

Direction dependent occipital and parietal activity during the perception of optic flows simulating eccentric headings.

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Abstract

In non-human primates, the central coding of spatial parameters such as the direction of a saccade or a sound source has been shown to rely upon neural maps. In humans, visuotopic and somatotopic organization has been demonstrated for primary sensory and motor areas; however there is no direct evidence that high-order spatial parameters may have a map-like representation in the human brain. We measured changes in cerebral metabolic activity by f-MRI evoked by optic flows simulating ego-motion to determine whether activations depend on the specific heading direction. Optic flows simulating heading toward a cloud of stationary dots either in the gaze direction or in an eccentric direction were presented. Activation within the cuneus - superior and medial occipital gyrus and the superior parietal lobule and precuneus was found during the perception of eccentric headings. Furthermore, rightward headings activated these regions within the left hemisphere, and leftward headings activated the corresponding areas in the right hemisphere. Both hemispheres were activated during the presentation of up and down headings. The results indicate a spatial organization for the central representation of heading.

When navigating humans can recover the direction of self motion from visual cues. It has long been contended that the most important source of visual information for heading estimation is optic flow (1), namely the set of instantaneous velocities, within the image plane, of the elements comprising the visual scene. While a number of algorithms for the estimation of heading from optic flow have been suggested (e.g. 2), and numerous neurophysiological investigations have addressed the properties of single units in areas putatively involved in heading estimation (3, 4, 5) the question of how the directional components of heading may be represented centrally has received scant attention until recently (6, 7). The only psychophysical data relevant to this specific issue have shown that the principal components of the errors made by human subjects in the estimation of heading, based on the focus of expansion, are aligned with azimuth and elevation (8). Furthermore, inhomogeneities have been found in the estimation of azimuth and elevation, the azimuth being estimated more accurately for headings toward the lower visual field and elevation being estimated more accurately for headings toward the upper visual field. These results were taken to imply that a) there are two populations of units tuned to azimuth and elevation respectively and that b) these units may share a common cortical map (8).

Germane to the concept of a map is the notion of spatial coding, namely that different values of a parameter are represented within different regions of a given cortical area (9). Also neural maps may contain representations for a number of different parameters (9). If indeed heading has a map-like neural representation, then one would predict that homologous areas of each hemisphere would encode headings towards the opposite side of space; otherwise if a non-spatial representation is used, the two hemispheres should not be expected to engage differentially in the estimation of rightward and leftward headings. Secondly, the azimuth and elevation of heading may be represented within a single map, have separate neural representations, or different maps may be used to represent upward and downward headings. We present psychophysical and neuroimaging data relevant to the issue of hemispheric differences in heading estimation and neuroimaging data concerning the mapping of azimuthal and elevational components of heading.

Results

The first report of a difference in the estimation of leftward vs. rightward heading is due to Crowell and Banks (10). These authors found that the accuracy in heading discrimination was significantly better for rightward headings than leftward headings when optic flows were presented at 40° of eccentricity on either side of the vertical meridian. It was suggested that these differences may be due to retinal inhomogeneity, the nasal portion of the retina being known to contain a larger number of photoreceptors than the temporal retina. However, since their conclusion was based solely on data for one subject with only right eye viewing, it cannot be ruled out that the difference in heading discrimination accuracy might rather depend on a hemispheric difference. Indeed hemispheric differences may better account for the finding that when optic flows were presented in central vision this same subject was more accurate in the discrimination of rightward than leftward headings for headings whose eccentricity was between 10° and 40° (10).

We designed a psychophysical experiment to determine whether the difference in the estimation of rightward and leftward headings is due to a retinal or a visual field inhomogeneity. Subjects viewed monocularly optic flows, centered at the fovea, simulating self-motion relative to a cloud of stationary dots and were asked to estimate the simulated heading at the end of each trial by placing a cursor in the perceived direction of the focus of expansion at the end of each trial. As shown in Fig. 1, the cumulative variance in the estimation of both azimuth and elevation is lower for rightward headings than leftward headings regardless whether the left eye (for azimuth $F(1480,1477)=1.113$; $p<0.05$; for elevation $F(1480,1477)=1.089$ $p<0.1$) or the right eye was used ($F(1473,1469)=1.142$, $p<0.05$; $F(1473,1469)=1.103$, $p<0.1$). Also, subjects underestimated on average the true heading, the magnitude of the squared constant error having been found to be less for rightward than leftward headings both for left eye (for azimuth $F(1,46)=1.94$, $p<0.2$; for elevation $F(1,46)=1.757$, $p<0.2$) and right eye viewing ($F(1,46)=7.270$, $p<0.02$; $F(1,46)=1.746$ $p<0.2$). These data imply that the difference in the accuracy of the estimation of rightward and leftward headings, for the azimuthal component at least, cannot be accounted only by retinal inhomogeneities. Rather, there must be a difference in the way each hemisphere is able to process heading information; the higher accuracy in estimation of rightward

