

Rats maintain an overhead binocular field at the expense of constant fusion

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Fusing left and right eye images into a single view is dependent on precise ocular alignment, which relies on coordinated eye movements. During movements of the head this alignment is maintained by numerous reflexes. Although rodents share with other mammals the key components of eye movement control, the coordination of eye movements in freely moving rodents is unknown. Here we show that movements of the two eyes in freely moving rats differ fundamentally from the precisely controlled eye movements used by other mammals to maintain continuous binocular fusion. The observed eye movements serve to keep the visual fields of the two eyes continuously overlapping above the animal during free movement, but not continuously aligned. Overhead visual stimuli presented to rats freely exploring an open arena evoke an immediate shelter-seeking behaviour, but are ineffective when presented beside the arena. We suggest that continuously overlapping visual fields overhead would be of evolutionary benefit for predator detection by minimizing blind spots.

Rats are commonly used as a model for studies of the mammalian visual system^{1–4}. They have laterally facing eyes and a panoramic field of view extending in front, above and behind the animal's head¹. Eye movements in head-restrained rats are conjugate⁵, but studies of the vestibulo-ocular reflex in rats suggest that this only describes a fraction of their eye movements^{6,7}. Rats can visually estimate distance for gap jumping^{2,8} and perform object discrimination tasks⁴, but in their natural environment also have to avoid predation from both airborne⁹ and ground-dwelling predators¹⁰. This leads to conflicting demands on their visual system: on the one hand, maximum coverage of the environment for predator detection; on the other, detailed vision for object recognition and depth perception. Eye movements in freely moving rats have not been characterized so far, and in view of the conflicting pressures on their visual system it is unknown to what extent the trade-off between detailed vision and panoramic surveillance compromises their capacity for binocular fusion.

Eye movements in freely moving animals

To record eye movements in freely moving rats, we developed a miniaturized ocular-videography system that consisted of two light-weight head-mounted cameras (Supplementary Fig. 1). Pupil positions in the acquired images were tracked using custom-written algorithms. To allow analyses of the observed eye movements in the context of the rat's pose and location, we also tracked the position and orientation (pitch, roll and yaw) of the animal's head using a custom-built tracking system (see Supplementary Methods).

In freely moving animals, both eyes were highly mobile (Fig. 1a, b and Supplementary Video 1), with large horizontal and vertical excursions of the pupil (Fig. 1b). Both eyes moved continuously while the animal was exploring, but movements markedly reduced in amplitude when the animal stopped making large movements of its head. The dynamics of the movements were complex, regularly disconjugate and often asymmetrical. In addition to measuring horizontal and vertical pupil positions, we developed a method for tracking the irregular edge of the pupil in each frame which allowed measurement

of ocular torsion (rotation around the optical axis) and quantification of torsional rotations (Fig. 1c, see Supplementary Methods). Torsional rotations occurred frequently, and reached relatively large amplitudes (20–30°; Fig. 1d and Supplementary Video 2). The dynamics of torsional rotations were also complex, and both cyclovergence (rotation of both eyes in the same direction) and cyclovergence (rotation of the eyes in opposite directions) were observed (see *a* and *b* in Fig. 1d). On average there was a weak correlation between left and right eye torsion angles; however, the range of angles recorded for one eye for any given angle recorded for the other eye was very broad (Supplementary Fig. 2). In contrast to free movement, eyes movements in head-restrained rats were conjugate and infrequent, even when the animal was running on a spherical treadmill (Supplementary Fig. 3 and Supplementary Video 3).

