Eye–Head Coordination during Free Exploration in Human and Cat

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Eye, head, and body movements jointly control the direction of gaze and the stability of retinal images in most mammalian species. The contribution of the individual movement components, however, will largely depend on the ecological niche the animal occupies and the layout of the animal's retina, in particular its photoreceptor density distribution. Here the relative contribution of eye-in-head and head-in-world movements in cats is measured, and the results are compared to recent human data. For the cat, a lightweight custom-made head-mounted video setup was used (CatCam). Human data were acquired with the novel EyeSeeCam device, which measures eye position to control a gaze-contingent camera in real time. For both species, analysis was based on simultaneous recordings of eye and head movements during free exploration of a natural environment. Despite the substantial differences in ecological niche, photoreceptor density, and saccade frequency, eye-movement characteristics in both species are remarkably similar. Coordinated eye and head movements dominate the dynamics of the retinal input. Interestingly, compensatory (gaze-stabilizing) movements play a more dominant role in humans than they do in cats. This finding was interpreted to be a consequence of substantially different timescales for head movements, with cats' head movements showing about a 5-fold faster dynamics than humans. For both species, models and laboratory experiments therefore need to account for this rich input dynamic to obtain validity for ecologically realistic settings.

Key words: **eye movements; cat; human; oculomotor; natural stimuli; free behavior; head movements**

Introduction

Most mammalian species use a combination of eye-in-head and head-in-world movements to orient gaze to regions of interest and to stabilize their retinal image. A variety of constraints on body shape, visual system architecture, oculomotor range, and eye location may influence the degree to which these different systems are recruited for a particular gaze-orienting behavior. Here we compare eye and head movement statistics of cats and humans during free exploration of natural environments.

Cats and humans share the characteristic of front-facing eyes, and for that reason cats have been serving as models for human vision for a long time.[1–3] A variety of differences, however, are striking: While humans can move their eyes over an oculomotor range of 100°,[4] the cat's range covers only about 50°.[5] The region of highest acuity spans approximately 1° of visual angle in humans (fovea) and approximately 5° in cats (area centralis).[6,7] Whereas

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Basic and Clinical Aspects of Vertigo and Dizziness: Ann. N.Y. Acad. Sci. 1164: 353–366 (2009).
doi: 10.1111/j.1749-6632.2008.03709.x

humans' highest visual acuity is at roughly 50–60 cycles/degree,[7,8] cats' acuity is about ten times worse.[9,10] In addition, cats have only dichromatic vision, but higher critical flicker fusion frequencies[3] and—as nocturnal animals—about a 6-fold lower absolute luminance threshold.[11] Provided that eye movements optimize visual processing, these differences render a dramatically different eye-movement pattern between humans and cats likely, and a comparison of both under natural conditions may shed light on the underlying criteria for optimality.

Besides fixational eye movements (microsaccades, tremor, and drift), two classes of larger eye movements are typically distinguished: volitional saccades and smooth movements. Major examples for the latter are smooth pursuit, the optokinetic nystagmus (OKN), and the vestibular–ocular reflex (VOR). In contrast to volitional saccades, these movements stabilize the retinal image, either of a small moving target (smooth pursuit) or of the whole scene (OKN) or during head movements (VOR). The interplay between gaze-shifting (through eye-in-head and head-in-world movements) and stabilizing movements is thus of central interest for understanding the dynamics of visual input during natural vision.

The VOR is of particular importance for eye–head coordination under free-behavior conditions. The VOR is directly controlled by the vestibular system and provides retinal stabilization of the visual world by a counterrotatory eye movement of equal amplitude to the head movement. It has been suggested that the VOR is (partially) absent during volitional gaze shifts.[12–14] Hence, only a small proportion of large gaze shifts are influenced by vestibular-driven compensatory eye movements. Instead, the VOR is only active when the gaze reaches the target and the head is completing its movement. In this view, the partial attenuation of the VOR during volitional shifts solves the dilemma between gaze stabilization and gaze shift.

Several studies have examined eye movements under head-free conditions in the laboratory for a variety of species. Collewijn[15] recorded eye movements in unrestrained rabbits, and found no evidence for isolated eye movements in the absence of head movements. Hence, in the rabbit, eye movements may have a purely gaze-stabilizing function. Similarly, under laboratory conditions cats rarely exhibit eye movements in the absence of head movements.[5] For large eccentricities (>20°, according to Freedman and Sparks[16]), monkeys use combined eye and head movements. Typically, those start with an eye movement, followed by a head shift, whose overshoot beyond the target is compensated for by a reflexive eye movement.[17] Humans also use a similar strategy to adjust gaze,[4,18] although the threshold up to which eye movements are exclusively used exhibits high interobserver variability,[12,19] and drifting head movements can compensate for lacking eye movements in clinical cases.[20] While all of these studies stress the importance of head movements, it remains to be assessed whether or not the results hold for free exploration in different species. In particular, body-in-world movements contribute to head-in-world movements, and might differ between free exploration and laboratory settings. Hence, the effect of head-in-world movements on eye-in-head movements needs to be considered for natural conditions.