headings suggesting a left hemisphere superiority in this task. Stated otherwise, these psychophysical data indicate that each hemisphere does not contribute equally to the estimation of leftward and rightward headings.

In order to directly test the hypothesis that eccentric headings lead to the activation of the contralateral hemisphere and to determine whether heading azimuth and elevation are represented in a common cortical area, we resorted to functional Magnetic Resonance Imaging (f-MRI). In these experiments, four sequences were presented to the subjects. Each sequence consisted of alternating optic flows simulating self-motion either straight ahead, that is in the direction of the fixation point, or motion in one of four eccentric directions, i.e. 3° to the left, right, above and below the fixation point. The activations during the presentation of individual sequences were computed by cross correlating the f-MRI signal with the stimulus sequence.

Since we did not monitor eye movements it is possible that the activation during the presentation of the eccentric headings were due to eye movements made by subjects to bring the focus of expansion on the fovea (despite the instruction to keep their gaze on the fixation cross). Even in the absence of overt eye movements, attentional mechanisms might have been engaged during the presentation of eccentric headings. Previous work has shown that while the neural networks which subserve saccadic eye movements and shifts in attention are largely coextensive and comprise both anterior and posterior areas of the brain(11, 12), the presentation of optic flows simulating forward motion causes activations in the posterior regions of the brain with little activation in the anterior regions (13).

We compared the number of voxels activated in the anterior and posterior portions of the left and right hemisphere of six subjects who took part in the experiment (see Methods) after the anatomical images had been warped into a common coordinate system. Greater activation, in both the anterior and posterior quadrants of the right hemisphere than the homologous quadrants of the contralateral hemisphere, was found when the sequence containing leftward headings were presented. However, during the presentation of the sequence with rightward heading, the left posterior and right anterior quadrant showed greater activation. Thus the lateralization in the posterior quadrants of the brain covaried with the heading direction whereas the anterior regions showed a right hemisphere lateralization irrespective of the heading direction. Any activation in the anterior regions

may, at this point, be best explained by the engagement of attentional mechanisms during the perception of eccentric headings possibly resulting from the additional effort to keep steady fixation. Attentional mechanisms cannot account for the pattern of activation in the posterior regions since a right parietal dominance has been shown in tasks involving shifts in attention to both visual hemifields (11, 12).

Next, foci of activation were localized by superimposing individual subjects' activation maps on anatomical images (see Fig. 3) and scaling each subject's brain volumetric reconstruction to a common coordinate system. The "average" coordinates of the activations that are consistent across subjects were calculated by cluster analysis (see Methods). As shown in the table, the group analysis revealed activation in the cuneus and superior occipital gyrus of the right hemisphere when leftward headings were presented. When rightward headings were presented, the cuneus and superior parietal lobule of the left hemisphere were activated. With upward heading we found bilateral activation in the cuneus - superior occipital gyrus. When downward headings were presented we found bilateral activation in the precuneus - superior parietal lobule and superior occipital gyrus - medial occipital gyrus.

These data confirm the pattern of lateralization found in the comparison of the activations of the anterior and posterior regions of the brain and most importantly lend support to the hypothesis of a spatial code for heading. Interestingly, both optic flows simulating upward and downward as well as sideways headings activated overlapping areas of the occipital and (upward headings excluded) parietal cortex.

Discussion

These data are consistent with our previous speculation (8) that a cortical area may contain a complete map for both azimuthal and elevational components of heading, as we found to be for the superior and medial occipital cortex. A point of interest is the functional localization of this occipital activation. In a PET study by de Jong et al. (13) of the cerebral blood perfusion changes evoked by optic flows simulating straight ahead headings on a ground plane vs. stimuli in which the velocity directions had been randomized, it was suggested that the occipital focus of activation may correspond to area V3. More recently, it has been shown that area V3a, which shares posteriorly the representation of the lower meridian with area V3, has greater sensitivity to motion than area

V3 (14). Furthermore, whereas area V3 has a retinotopic representation of the lower visual field only, area V3a contains a representation of both upper and lower visual fields (14). The finding that activations take place in overlapping regions of the occipital cortex for optic flows simulating both upward and downward headings suggests to us that they may take place in area V3a rather than area V3.