Influence of head movements

Numerous sensory inputs and reflexes contribute to the regulation of eye position or gaze direction^{6,11,12}. Particularly obvious in the current study was the role of the vestibulo-ocular reflex⁶. As previously observed in restrained rats, roll of the head to the right resulted in elevation of the right pupil and declination of the left pupil and vice versa for roll to the left (Fig. 2a, b). For both freely moving and head-restrained animals, these eye positions were maintained for as long as the roll was maintained (Supplementary Fig. 4 and Supplementary Video 4). Pitching of the head nose-up or -down resulted in strong convergent and divergent eye movements, respectively (Fig. 2c, d), and these positions were maintained while the pitch angle was maintained (Supplementary Fig. 4 and Supplementary Video 4). In addition, pitching of the head also resulted in complementary torsional rotation of the left and right eyes (Fig. 2e, f). To assess the extent to which the vestibulo-ocular reflex controlled the observed eye positions, we built a simple predictive model (see Supplementary Methods) which predicted eye positions based on pitch and roll of the head. The model was able to predict a large proportion of the tracked eye movements for both vertical (78 ± 2% variance reduction, *n* = 3 animals) and horizontal axes (69 ± 3% variance reduction, *n* = 3 animals; Supplementary Fig. 5).

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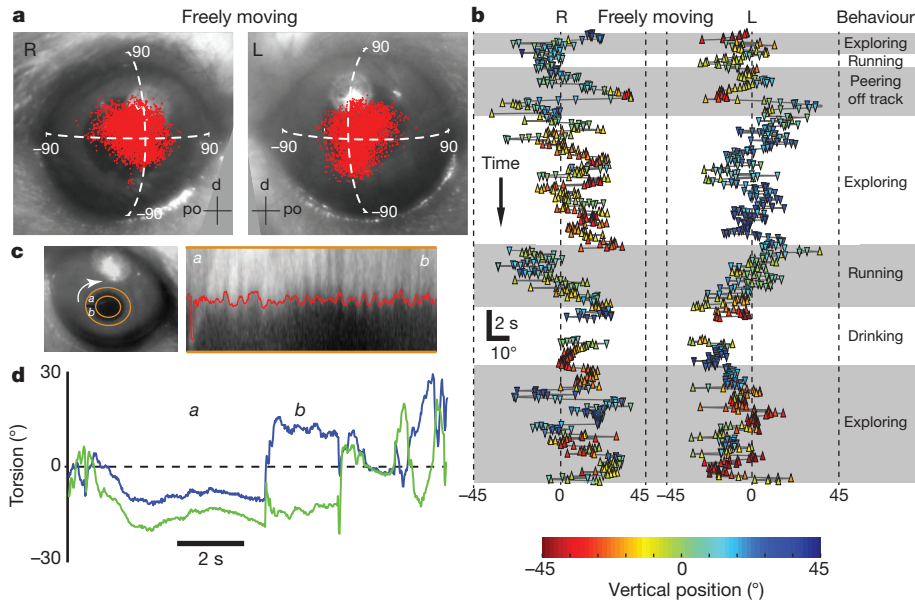


Figure 1 | Eye movements in freely exploring rats. **a**, Left and right eye images during free movement with individual pupil positions (red dots, approximately 5,000 data points) (dorsal (d) and posterior (po)). **b**, Vertical (marker colour) and horizontal (x axis position) kinetics (y axis) of eye movements during free movement (excerpt from **a**). Positive and negative vertical movements are denoted (up and down markers). Magnitude is

represented (marker colour). Behavioural periods are indicated. **c**, Eye image (upper) showing the pupil margin used for torsional tracking (outlined in orange) and the extracted section (lower image) from upper image including tracked pupil margin (red). **d**, Torsion of right (green) and left (blue) eyes during free movement. Note eyes can both rotate in the same direction (**a**), opposite directions (**b**) and combinations thereof.

From this, we conclude that a large proportion of the eye movements we observed in freely moving animals were driven by vestibulo-ocular reflex.

Consequences for matching retinal images

One obvious feature of the observed eye movements was that the pointing directions of the two eyes often differed substantially (Supplementary Video 1). This observation implies that both the fraction