Recent advances in eye-tracking technology have spurred a variety of studies with unrestrained humans. Typically such studies focused on a well-controlled but specific task, such as making tea, preparing food,[21,22] washing hands,[23] throwing and catching a ball,[24] playing cricket,[25] and so forth. Here we take a complementary approach and ask a human observer to freely explore her environment, while gaze- and head-centered videos are simultaneously recorded with a wearable setup (EyeSeeCam). These data are compared to eye and head movements of a freely behaving cat in a similar outdoor environment, which we record with a wearable light-weight custom-made setup. The human data consist of a subset of those recorded for a previous study,[26] which here is analyzed for eye–head coordination rather than for static features. Unlike a previous study on eye–head coordination,[27] which used a different data set, and an earlier stage of setup development, we here focus on the comparison between the two species, cat and human. To our knowledge, this is the first study to directly compare cat and human gaze data under free exploration conditions.

Methods

Data Acquisition in the Freely Behaving Cat

We developed a system to simultaneously record eye-in-head and head-in-world movements during free exploration outdoors. The data presented here are based on a total of six recording sessions in three adult cats. For safety reasons, animals were accompanied by the investigator and secured with a leash, but care was taken to minimize any restraints on their behavior. Indeed, the cats appeared relaxed and tolerated the experimental apparatus well. All procedures were compliant with university and governmental regulatory guidelines for experimental animal care and were approved by the responsible authority (Kantonales Veterinäramt Zurich).

The setup was based on the CatCam setup[28] and extended it to simultaneously perform eye-movement recordings. The setup consisted of two identical charge-coupled device (CCD) cameras (DFM 5303, The Imaging Source, Germany) of dimensions 1.8 cm × 4.2 cm × 4.2 cm (depth, height, width), weighing 35 g each. One camera ("feline HeadCam") pointed parallel to the cat's line of sight and captured a large part of the cat's frontal visual field (80°, as compared to about 135° horizontally in the cat[29]). The other camera ("feline EyeCam") recorded one of the animal's eyes through a small magnifying mirror (Fig. 1A). The cameras were mounted to the head via a cranial implant, which had been surgically prepared for the purposes of a separate experiment. The whole setup weighed 89 g (including cameras, mirror, and mount). To minimize the setup's influence on head movements, priority in design was given to low weight, even if this required sacrificing some spatial and temporal resolution at the time the experiments were conducted.

The CCD cameras were each equipped with a Sony ICX059CK image sensor of 752 (horizontal) × 582 (vertical) pixels resolution. The image sensors perform a global gain control, which allows them to capture a wide dynamic range of intensity without affecting relative luminance (contrast) measurements. This is favorable for outside recordings, for which light intensities may vary over several orders of magnitude. Each camera was wired to a standard VHS video recorder [phase alternating line (PAL)], carried by the investigator. Videos were digitized off-line at a rate of 25 frames/s, a spatial resolution of 360 × 270 pixels, and a color depth of 16 bits (Fig. 1C and 1D). For analysis, the images were converted to 8-bit gray scale, using Matlab's rgb2gray function with default mapping.

Precise temporal alignment between the cameras was achieved by a custom-made electronic synchronization device. The device counted the frames in the HeadCam, and triggered the inversion of the color look-up table (CLUT), whenever the frame count was divisible by 250 (i.e., every 10 s). The thus color-inverted frames were detected in the video streams, were reinverted—without loss of information—and ensured temporal alignment of both videos with a temporal error guaranteed to be smaller than half a frame's duration (20 ms).

Data Acquisition in Freely Behaving Humans

For data acquisition in humans, we used the EyeSeeCam setup (Fig. 1E), whose technical details and development are described in detail elsewhere.[30–33] In brief, eye position is tracked with a head-mounted infrared eye-tracking