It has been contended that self-motion estimation must depend upon the integration of wide areas of the optic flow (e.g. 15), the information provided by peripheral vision being most important, and that cortical area MST (3, 4, 5) and parietal area 7 (6), which contain neurons with large receptive fields, are the best suited for this task. However, psychophysical data have shown that the accuracy of heading estimation is best when optic flows are presented at the fovea with no improvement in accuracy being noted when larger optic flows are presented (16, 17, 18). Furthermore, most of the information relevant to the estimation of heading is limited to those regions of the optic flow whose visual direction is in the proximity of the direction of self-motion (19). Thus, the relatively small size of the receptive fields in area V3a, intermediate between that of primary visual cortex and area V5 (14), may not be the limiting factor on heading accuracy .

Parietal activations behaved similarly to the occipital activations except that no activation was found for upward headings. The implications of this result are unclear at this point. We shall only point out that in non-human primates, single unit recordings in parietal area 7a have shown the presence of cells responding to large field optic flows and possibly tuned to heading (20).

Two areas in which we did not find activations are worth mentioning. Firstly, in area V5 (MT/MST) no activity is evoked by a change in heading. This result seems to negate the existence of a heading map in this area. Also, no greater activity is evoked in area V5 by optic flow stimuli as compared to randomized motion fields (13). These data are probably in keeping with the non-selective nature of V5 activations relative to stimuli with high temporal frequency content (21).

Secondly, De Jong at al. (13) reported ventral occipito-temporal activations. The lack of activation in these areas in the present study may be attributed to differences in the nature of the simulated environment (a cloud in this experiment versus ground plane in de Jong's), or the nature of the

control stimulus (randomized motion fields versus optic flows). Regardless of the reason, the implication of this result remains the same; namely no heading map is likely to exist in the ventral division of visual extrastriate cortex.

Methods

Psychophysics

The stimuli were generated off-line on a Macintosh IIfx and were displayed on a Hitachi monitor (SM-19B) with a refresh rate of 67 frames/second. The optic flows subtended 45° of visual angle and contained 200 dots in positive contrast, each dot's image size being 6.7'. The dots' initial x-y screen coordinates and Z coordinate, that is the virtual distance from the observer, were assigned by sampling a pseudo random uniform distribution and were contained within a volume of a truncated cone whose smaller base was three focal lengths away from the observer and greater base seven focal lengths away. The screen position of half of the dots was updated every frame and once a dot reached a position outside the field of view a new dot was generated. Sixty-one possible heading directions were simulated (see fig. 1) and the speed of self-motion matched the one that would have resulted if a smooth force pulse had been applied to the observer in a frictionless environment. Following the presentation of each trial, which lasted 820 msec., the subjects were instructed to position a cursor in the direction corresponding to the perceived heading. Clicking on the mouse prompted the computer to acquire the position of the cursor and to initiate a new trial.

Three students belonging to the psychology graduate program and one faculty member from a different institution took part in the experiments. All four subjects had normal or corrected to normal vision and gave informed consent. During the experiments the subjects were comfortably seated and viewed the computer screen through a circular aperture obtained in the front panel of a viewing box. The subjects were instructed to maintain a firm hold of a bite bar to ensure a fixed position of the head. For each condition the subjects engaged in two sessions of data collection. In each session 488 trials were presented, each session lasting ~50'. had to position a cursor in the direction of the perceived heading. We quantified the reliability in the judgments by computing the variances in the cursor's position for each heading direction. Settings that differed by more than 3 standard deviations from the mean setting were discarded. This resulted in between 0.4% and 1.6% of the trials,

depending on the subject, not being included in the final analysis. Cumulative variances were obtained by averaging the individual variances in the estimation of a given heading weighted by the subject's cumulative variance. To quantify the magnitude of bias in the estimation of heading we calculated the squared constant error, that is the squared difference between the true heading and the mean settings' direction, averaged across subjects. The effect of heading was evaluated with a mixed linear model where the continuous variables were the squared azimuth and elevation of the simulated heading and the factor was the side (i.e. left vs right heading).