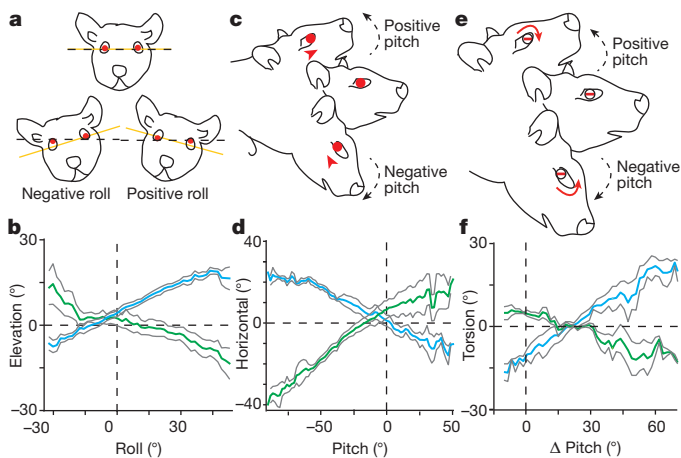


Figure 2 | Eye movements are dictated by head movement and position in freely moving animals. **a**, Schematic detailing how pupil elevation and depression (red pupils) can counteract head roll (yellow) compared with a horizon (black dashed). **b**, Comparison of pupil elevation for left (blue) and right (green) eyes in relation to head roll in a freely moving animal (average and s.e.m., $n = 4$ animals). **c**, Schematic detailing how eye movements in the horizontal plane (red arrowhead) occur during head pitch. **d**, Horizontal pupil position for left (blue) and right (green) eyes in relation to head pitch in a freely moving animal (average and s.e.m., $n = 4$ animals). **e**, Schematic detailing how ocular torsion (red arrows depict torsion direction) counteracts head pitch (black arrow) compared with horizon (red line). **f**, Ocular torsion for both left (blue) and right (green) eyes in relation to head pitch during free movement (average and s.e.m., $n = 4$ animals).

of left and right eye retinal images that are matching and the location on the retina of any matching regions may vary from moment to moment. To begin to quantify this, we first measured the difference in pupil positions (right pupil position minus left pupil position; Fig. 3a and see Supplementary Methods for details). If this measure was used for animals with conjugate eye movements (human, primate, cat, etc.), differences in pupil positions would be minimal, other than during convergence and divergence. In the freely moving rat, the horizontal pupil position differences were both negative (one or both eyes rotating temporally away from the nose) and positive (convergent eye positions). This was also the case for the vertical plane, where positive differences represented a vertical divergence with the right eye more dorsal than the left, and vice versa for negative differences. The range of pupil position differences was large in both planes, with an average standard deviation of almost 20° (Supplementary Fig. 6). Furthermore, the differences in pupil positions in both planes changed continuously as the animal was moving (Supplementary Video 5), with the horizontal difference being strongly related to head pitch (Supplementary Fig. 7). In contrast, in head-restrained animals the differences in pupil positions were minimal (Fig. 3a), with the standard deviation nearly one-quarter that for freely moving animals (Supplementary Fig. 6). We also confirmed that these differences in pointing direction (gaze vectors) occurred when measured in a 'world coordinate' system (Fig. 3b; see Supplementary Methods and Supplementary Fig. 8) and the difference changed continuously, with shifts of more than 20° occurring several times per second (Fig. 3c).

We next estimated the extent to which the observed eye movements may represent shifts in fixation onto different objects around the track as the animal performed a single cross of the gap. Because rats have no fovea or pronounced retinal specializations¹³, measuring the extent to which fixation was maintained required an alternative reference point for re-projection over time. We therefore identified a time point shortly before the gap crossing when the animal's head position was at median pitch and roll, and then defined a reference visual target on the jumping track in the animal's field of view (Fig. 4a). Projection lines from this reference target into the centres of the left and right eyeballs were used to define the point on the surface of the eyeball to