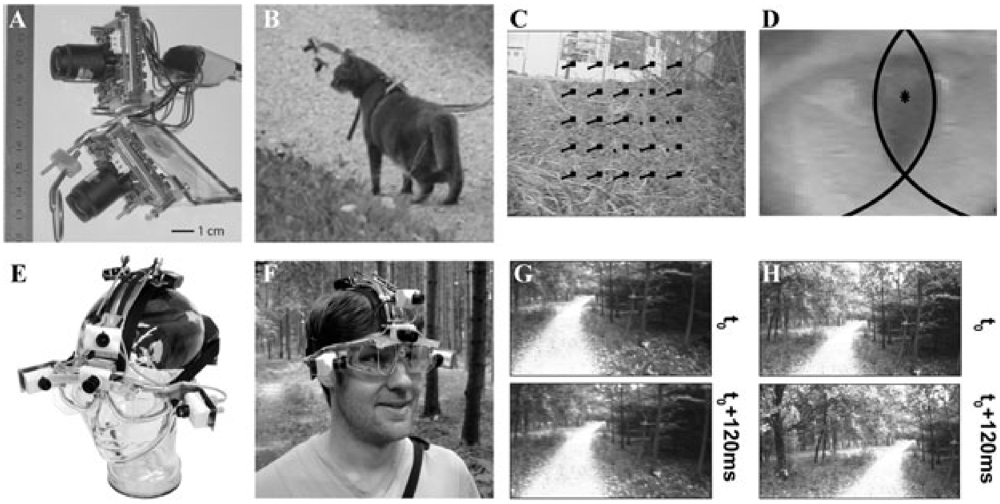

Figure 1. Setups. (**A**) CatCam setup, consisting of the "feline HeadCam" (*top*) pointing in parallel to the animal's line of sight and the feline EyeCam (*bottom*) pointing toward the animal's eye by a magnifying mirror, while only minimally obstructing the field of view. (**B**) Experimental cat during recording. (**C**) Frame of feline HeadCam with local flow vectors superimposed (*arrows*). (**D**) Frame of feline EyeCam with pupil fit (*black circles*) and computed eye position (*black star*) superimposed. (**E**) "EyeSeeCam" setup, consisting of the eye-tracking cameras (*left* and *right*), the "human HeadCam" (*center*), and the human GazeCam (*top*) that is directed in parallel to the observer's line of sight in real real-time. (**F**) Observer during recording session in the forest. (**G**) Two frames of the human HeadCam, spaced 120 ms (3 frames) apart. (**H**) Two frames of the human GazeCam, recorded simultaneously with the frames in part G. Note the large saccade between the two frames.

device, which controls a gaze-contingent camera in near real-time (human GazeCam). Simultaneously, head-centered videos are obtained by a camera fixed with respect to the head (human HeadCam). Recording was performed fully digitally using the IEEE1394 ("FireWire") standard and Bayer encoding to efficiently transmit and store the data. Resolution of the videos was 752 × 432 pixels, sampled at 25 Hz. To approximate the environment of the cat recordings, a park and forest surrounding the cat's animal facility (Fig. 1C), the human videos used here are a subset (environment "forest") of the data presented earlier in the context of static feature distributions.[26]

Computing Feline and Human Head-in-World and Human Eye-in-Head Movements

We computed head-in-world movements of both species as well as eye-in-head movements of humans based on the optic flow between subsequent video frames. Due to the difference in resolution (owed to technical constraints, such as minimizing setup weight), we applied slightly different techniques to compute optical flow. In the feline HeadCam we selected 25 equally spaced image patches of 25 × 25 pixels resolution, spaced 40 pixels apart in the center of each frame. For each of these patches the cross-correlation between two subsequent frames defines the local flow, as visualized by the black arrows in Figure 1C. A local field vector was discarded as invalid if its length exceeded 100 pixels, since such cases usually corresponded to an incorrect match between the two frames. When fewer than 8 of 25 of the local flow-field vectors were valid the frame was discarded, otherwise the global flow was defined by computing the bilinear transform (8-dof) that minimizes the mean squared error of the transformed grid-points with respect to the transform given by each valid local flow vector. Of this bilinear transform, we only considered the translational components further.

This procedure minimizes biases towards areas, in which more valid vectors exist, and avoids mistaking expanding flow for translations, when only part of the image contributes valid data. For analysis of both human cameras we computed local flow at the center of the image by cross-correlating the central 128 × 128 patches of 2 subsequent frames (see Ref. 27 for details).

Computing Feline Eye-in-Head Movements

Unlike for the EyeSeeCam, the CatCam equipment does not actively control a gaze-centered camera. Hence, feline eye-in-head movements were computed off-line from the EyeCam videos. The pupil in each frame was modeled as the black region ($<70\%$ of the mean frame luminance) at the intersection of two circles. The circles were of equal radius and centered on the same horizontal line (Fig. 1D). The radius, the position of one circle center, and its distance to the second circle center were fitted. Eye position was defined as the center of the intersection. When fit quality was beneath a certain threshold, the frame was deemed invalid and discarded. Most invalid frames resulted from blinking and occasionally from grass obstructing the camera's view of the eye. Since the slit-shaped pupil makes precise measurements of vertical eye position difficult, we focused all analysis on horizontal movements.

Calibration

Since cats are not easily trained to fixate targets and our present study is concerned with eye movements rather than absolute position measurements, we focused the calibration procedure on relative positions in the cat. We moved a highly salient target (a laser pointer or bells) over a fixed horizontal range (35 cm) at a fixed distance (70 cm) from the cat's eyes. From these data we estimated 1 image pixel to map to 2° of angular deviation of the eye in the orbit. With the observed oculomotor range of 25 pixels being consistent with laboratory measurements (50°), we have confidence in this mapping, despite the clear limitations of such outdoor calibration. The *absolute* scale of eye movements in cats based on this calibration therefore has to be taken with care, whereas the analysis of the *direction* of eye movements is unaffected by any calibration errors, and will be at the focus of the analysis. The EyeSeeCam has a built-in calibration function that computes the mapping from camera control to eye position based on 25 fixations on a predefined laser grid, projected by the device on a wall. The average precision of the motors moving the HeadCam is 0.09° RMS. The precision of the whole device, including eye-position measurement and slippage of the HeadCam is—measured in a stationary laboratory setup—0.5° RMS.[34]

Results

Behavior

All three cats behaved similarly through the course of each experimental session. They showed no sign of irritation by the cameras or the accompanying investigator. At the beginning of each session the animals displayed accommodation behavior, staying close to the building from which they were released. After familiarization with the environment, the cats moved along paths, through fields and woodlands. Frequently, the cats lay down, stalked, and prowled.