f-MRI experiments

The stimuli were presented on a screen with a projector (?) attached to a Macintosh 8500. The refresh rate was 60 frames/minute. The stimuli were similar to those used in the previous experiment, except that 50 dots were displayed in each frame, the dots' image size being 12' and the flow size being 12°. Five different heading directions were simulated, respectively toward the fixation point or 3° in each of the four cardinal directions. Each optic flow lasted 20 sec. Paired optic flows simulating straight ahead and one of the eccentric headings were presented consecutively six times

Six naive subjects were recruited from the academic community at the University of Minnesota. Before the experiment they were shown the stimuli and were instructed to keep their gaze on a fixation cross displayed at the center of the flow field. Then they were placed in the scanner and anatomical images were obtained prior to the actual experimental session. During the experiment the subjects were presented with four sequences, each sequence containing alternating optic flows simulating self motion straight ahead and in one of the eccentric headings. Each sequence lasted four minutes.

The data were acquired using T2* weighted multi slice echoplanar imaging. The experiments were done on a 1.5 T Siemens Vision Scanner (Siemens Medical Systems Inc.). During each block, 110 images were obtained in 11 interleaved oblique axial images. A TR of 2.1 sec. and an echo time of 51 msec. were used (FOV: 256x256 mm², matrix size: 128x128, voxel size: 2.0x2.0x7.0 mm³ with a 1.05 gap between slices). The anatomy images were obtained using a 3D-MPRAGE sequence giving a resolution of 1.0x1.0x2.0 mm³. They were acquired along the same orientation and with the same field of view as the functional images.

Activation maps were computed by correlating the f-MRI signal to a 'box-car' function that matched the temporal course of the experimental paradigm. A 4 sec. (2 images) shift was allotted for hemodynamic response in the correlational analysis. A correlation coefficient threshold of 0.26, corresponding to a p-value of 0.01, was used. Voxels that did not have at least an activated neighbor in the 8 adjoining voxels were not considered in further analysis. The individual activation maps were normalized to Talairach space.

To determine consistent activations across subjects and their mean Talairach coordinates we employed cluster analysis. The number of clusters was established for each condition by comparing the variance of the residuals for n versus n+1 clusters until no significant decrease ($p > 0.05$) in residuals variance was found.

