Overt attention toward oriented objects in free-viewing barn owls

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Visual saliency based on orientation contrast is a perceptual product attributed to the functional organization of the mammalian brain. We examined this visual phenomenon in barn owls by mounting a wireless video microcamera on the owls' heads and confronting them with visual scenes that contained one differently oriented target among similarly oriented distracters. Without being confined by any particular task, the owls looked significantly longer, more often, and earlier at the target, thus exhibiting visual search strategies so far demonstrated in similar conditions only in primates. Given the considerable differences in phylogeny and the structure of visual pathways between owls and humans, these findings suggest that orientation saliency has computational optimality in a wide variety of ecological contexts, and thus constitutes a universal building block for efficient visual information processing in general.

feature search | gaze map | pop-out | visual behavior | avian vision

In his now-classic experiments, Yarbus (1) showed that humans who freely view visual scenes move their eyes between salient, discretely spaced features (e.g., eyes and mouth in face scenes, people and objects in indoor scenes). Similar behavior in other environments has been observed in primates (2, 3) and even in birds (4–7). Indeed, the visual systems of humans and other animals have mechanisms to overtly shift attention to salient parts of visual stimuli, a selective process that helps allocate the brain's limited computational resources to potentially important sensory information (for a review see refs. 8 and 9). The selective nature of the visual system perhaps is best expressed in what has been termed "visual search" (10, 11).

Although visual search is a visual behavior occurring with natural and synthetic stimuli, controlled scientific studies of visual search typically make use of well-defined, simple objects. In such experiments, the subject's task is to detect one outstanding object (the target) embedded among many similar objects (the distracters) (12). Studies in which the target differs from the distracters in one visual feature are referred to as feature search (11). A typical feature would be an early visual cue, such as contrast, color, motion, orientation, or even shape. When feature search exhibits reaction times that do not change much with the number of distracters, the behavior is usually characterized as "pop-out," which is indicative of a parallel preattentive process that precedes any subsequent serial attentive processing (12).

Although much is known about the properties and the neural networks involved in visual search in humans and primates (11–15), knowledge of this process (especially its neural substrate) in nonprimate animals is limited. This is in stark contrast to the important ecological function of search strategies in all animals, which should have been optimized according to the ecological and survival needs of a species in the course of evolution. Notable exceptions are visual search strategies reported in pigeons (4, 5) and recent orientation-saliency behavior found in archer fish (16).

In the present work we studied visual search in free-viewing barn owls, which, as we argue, may become a model animal with several important advantages for exploring this visual attentive behavior in animals. First, barn owls' eye movements are either absent or very small, allowing the study of overt attention with an external camera fixed to owls' heads (6). Second, barn owls are known to make conspicuous peering movements (17) and can also covertly shift attention toward interesting targets (18), meaning that their vision is likely to incorporate attention mechanisms. Third, much is known about barn owls' visual system (19, 20), and the neural circuits underlying visual perception in this species have been studied in some detail (21–27). With this in mind, we asked whether barn owls exhibit similar visual search behavior as humans. The data presented here indeed show such similarities.

Results

In our barn owl experiments, the setup and procedures were chosen to resemble the classical visual search studies performed with humans (1, 12), with a specific focus on saliency due to orientation. Two barn owls (subjects HB and WH) were trained to carry the OwlCam, a head-mounted wireless microcamera (Fig. 1A). In a typical experimental trial (Fig. 1B), the owl was placed on a perch in a large illuminated room and was confronted with an extended open-field stimulus that contained several visual objects (oriented bars), one of which differed in its critical visual feature (orientation). No specific task was given, and the owls could freely view the scene in the room. We measured and analyzed the owls' gaze that could be derived directly from the camera view, given that eye movements are negligible.

Because barn owls lack a visible fovea (28, 29), their true gaze direction cannot be resolved by optical and geometrical analysis, and thus the OwlCam must be calibrated by other means after it is mounted and fixed to an owl's head (Materials and Methods and Fig. 1 B and C). This yields the "functional fixation point" of the owl in camera-frame coordinates, which serves as a reference frame for all of our reported data. As discussed in Materials and Methods, both of our owl subjects were found to have a similar fixation spot of ~2.3° of visual angle and steep flanks. In our OwlCam image plane, this amounts to a disk of 25 pixels in diameter, which was used in all of our subsequent analyses.

