.23	0.32		0.11
101	79	0.23	0.38	0.32	0.30	0.31		0.10
123.5	90	0.27	0.23	0.21	0.29	0.25		0.10
22.5	0	-0.20	-0.37	-0.35	-0.35	-0.33		0.10
34	11	-0.27	-0.28	-0.26	-0.43	-0.31		0.13
45	22.5	-0.20	-0.51	-0.40	-0.33	-0.36		0.16
56	34	-0.22	-0.38	-0.45	-0.28	-0.34		0.15
67.5	45	-0.27	-0.32	-0.46	-0.31	-0.34		0.13
79	56	-0.22	-0.32	-0.47	-0.25	-0.32		0.14
90	67.5	-0.18	-0.41	-0.45	-0.17	-0.30		0.14
101	79	-0.24	-0.26	-0.36	-0.23	-0.27		0.12
112.5	90	-0.25	-0.40	-0.32	-0.38	-0.34		0.12
Eyes looking straight ahead								
0	0	0.24	0.56	0.37	0.46	0.413		0.18
11	11	0.29	0.49	0.55	0.40	0.438		0.22
22.5	22.5	0.35	0.50	0.36	0.31	0.387		0.12
34	34	0.30	0.37	0.18	0.27	0.285		0.10
45	45	0.25	0.39	0.32	0.30	0.318		0.16
56	56	0.31	0.23	0.23	0.26	0.262		0.08
67.5	67.5	0.31	0.25	0.35	0.22	0.286		0.12
79	79	0.24	0.31	0.33	0.29	0.297		0.13
90	90	0.28	0.29	0.41	0.23	0.306		0.12
0	0	-0.23	-0.40	-0.38	-0.36	-0.34		0.16
11	11	-0.33	-0.56	-0.36	-0.40	-0.41		0.18
22.5	22.5	-0.26	-0.46	-0.39	-0.52	-0.41		0.18
34	34	-0.25	-0.48	-0.41	-0.25	-0.35		0.16
45	45	-0.22	-0.53	-0.34	-0.33	-0.35		0.15
56	56	-0.26	-0.44	-0.36	-0.21	-0.32		0.14
67.5	67.5	-0.19	-0.33	-0.41	-0.21	-0.29		0.12
79	79	-0.22	-0.28	-0.39	-0.23	-0.28		0.12
90	90	-0.19	-0.30	-0.40	-0.21	-0.27		0.12