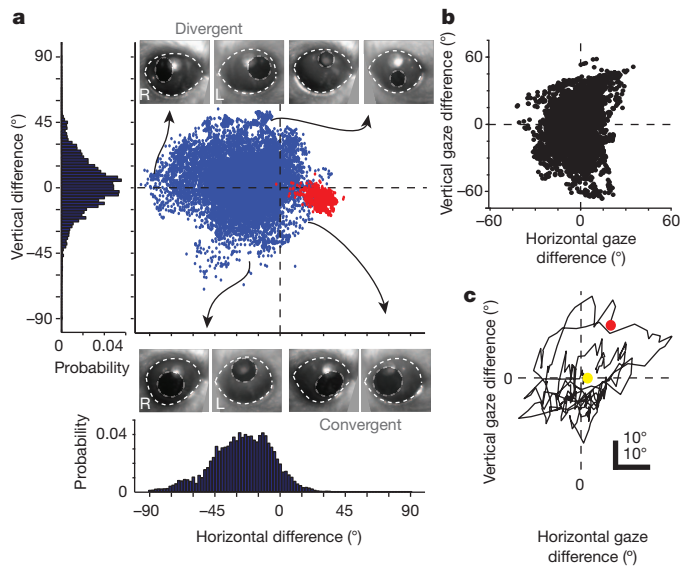


Figure 3 | Asymmetrical eye movements in freely moving rats. **a**, Distributions of the difference between left and right eye positions for a freely moving (blue) and head-restrained (red) rat. Each point represents the right eye position minus the left eye position for a single frame. Histograms are shown for *x* and *y* axes. Example image pairs (inset) from positions in the distribution (arrows). Conventions for eye images as in Fig. 1a. **b**, Scatter plot of the difference in left and right eye gaze vectors during free movement. **c**, Plot of the difference in left and right eye gaze vectors during free movement for a single continuous 1.7 s data segment including a gap cross.

be used for re-projection as the eye moved. To gauge the extent to which the observed ocular misalignment caused differences in potential visual targets of the two eyes, we rendered the environment around the rat, and followed the location where the re-projection lines contacted objects in the rendered environment (Fig. 4b, see Supplementary Methods). Over the 1.7 s required for the animal to perform the gap cross, most eye movements were disconjugate, resulting in a broad range of differences in both eye positions (Fig. 4c) and gaze vectors (Supplementary Fig. 9). The pupil projection points varied widely over the track (Fig. 4b), and there was very little coordination of the two points on single objects or locations (for rendered visualization see Supplementary Video 6). Note that the projections points

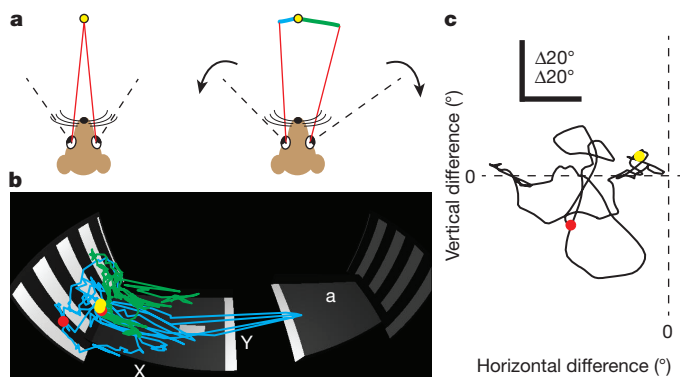


Figure 4 | Eye movements in freely moving animals are not consistent with those needed for binocular fusion. **a**, Schematic for defining lines of sight for re-projection. Left, reference visual target (yellow spot), optical axis (black), projections from visual target to eyeball centres (red). Right, relative changes of right (green) and left (blue) eye re-projections (red). **b**, Rendering of jumping arena showing monitors (far left and right stripes), initial animal position (a), initial gaze position (yellow dot for each eye) and subsequent gaze positions of the two eyes (left, green lines; right, blue lines; end gaze positions over 1.7 s ending with red dot). Same data as Fig. 3c. **c**, Difference between left and right eye positions for the data shown in **b** (conventions as Fig. 3a).

were precisely aligned on the reference visual target just before the jump. We next calculated the physical distance between the left and right eye projection points down the length and across the width of the track (Supplementary Fig. 9). In the animal’s viewable environment, the distances separating the two projection points ranged from 0 to approximately 70 cm on the jumping track. Although we were not able to predict exactly what part of the visual space the animal was attending to, the constant changes in ocular alignment in both eye axes were not consistent with the animal shifting its gaze onto different objects of interest. We conclude that the coordination of eye movements in rats is not specialized for maintaining a fixed relationship between the eyes.