The human observer, accustomed to wearing the setup, did not report any disturbance by the setup or any effect on the freedom to move their head; contact with other people in the forest environment was infrequent and did not affect behavior. The human observer was instructed to behave "naturally" while walking through the forest. Leaving the different vantage point and gait aside, human behavior and environment and path selection (on a path, through forest off path, etc.) was as closely matched to the animal as possible.

Data Quality

The cat recordings consisted of six separate outdoor sessions. Due to the analog recording setup, susceptibility of the equipment to glare, nonnegligible line-of-sight differences between HeadCam and eye for close objects, mirror misalignments as a consequence of obstacle contact, view obstruction by high grass, parts of the data had to be excluded for technical reasons prior to analysis. Rare events of pursuit eye movement in the presence of a bird (6 in total over the recording sessions) were also excluded (as the real target path is unknown), as the flow-field algorithm considers global motion only. These short episodes, however, would not substantially alter the overall statistics. After applying these exclusion criteria, the analysis was based on 70,897 video frames, corresponding to 47 minutes of data. After applying the strict criteria for flow-field and eye-movement detection quality, an additional 30,688 valid frame pairs remained. All cat data analysis refers to these frames, corresponding to effectively 20 minutes of video. In humans, we selected 40 minutes (60,641 frames) of gaze and head movement recordings in a forest, which most closely resembles the cat's environment. These data were a subset of that presented in Ref. 26, but here analysis focused on eye–head coordination, rather than on spatial stimulus properties.

Velocity Distributions

The analysis focuses on horizontal eye, head, and gaze velocities. Head velocities were measured directly in both species by optic flow analysis. For cats, the mean speed of the head is 52°/s (9 pixels/frame), which is considerably larger than the 32°/s of the human observer. By thresholding the velocity at the resolution of the human analysis (0.5 pixel/frame = 6°/s), we find no measurable movement for 29.2% of the data, whereas head movements in cats stay below the 6°/s threshold for 36.3% of data (Fig. 2A). From this distribution of velocities we conclude that, for our experimental setting, cats make fewer but faster head movements than the human observer.

Eye movements were measured directly in the cat, with the threshold for no measurable movement at 25°/s (0.5 pixel/frame). Using this threshold, in 53.8% of the cat data, no measurable movement was observed (Fig. 2B). Applying the same analysis to human eye movements, as computed by subtracting head from gaze movements, we find 63.1% of valid data at 24°/s or below, with the 24°/s bin accounting for 14.6 percentage points. This is, the fraction of eye movements falling below the measurement threshold for cats is in the same range as for the human observer. Also, for very fast movements beyond 120°/s we find humans (10.0%) and cats (11.2%) to be similar. Although precise quantitative analysis is hampered by technical constraints, we have no indication of a systematic difference between human and feline horizontal eye velocity distribution.

In summary, cats make fewer but faster head-in-world movements than humans, but the species exhibits no obvious difference with respect to eye-in-head velocities.

Simultaneous Movements of Eye and Head

To what extent are eye movements determined by co-occurring head movements? Using the same thresholds as before (6°/s for head, 25°/s for eye movements), the assumption of independence would predict that the cats move their eyes in the absence of head movements in $(100\% - 53.8\%) \times 36.3\% = 16.8\%$ of the valid data. In the actual data, however, such isolated eye movements occur about half less frequently (8.9% of data) than predicted by independence. Similarly, for humans independence would predict $(100\% - 63.1\%) \times 29.2\% = 10.7\%$, while the actual data show isolated eye movements only in 4.5% of the data, again less than half the independence prediction. In turn, simultaneous movements are more