In the visual search experiment, the room contained 25 oriented bars scattered on the floor in a 5 × 5 jittered configuration (Fig. 2). Of these 25 bars, 24 bars—the distracters— had a similar orientation (up to a small jitter, to avoid possible confounds from strict regularity), and one bar—the target—was placed at a very different orientation (Materials and Methods). The owl was allowed to freely view the scene without any prescribed task. Once the owl oriented its head toward the scene (usually immediately after stimulus onset), it clearly moved its gaze from one bar to another, sometimes returning to a bar on which it had
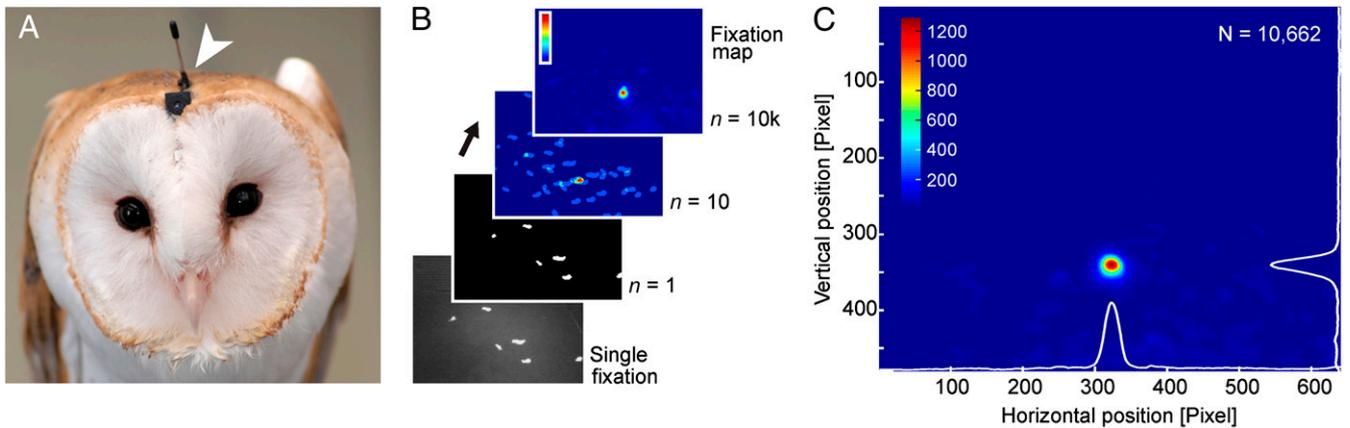
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Fig. 1. (*A*) OwlCam (indicated by the white arrow) attached to the head of a barn owl. Only the antenna and the frontal part of the camera unit are visible. The total weight of the setup, including the battery, is 5.5 g. (*B*) Fixation spot calibration procedure. Single fixation images (*Bottom*) are binarized into target and background regions (*n* = 1). When several binarized frames are accumulated into a single normalized map, a 2D probability density function of target locations within the camera frame begins to form (*n* = 10). A marked fixation spot emerges after several thousand fixation images are processed (*n* = 10,000). (*C*) Fixation map of one of our owls (WH) after calibration. Absolute occurrences of targets within each pixel (in camera frame coordinates) are color-coded (compare *Inset*). In this example, 10,662 fixations were accumulated to yield a peak probability at pixel 322/339 of the image (horizontal/vertical coordinates). The 1D probability functions along both axes are given as well (bright lines).

already fixated earlier. An example of a typical fixation-saccade behavior is shown in Movie S1. In a total of 97 experimental trials, ~120 min (217,309 frames) of OwlCam video material was recorded and analyzed from the two owls. To present data corresponding to both owls in a simple and clear fashion, in what follows we present all results using the notation "HB/WH."