Maintenance of binocular field

The large collection angle of the rat eye (approximately 200°) combined with the lateral position of the eye on the head result in rats having large monocular visual fields, that share a large overlapping area extending in front, above and behind the animal’s head¹ (Fig. 5a). To investigate the extent to which eye movements change the size, shape and location of the overlap of the monocular visual fields, we first generated a model of the animal’s monocular visual fields based on optical and physiological properties of the rat eye¹. The width of the overlapping fields at three different locations around the animal’s head (Fig. 5b) varied strongly with the pitch of the animal’s head (Fig. 5c, d and Supplementary Fig. 10). The width of the binocular field directly in front of the animal’s nose, which is generally considered the animal’s binocular viewing area¹⁴, ranged from approximately 40° to 110° depending on head pitch. Changes in the extent of the visual field overlap measured at the inferior and posterior locations had strong but complementary dependence on head pitch

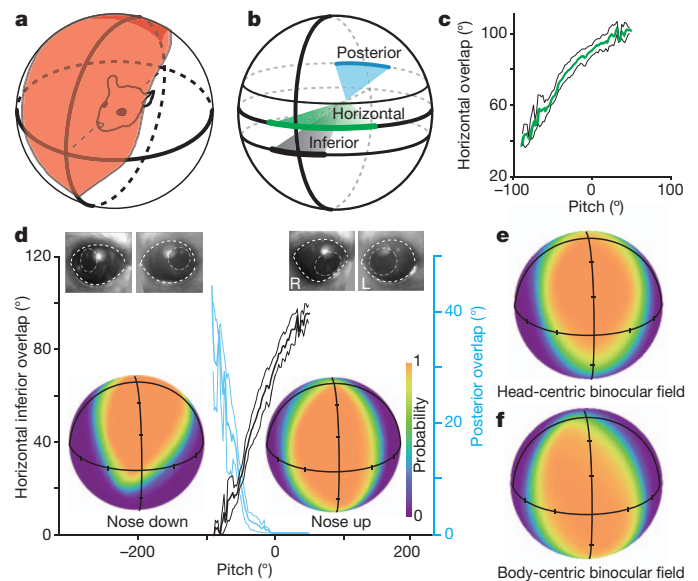


Figure 5 | Overhead binocular overlap. **a**, Schematic outlining binocular overlap (red, modified from ref. 1). **b**, Schematic for data in **c** and **d**. **c**, Average (green) dependence of horizontal overlap on head pitch (s.e.m., thin black lines, *n* = 4 animals). **d**, Dependence of horizontal inferior (black) and posterior (blue) overlap on head pitch (s.e.m., thin black lines, *n* = 4 animals). Head-centric density plots (insets) showing probability of visual field overlap (pseudo-colour) when animal is pitched down (≤ 10 th centile of head pitch angles, insert left) or pitched up (≥ 90 th centile, insert right, 30° ticks on vertical and horizontal axes). Note that average head roll was $18 \pm 1^\circ$ during nose-down pitch. Images (upper insets) show example eye positions for negative and positive head pitch (same as in Fig. 3a). **e**, Head-centric density plot of average overlap of monocular visual fields during free movement for all head positions (conventions as in **d**, *n* = 4 animals). **f**, Body-centric density plot of the overlapping fields that includes head and eye movements (conventions as in **d**, **e**, *n* = 4 animals). See Supplementary Fig. 11 for body-centric definition.

(Fig. 5d), consistent with the location of the binocular field remaining above the animal as the animal pitched its head. In all animals, the eye movements constantly kept the average overlap of the monocular visual fields above the animal's head (Fig. 5e). The effect of pitch on the location of this region was most clear when it was calculated for the top and bottom 10% of head pitch positions (average $-42.4 \pm 0.1^\circ$ for pitch down and $30.2 \pm 0.2^\circ$ pitch up; Fig. 5d, inserts). To characterize this further, we next calculated the position of the average binocular visual field relative to the animal's body (see Supplementary Fig. 11 for schematic). This 'bird's eye view' of the average overlap shows its location after accounting for the changing location of the visual fields caused by pitch and roll of the animal's head (Fig. 5f). In this reference system, the visual field overlap is predominantly located in front of and above the animal (Fig. 5f), despite an average nose-down head pitch of 25° (range 80° down to 40° up; Supplementary Fig. 11).