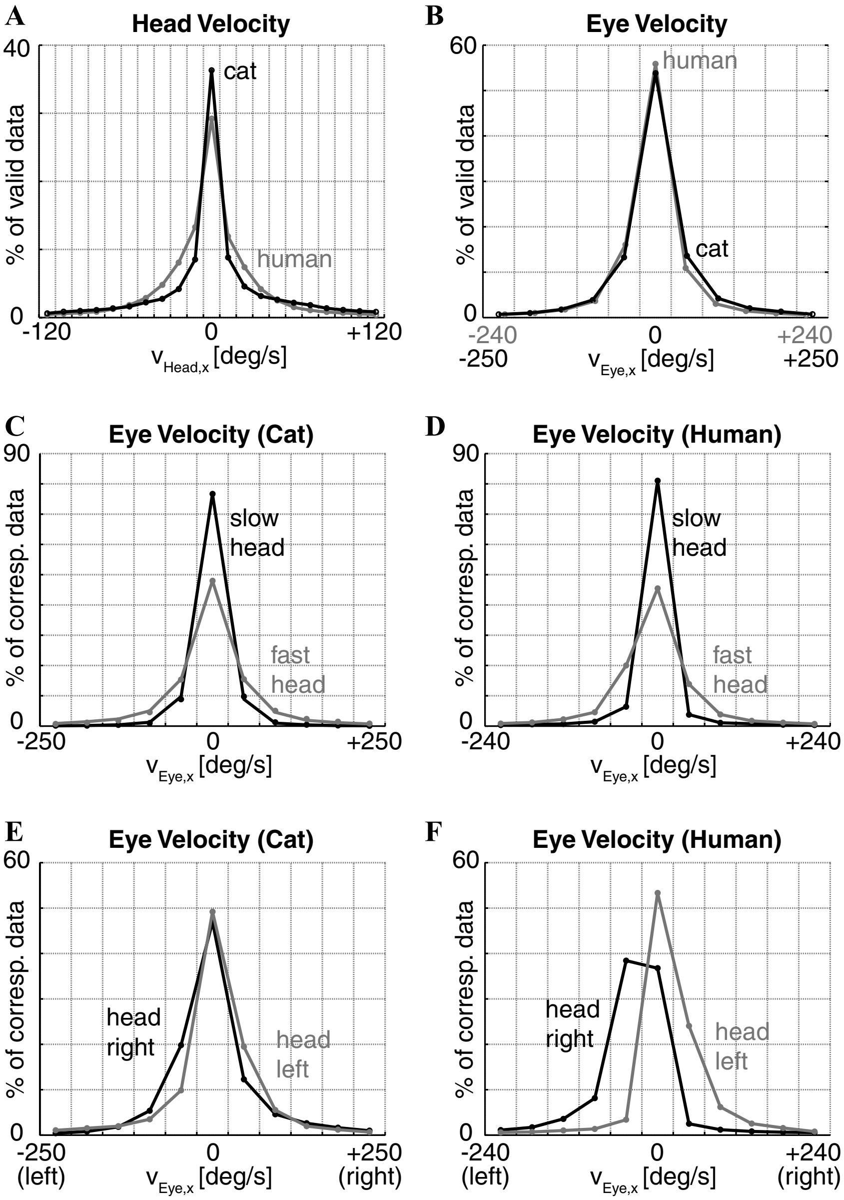

Figure 2. Velocity distributions. (**A**) Velocity distribution for head movements in cat (black) and human (gray); binning 12°/s (1 pixel/frame in humans), central bin [−6°/s, +6°/s]. Due to analysis of 25 local flow vectors, cat data are nearly continuous on the scale of human data. (**B**) Velocity distribution for eye movements in cat and human. Binning for cat 50°/s (1 pixel/frame), central bin [−25°/s, +25°/s]; binning for human 48°/s (4 pixels/frame), central bin [−24°/s, +24°/s]. (**C**) Distribution of cat eye velocities during fast (>6°/s, gray) and slow or no (<6°/s, black) head movements. Binning as in Figure 2B. (**D**) Distribution of human eye velocities during fast (>6°/s, gray) and slow or no (<6°/s, black) head movements. Binning as in Figure 2B. (**E**) Distribution of cat eye velocities during head movements (>6°/s) to the left (gray) or right (black). Positive values correspond to movements to the right. Binning as in Figure 2B. (**F**) Distribution of human eye velocities during head movements (>6°/s) to the left (gray) or right (black). Positive values correspond to movements to the right. Binning as in Figure 2B.

frequent than predicted by independence: eye and head movements co-occur in 32.1% (cat) and 32.5% (human), respectively, compared to the independence prediction of 29.4% = (100% − 36.3%)(100% − 53.8%) for cats and 26.1% = (100% − 29.2%)(100% − 63.1%) for humans. This quantifies that eye and head movements may not be considered in isolation, but their coordination is of relevance.

We therefore compare the distribution of eye-movement velocities in the presence of head movements larger than 6°/s to the distribution in their absence (Fig. 2C and 2D). In line with the aforementioned data, for no or slow head movements, there are no eye movements in the majority of cases (76.7% in cats, 81.1% in humans), while in the presence of head movements these values drop to 48.0% and 45.5%, respectively. By this separation of eye movements according to head velocity, the velocity distributions in humans and cats are remarkably similar, suggesting that differences in eye-movement behavior are attributable to differences in head velocity distributions. In any case, these figures confirm the importance of coordinated movements of eye and head as compared to isolated movements of either.