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Figures

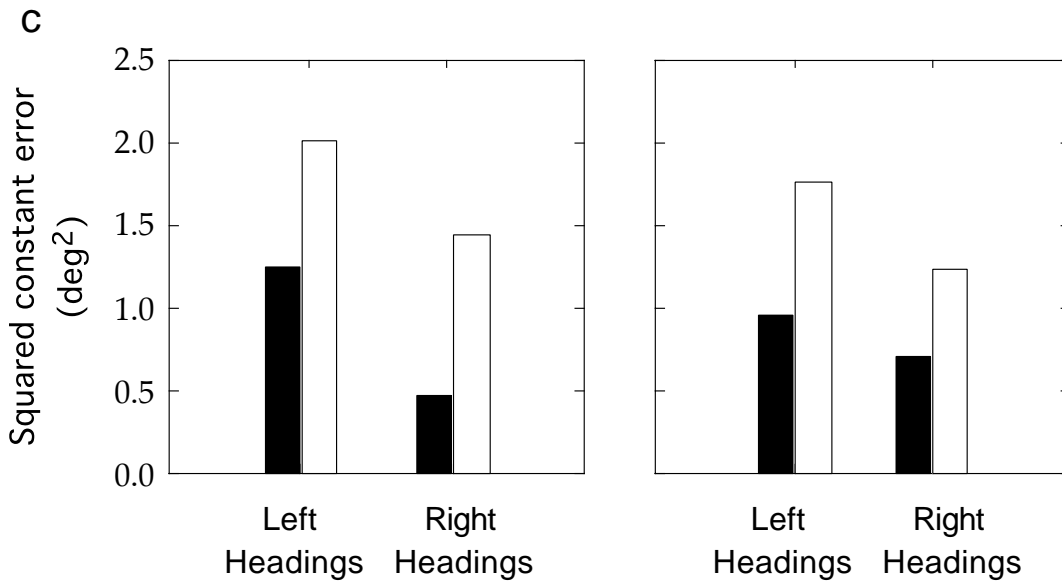
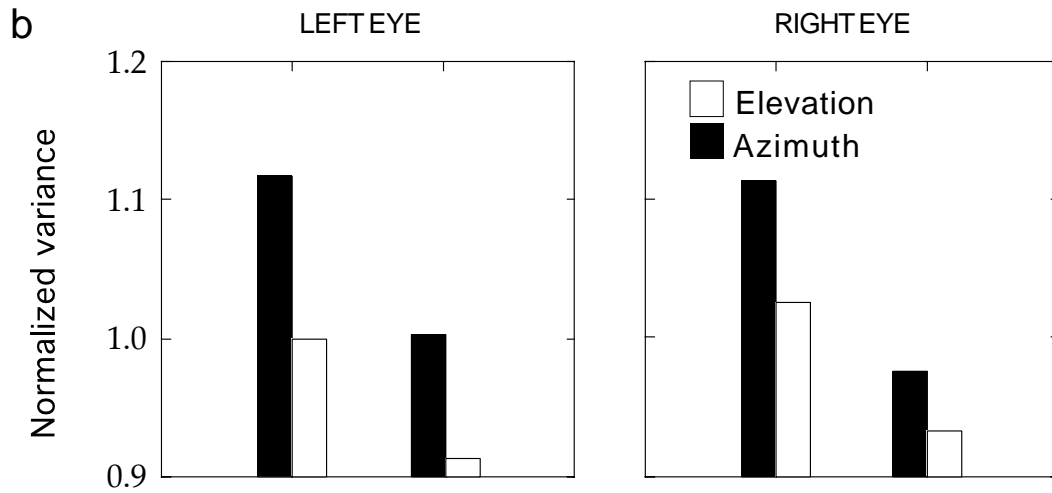
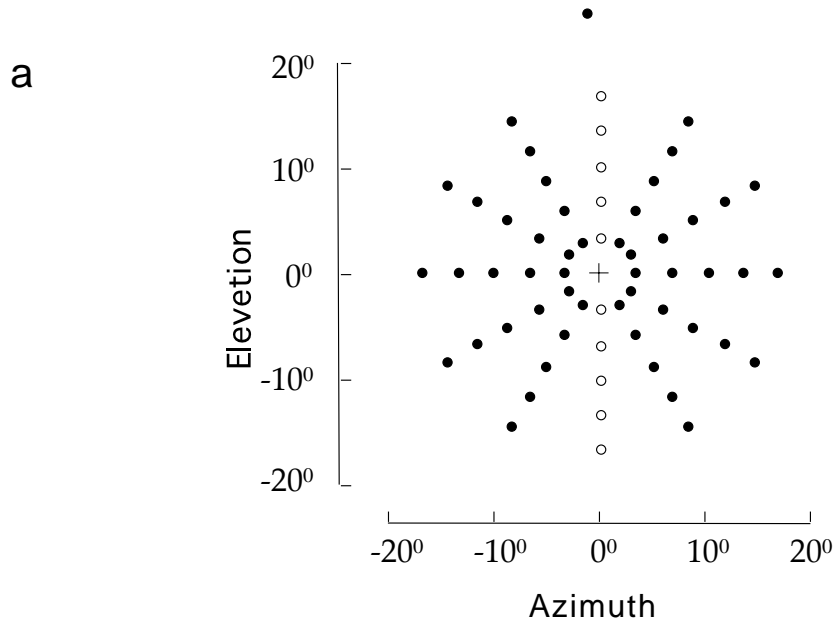
Fig. 1 In the psychophysical experiments, subjects viewed optic flows simulating heading in one of 61 possible directions. a) The set of simulated heading directions the cross shows the gaze direction. Only data for headings lying on either side of the vertical meridian are presented (filled dots). The headings were placed along meridians through the fixation point whose orientation differed by 30° at incremental steps of 3.5° in eccentricity. b) The variances in the estimation of azimuth and elevation for leftward and rightward headings are shown when subjects viewed the stimuli with their left and right eyes, respectively. The variance in the estimation of heading azimuth and elevation was significantly better for rightward headings than leftward headings either when the left eye or the right eye was used. c) The subjects also underestimated the true heading, the magnitude of this constant error being greater for leftward than rightward headings

Fig. 2. Each subject's activation maps were divided in four quadrants by the mid-sagittal plane and the frontal plane passing through the VCP line. This plane divides the brain in approximately two equal volumes and passes posteriorly to the central sulcus except at the superior medial edge where it crosses the motor strip in the area of the lower limb representation. The number of significantly activated voxels ($r > 0.26$, $p < 0.01$) was calculated for each quadrant and summed across subjects. The figure shows the number of voxels activated as a function of heading direction. Posterior quadrants show clear tuning for headings with greater activations for downward and contralateral headings. Little differential activation is present in the anterior quadrants.