Together these results indicate that one of the key consequences of the eye movements observed in freely moving rats is that the region of overlap of the left and right visual fields is kept continuously above the animal, consistent with the suggestion that a major function of the rat visual system is to provide the animal with comprehensive overhead surveillance for predator detection¹⁴.

Behavioural response to overhead stimuli

We next tested whether visual stimuli presented above the animal were capable of eliciting behavioural responses. Naive rats were placed in an open-field arena surrounded on three sides and above by stimulus monitors (Fig. 6a). The only object inside the open field was a shelter under which the animal could hide. Stimuli presented on the monitors beside the arena failed to elicit any detectable changes in the animals' behaviour (Fig. 6b). In stark contrast, black moving stimuli presented overhead (Fig. 6c) elicited an immediate shelter-seeking behaviour from all animals tested (Fig. 6d and Supplementary Video 7). The

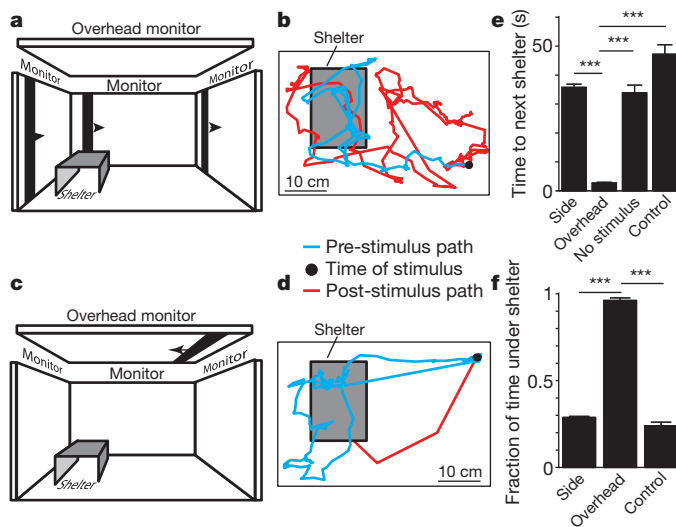


Figure 6 | Shapes moving overhead selectively evoke shelter-seeking behaviour. **a**, Schematic of side stimulus presentation. **b**, Animal's trajectory before (blue) and after (red) the onset (black circle) of a black moving bar stimulus presented on one of the side monitors. **c**, Schematic showing stimulus presentation above the rat. **d**, Trajectory before and after the onset of an overhead stimulus. Plot conventions as in **b**. **e**, Average time (bars, s.e.m.) before the rat's next visit underneath the shelter after stimulus presentation on monitors located beside the arena (Side), above the animal (Overhead), without stimulus presentation (No stimulus) or after a randomly chosen time in the data set (Control). **f**, Fraction of time spent underneath the shelter after stimuli presented on monitors beside the arena or overhead and for the same control condition described for **e**. Statistically significant group differences ($P < 0.01$) in **e** and **f** are denoted (stars, $n = 3$ animals).

rats ran immediately and directly to the shelter (Fig. 6e, 20 trials from three rats for side stimuli, 12 trials from three rats for overhead stimuli), and once there remained under the shelter for significantly extended periods (Fig. 6f, data sets as for Fig. 6e). As these behavioural responses may not necessarily require binocular viewing of the stimulus, one possibility is that the seemingly disconjugate eye movements, by continuously maintaining overlap of the monocular visual fields, help provide comprehensive surveillance of the region overhead by minimizing or eliminating 'blind spots'. However, it has also been shown for freely moving rats that certain aspects of their visual function, such as visual acuity, are enhanced in the binocular field compared with the monocular field¹²; thus it is also possible that these eye movements provide a direct enhancement of their vision by maintaining binocularity overhead. In summary, we conclude that although the observed eye movements preclude the possibility that rats continuously maintain binocular fusion while moving, they provide a benefit to the animal by facilitating comprehensive overhead surveillance as a defence against predation.