Relative Direction of Eye and Head Movements

Whereas the absolute speeds considered so far can be subject to calibration errors, a robust measure is provided by the relative direction of eye and head movements. How does the direction of eye movements depend on the simultaneous head movement? By separating eye-movement analysis according to the direction of head movement (left or right), we find that there is only a slight dominance for potentially compensatory eye movements in cats (Fig. 2E). Only considering substantial movements (head movements larger 6°/s, eye movements larger 25°/s) for rightward head movements, 44.4% of eye movements go to the right, and 55.6% to the left. Analogously, for leftward head movements, 40.4% of eye movements go to the left, and 59.6% go the right. Consequently, a slight majority of eye movements opposes head movements, indicating a slight bias to potentially compensatory, gaze-stabilizing eye movements. Even if all these were indeed stabilizing, however, more than 40% of the eye movements in cats cannot be accounted for by a purely gaze-stabilizing function, but instead act synergistically with head movements. Surprisingly, the fraction of potentially gaze-stabilizing eye movements is larger in humans than in cats (Fig. 2F): for our data, 83.3% of fast eye movements go to the left when the head moves to the right, and 88.7% of fast eye movements point rightwards when the head moves to the left. Hence, potentially stabilizing eye movements are more abundant in humans than they are in cats, and the human data provide a reference for comparing the cat data to. The cat data stresses that exploratory eye movements, which act synergistically with head movements to readjust gaze to a different location in the world, constitute a substantial fraction of the eye movements occurring in cats during natural exploration behavior.

Direction and Speed

So far, we have considered absolute velocities and directions separately. Next, we analyze them simultaneously by histogramming simultaneous head and eye movements (Fig. 3). If the only function of eye movements would be stabilization of the retinal image, all data in such histograms would fall on the second diagonal, independence would be reflected by separability of the axes, and a predominantly exploratory component of eye movements by peaks in the first and thitd quadrant. In humans (Fig. 3B), we find a predominantly gaze-stabilizing role of eye movements, with 42.7% of the data on the second diagonal; this for 42.7% eye velocity equals the negative head velocity within 12°/s (or in other words: gaze moves less than 12°/s). In cats, the corresponding value is similar, with

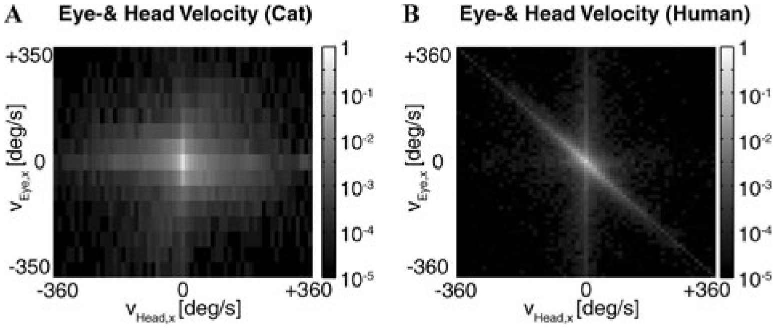

Figure 3. Eye movements and head movements. Two-dimensional histograms of co-occurring eye and head velocities; binning for each axis as in Figure 2. (**A**) Cat, (**B**) human.

39.7%. When excluding times of slow movement (defined as previously), however, 29.3% of the human data show gaze shifts slower than 12°/s, compared to 8% in the cat. This quantifies the visual inspection of Figure 3 and verifies the analysis of directions: in humans potentially gaze-stabilizing movements are much more abundant than in cats. This challenges the notion that gaze stabilization is the dominant role of eye movements in cats under natural conditions.

Temporal Correlations of Movements

So far, we have considered only individual time points. However, movements are usually longer than the 40 ms of a video frame. To quantify the typical duration of a movement, we analyze the autocorrelation of head and eye movements as well as their cross-correlation. First, we consider absolute speeds, irrespective of direction. Cats' head movements are correlated over 99 ms [full width at half maximum (FWHM)] of correlation; Fig. 4A), while the human's head movement is correlated over nearly 362 ms (Fig. 4B). When considering direction and speed, the cats' head movement correlation width drops to 77 ms (Fig. 4C), while the humans correlation length increases to 425 ms (Fig. 4D). This shows that head movements operate on different time scales for both species. Consistent with the faster and less frequent head movements in cats, human head movements tend to be inert, going in the same direction for nearly half a second, while cat head movements are faster and may change direction more frequently.

Eye movements have shorter correlation time constants than head movements in both species: considering only speed we find 69 ms in cats (Fig. 4A) and 54 ms (Fig. 4B) in humans; when also accounting for direction, the cat value drops to 32 ms (Fig. 4C) and the human value to 46 ms (Fig. 4D). This implies that for humans eye movements operate on a six to ten times faster timescale than head movements, while for cats this difference is less pronounced. In addition, the correlation in humans is positive in the whole time window (400 ms) investigated, while cat eye movements show a substantial anticorrelation (Fig. 4C). A possible explanation for this correlation is found in preparatory eye movements: eye and head movements are coordinated for exploration: after the head starts to shift, gaze allocation starts with a compensatory movement, then the eye may "overtake" the head in gaze allocation and needs to make an opposing movement to counteract this overshoot. Although this explanation is consistent with the literature, the nearly flat cross-correlation between eye and head movements (Fig. 4C) suggests that other mechanisms of eye–head coordination are in place that compensate for this behavior, which would result in a positive cross-correlation between eye and head movements. Hence, with respect to the coordination of eye and head movements, compensatory (gaze-stabilizing)