In 28/69 experimental trials, a total of 45/75 min (82,090/135,219 frames) of video material was recorded. The average length of each trial was 97.7/65.3 s (2,931.8/1,959.7 frames). The experimental video material was separated into segments of image motion and nonmotion (17), corresponding to the phases of head movement (saccades) and nonmovement (fixations). Note that by such a definition, an equal number of saccades and fixations must occur, because each saccade is bracketed by two fixations and vice versa. A total number of 985/1,236 fixations were analyzed, which lasted a total of 71,673/120,567 frames and averaged 72.76/97.55 frames per fixation. Thus, the owls spent 87%/92% of the total recording time on fixations, with an average fixation time of 2.43/3.25 s. The average duration of a saccade was 0.35/0.28 s.

Because of the static nature of fixation segments, only one frame was used to represent the content of each fixation. For our analysis, we extracted the middle frame of each fixation, on which the fixation spot of 25 pixels in diameter was marked for further analysis. First, fixations were classified into four classes based on their visual content (Fig. 2):

i) Target fixations, in which the target item appeared within or immediately at the border of the fixation spot mark (with up to 1 pixel tolerance).
ii) Control fixations, in which the control item appeared within or immediately at the border of the fixation spot mark (1 pixel tolerance). The position of the control item was defined by mirroring the target position about the center of the 3 × 3 array, and thus was trial-dependent and changed its position according to the target position in each trial.
iii) Frontal fixations, directed toward the stimulus scene while being neither target nor control fixations. Frontal fixations include cases in which bars other than the target and the control items were looked at, along with cases in which the gaze was directed toward the stimulus but the animal fixated at no specific bar. In general, frontal fixations were the most frequent of all fixations.

iv) Back fixations, directed at locations where no bars were visible within the entire camera field of view. Such fixations were directed at the walls, ceiling, or door of the experiment room.

For simplicity of presentation, we also designate all nonback fixations (i.e., the sum of target, control, and frontal fixations) as scene fixations.

Out of all 985/1,236 fixations recorded, 347/264 (35%/21%) were back fixations. Such fixations occurred due to the owl's overall state of alertness (or lack thereof) and its natural visual scanning behavior. Naturally, these fixations did not show useful visual content that could be used to examine fixations on target or distracter items, and thus they were excluded from further analysis.

The remaining scene fixations were used for our main analyses, as described next. Out of all scene fixations, 7%/8% were outside of the region covered by the 25 bar items.

For stimulus presentation, we divided the scene into two compartments: the total region of 5 × 5 items and a central subarray of 3 × 3 items. Targets were placed only within the central 3 × 3 subarray of items, to avoid possible margin effects due to the fact that items outside the central subarray did not have neighbors on all sides. Interestingly, increased saliency for the bordering items was not observed. Moreover, both owls had a tendency to focus their overt attention to the central 3 × 3 subarray, where indeed 76%/62% of their scene fixations were directed. This bias toward the central subarray was confirmed in a number of control trials in which no target bar was present and all bars were oriented similarly, where 79%/60% of all scene fixations were directed to the central subarray. Thus, the expectations for randomly hitting one of the central items would be 0.76/9 = 0.08 and 0.62/9 = 0.07. With this in mind, the proportion of target and control fixations out of the total number of scene fixations was calculated and compared for each experimental trial separately. The mean proportion of target fixations was 0.21/0.16, whereas that of control fixations was 0.07/0.08 (Fig. 3*A*). More quantitatively, the mean proportion of fixations directed to the target was more than twice as high as those directed to the control bar.