Discussion

In primates, eye movements are precisely coordinated to maintain fixation of visual targets¹⁵. Precise ocular alignment is critical for binocular fusion. For foveal vision in humans misalignment of more than $1/3-1^\circ$ results in double vision¹⁶. For peripheral vision, fusion is more tolerant to ocular misalignment; however, even there misalignment of more than a few degrees results in diplopia¹⁷, and pupils moving in opposite vertical directions is associated with serious pathology¹⁸. In freely moving rats the difference in the gaze directions of the left and right eyes, which is a measure of the alignment of the eyes on a single target, has a range of more than 40° horizontally and more than 60° vertically. This range excludes the possibility that primate-like binocular fusion is continuously maintained when the animal is moving. Instead, eye movements in the rat are specialized for continuously maintaining overlap of the monocular visual fields above the animal as the head moves. It is clear from the low acuity¹⁹, lack of fovea¹³ and lack of significant capacity for accommodation²⁰ that rat vision is specialized along different lines to that of foveate mammals, and rats' strategy for eye movement control seems to be different as well. For the ground-dwelling rodent, foraging is actively pursued at dusk, and local changes in the environment are detected using mystacial vibrissae²¹ and olfaction²², both of which are associated with rapid head movements in all planes²³. For rats, birds of prey such as owls⁹ are a major predator, and as vision is the only sense that allows predator detection at a distance, the wide panoramic field of view^{1,20}, large depth of field²⁴ and maintenance of comprehensive overhead surveillance based on a system that counteracts the rapid head movements may be of substantial evolutionary advantage.

The eye movements observed here do not imply that rats are completely incapable of binocular fusion, stereoscopic depth perception or detailed vision. Rats can use their vision for depth perception^{2,8} and are capable of quite sophisticated visual object recognition⁴. The variable alignment of the gaze directions of the eyes during head movements do imply, however, that for rats to fuse the two monocular images or to have stereoscopic depth perception they must either use a behavioural strategy to align the two monocular images (orient their head in a position that allows or facilitates fusion) or have another mechanism that allows them to identify matching components in the two retinal images. Some non-predatory bird species combine both panoramic vision (predator detection) with stereoscopic vision of close-by objects (bill vision) by using multiple retinal specializations²⁵, and other birds have behavioural strategies involving a combination of head movements for switching between distinct modes of viewing²⁶. Rats may use similar strategies, in which the animal assumes a particular posture bringing both eye images into registration when detailed vision is required. An alternative proposal is that they can fuse left and right images without precise retinal

registration by using something like a corollary signal (for review, see ref. 27) to track the eye movements and identify matching retinal locations. This would be somewhat analogous to the mechanism suggested to explain shifting receptive field locations in monkey frontal cortex²⁷. However, such a mechanism would require an immense degree of connectivity in the visual areas, and so far there is no evidence for this.

In summary, eye movements in freely moving rats are asymmetrical and inconsistent with the animal maintaining continuous fixation of a visual target with both eyes while moving. Instead, the movements keep the animal's binocular visual field above it continuously while it is moving, consistent with a primary focus of the animal's visual system being efficient detection of predators coming from above.

METHODS SUMMARY

The miniaturized camera system was secured onto a custom-built headplate which was implanted on the head. The position of the pupil was tracked in each image frame, and the effects of movement of the cameras eliminated by simultaneously tracking anatomical features of the eye (Supplementary Fig. 12 and Supplementary Video 8). The accuracy of the pupil-detection algorithm was measured to be less than 1°, and errors associated with tracking the anatomical features estimated to be very much less than 3° (Supplementary Fig. 13). Head position and orientation were tracked by following the relative position of six infrared light-emitting diodes mounted with the camera system. Tracking accuracy was less than 1° for all three axes of head orientation (Supplementary Fig. 14). For full details of all error quantifications, methods and analyses, see Supplementary Methods.

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Supplementary Information is available in the online version of the paper.

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