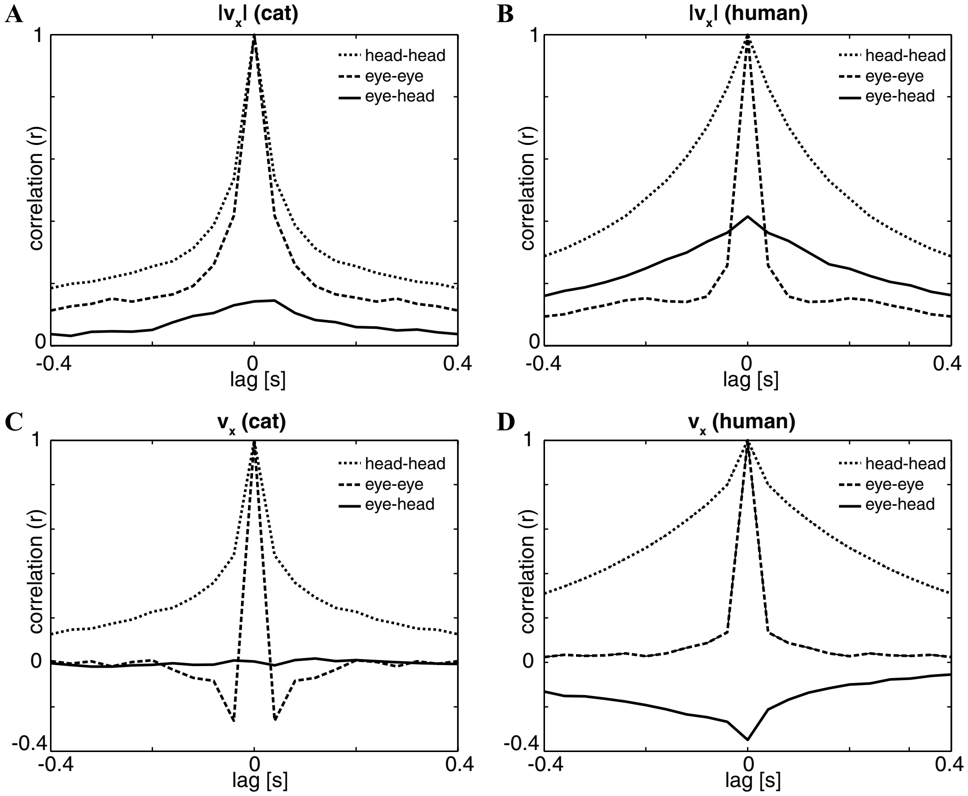

Figure 4. Temporal correlation. Autocorrelation of head (*dotted line*) and eye (*dashed line*) velocity and cross-correlation between eye and head velocity (*solid line*). (**A, B**) horizontal velocity, (**C, D**) absolute value of horizontal velocity; (**A, C**) cat, (**B, D**) human. Negative lags for cross-correlation implies head leading eye.

and synergistic (gaze-shifting) components cancel each other and are thus of similar importance.

Considering the cross-correlations for the other cases, it becomes evident that for absolute speeds in cats the cross-correlation is weak but positive (Fig. 4A), again reflecting the abundance of eye movements in the presence of head movements compared to an assumption of independence. Due to the low peak value, a time constant can only be approximated and the value of 331 ms for FWHM primarily reflects the nonzero correlation even after 400 ms, which is consistent with prolonged phases of rest and fixation interleaved by long exploratory phases. Interestingly, the cross-correlation is asymmetric, peaking at a lag of +40 ms, consistent with the eye slightly leading the head movement as discussed earlier in this chapter.

In humans, the cross-correlation between absolute eye and head speeds is stronger and rather symmetric (Fig. 4B), and has a long (546 ms FWHM) time constant, which exceeds the head's autocorrelation. This suggests that prolonged gaze shifts are often dominated by head movements and supported by eye-in-head movements, while isolated eye movements are responsible for quick shifts of gaze. This receives further support by including the direction. The cross-correlation between head and eye velocity is negative, underlining that prolonged coordinated eye and head movements in humans contain predominantly compensatory mechanisms, presumably similar to the one previously described for cats.

Discussion

Here we report eye and head movement data for freely behaving cats and compare them to free exploration data of a human observer in a similar natural environment. Despite the differences in oculomotor and visual system, basic eye-movement parameters, such as velocity, are remarkably similar between the two species. In contrast, head movements operate on substantially different time scales, presumably attributable to the human head's inertia. As a surprising consequence, eye movements that compensate for head movements play a more dominant role in humans than they do in cats.