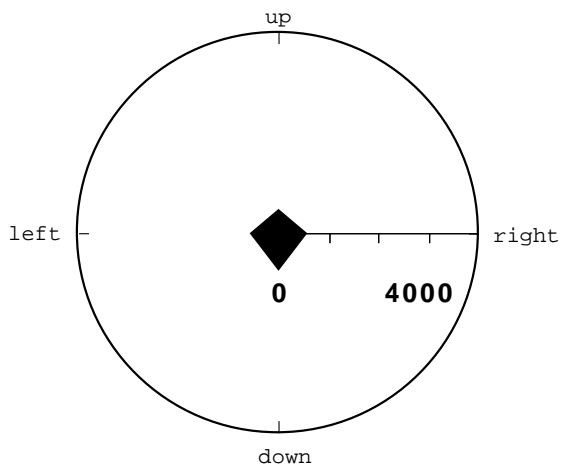
Fig. 3. Activations in one subject. The activation maps are superimposed upon the 3-D reconstruction of the subject's brain obtained from T-1 weighted anatomical images. Areas of activation are rendered in red. The cerebellum is left covering the ventral surface of the occipito-temporal lobes as no activation was observed in this area. The idealized optic flows representing the test and control stimuli used are displayed on the bottom. a) Activation evoked by leftward vs. straight-ahead heading; b) activation evoked by rightward vs. straight-ahead heading; c) activation evoked by leftward vs.

straight-ahead heading; d) activation evoked by leftward vs. straight-ahead heading. In this last condition only occipital activations are found.

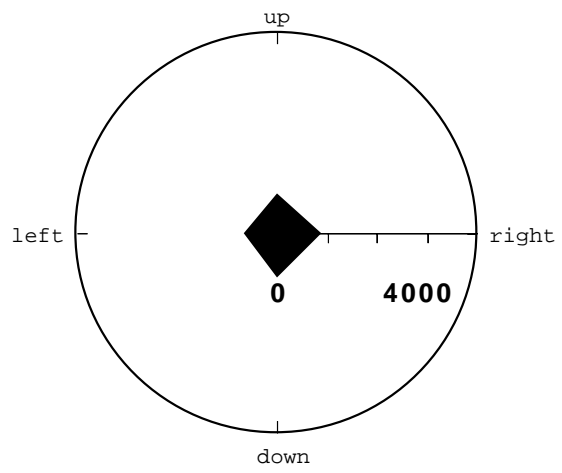
Table. The table reports the mean Talairach coordinates of the foci of activation. Only the coordinates of those clusters that encompassed activations at least three subjects are shown here. The anatomical structure and Brodman's area corresponding to the Talairach coordinates are provided and the standard deviations are reported in parentheses. The X and Z coordinates of the occipital activations were similar to those given for area V3a by Tootell et al. while the Y coordinate was 4 to 7 mm less than the one reported for the superior medial end of area V3a (i.e. 14,-84,19).



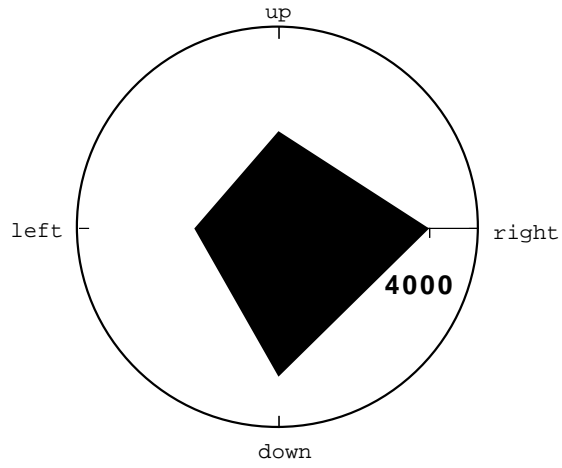
Left-Anterior Quadrant



Right-Anterior Quadrant



Left-Posterior Quadrant



Right-Posterior Quadrant