The cat data reveal several prominent dependencies between eye and head movements, but relatively weak evidence for eye movements that oppose the direction of head movements. The single most frequent behavior was of concomitant stability of head and eyes. Furthermore, eye movements tended to coincide with head movements, and vice versa. While the distribution of eye velocities is biased toward movements that oppose the direction of head movement, these movements—unlike in the human—are of short duration and confined to low velocities. All of these data considered, many of the potentially compensatory movements in cats would not be expected to stabilize the image on the retina within short timescales. Hence, our data argue against a primarily gaze-stabilizing role of eye movements in cats during free exploration behavior.

When considering the spatiotemporal statistics of natural stimuli, typically a uniform sampling of time is assumed. We therefore characterize the dynamics of eye, head, and gaze movements by treating all time points equally, rather than defining and categorizing individual epochs. In our scheme a fast saccade thus receives less weight than a slow movement, even if a categorization scheme would treat each as a single event. Hence, we do not take our data to suggest that saccades are unimportant in humans, rather we argue that slow eye and head movements are frequent and have to be considered in humans as they are in cats. Only under the assumption of a saccade-triggered time representation, periods around saccades may dominate and eye movements themselves can serve as a trigger signal for perception and learning.[35] In turn, the apparent abundance of "slow" eye movements in cats can be understood as a consequence of the opposite bias: cats move their head faster, yielding shorter individual gaze-shifting epochs. In this view, the apparent differences in eye-movement characteristics between humans and cats can be understood as a consequence of the different head-movement dynamics.

The present study is, to the best of our knowledge, the first to record eye movements in the cat under conditions of free behavior in a natural environment and without any restraints to head or body. This reveals technical limitations of our CatCam setup. The restriction imposed by the need for cameras being lightweight and small, allowed us to only a limited spatial and temporal resolution at the time of recording. Yet eye movements of head-restrained cats are relatively slow and more variable than human eye movement. Fixation may be of 1–3 s duration, compared to 150–300 ms for humans,[36–38] and intersaccade intervals may be up to 20 s.[39] Thus, we are confident that we have sampled the relatively low eye velocities at our resolution. Nevertheless, the given spatial and temporal resolution only allows us to deduce an upper boundary for the proportion of eye movements that potentially compensate for head movements, and it is worthwhile to improve upon such an upper boundary and determine the fraction of truly compensating eye movements.

The general shape of the eye-velocity autocorrelation in cats and the prolonged negativity of eye–head cross-correlation in humans is consistent with gaze-shifting behavior, described earlier for monkeys:[17] large gaze-shifts start with an eye movement, the less precise head movement follows, and is finally compensated for by a reflexive eye movement that stabilizes gaze. In line with these results, the VOR has been shown to be mainly active at the beginning and the end of large gaze shifts[12,40,41] and inactive otherwise. The absence of a substantial eye–head velocity cross-correlation in cats and the strictly positive eye-velocity autocorrelation in the human observer indicates that movements on different timescales play an important role in gaze allocation during free exploration, when not only the head, but also the body can move without restraints.

How can we explain why evidence for compensatory eye movement in our results is so weak for cats as compared to humans? Many previous studies demonstrated the task dependence of eye movements in humans.[42,43] Here, the free behavior in a natural environment emphasizes exploratory behavior. Neither humans nor cats were restricted by the experimental apparatus, and neither did we impose any specific explicit task. Instead, both species displayed self-paced active explorative behavior. This may explain the seeming discrepancy between our data and those obtained under more controlled conditions in the context of a specific task. This highlights how studying free behavior remains a necessary complement to restrained, albeit better controllable, laboratory experiments.

The perception of a stable world in the presence of movements is a challenge for the visual system. Eye movements play a dual role in this quest: on the one hand, oculormotor reflexes contribute to the stabilization of images on the retina, while on the other hand, eye movements actively contribute to shifts in gaze. Our present results show that this distinction is not strict, so seemingly reflexive movements may support exploratory behavior: eye movements that co-occur with head movements are most abundant, but, particularly in cats, not of purely gaze-stabilizing function. Our most remarkable finding is that precise image stabilization seems to be *less* frequent in cats than in humans, contrary to the intuitive expectation. It is tempting to speculate that the more precise compensation in humans reflects their smaller area of highest retinal resolution: whereas humans have to bring and keep detail precisely to their fovea, cats only need precision on the order of their area centralis's size. In this view, the higher need for precision in gaze allocation requires humans to precisely tune eye movements with respect to head movements during exploration, while in cats both mechanisms also act together, but with less need for precision. Whether this explanation fully accounts for our results or not, three interesting conclusions remain: eye movements in humans and cats have similar velocity characteristics, combined eye and head movements are most abundant in both species, and precise stabilization is found in humans more frequently than in cats.

Acknowledgments

We gratefully acknowledge the support by IST-027268-POP (Perception On Purpose, P.K.) and by Bayerische Forschungsstiftung (DOK-88-07 to J.V.). This work was financially supported in part within the DFG excellence initiative research cluster Cognition for Technical Systems – CoTeSys. Furthermore, we thank Tobe Freeman for assistance with the preparation of the manuscript.

Conflicts of Interest

The authors declare no conflicts of interest.

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