To demonstrate the difference in the number of fixations directed at the target and the control, we also counted the number of fixations for each category in each trial. For example, in the trial shown in Fig. 2*B*, the owl looked at the target three times, whereas the fixation spot appeared at the control item two times.
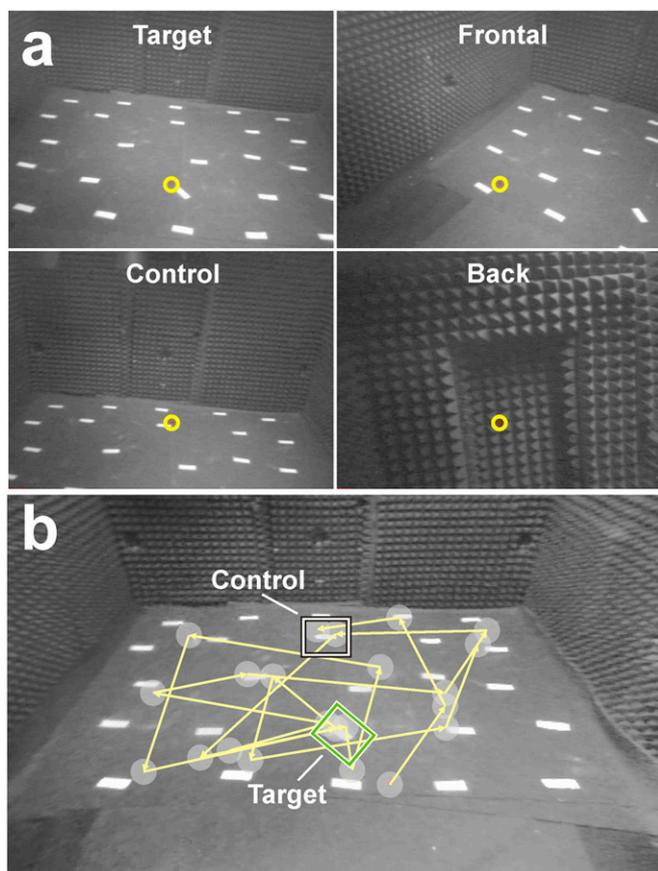
Fig. 2. (*A*) Classes of fixations. The fixation classes were determined by the content of the frame in the fixation spot (marked by the yellow circle) and away from it. In *target fixation*, the owl was looking toward the stimulus array, and the target item (in this case, rotated by 45° compared with all other items) appeared within or immediately at the border of the fixation spot. In *control fixation*, the owl was looking toward the stimulus array, and the control item appeared within (or immediately at the border of) the fixation spot. The position of the control item was defined by mirroring the target position about the center of the 3 × 3 array. In *frontal fixation*, the owl was looking toward the stimulus array, but neither the target nor the control items appeared within the fixation spot. This was the most frequent type of fixation. In *back fixation*, none of the foregoing held. In the demonstration case, the owl simply looked at the door of the experiment room. (*B*) An exemplary stimulus scene as reconstructed from many fixation frames (*Materials and Methods*). The walls of the experiment room are visible in the far end and along the sides. The reconstructed scan path of the owl during this experimental trial is denoted by circles (loci of fixations) connected by straight lines (saccades). Note how the owl repeatedly shifted its gaze between stimulus objects and often returned to specific locations/ items. Regions in which target and control fixations were registered are highlighted. Back fixations are not shown.

Fig. 3. Target advantage over control in terms of number and total fixation time. (*A*) Mean proportion of fixations on target (green, filled) and control items (white, open) out of all frontal fixations for both owl subjects (HB and WH). The difference between target and control conditions was highly significant in both cases ($P < 0.0001$, Wilcoxon matched-pair signed-rank test). Error bars are SEM. (*B*) Normalized cumulative occurrences of fixations directed to the target (green line) and to the control (dashed line) plotted against the number of fixations. In both owls, the right shift of the target graphs generally indicates more fixations. (*C*) Mean proportion of time spent on fixating the target and control items out of all frontal fixations/ differences between target and control conditions (color-coded as in A), again highly significant for both owls ($P < 0.002$). (*D*) Normalized cumulative occurrences of frames directed to the target and to the control plotted against fixation time given in the frames for both owls. A right shift denotes longer fixations.

A Wilcoxon matched-pair signed-rank test including all trials revealed a highly significant difference in the target and control fixations per trial ($P < 0.001$ for both owls). To demonstrate this perceptual advantage of the target over the control in another way, we also plotted the data as cumulative probability distributions (Fig. 3*B*). These curves demonstrated a rightward shift of the target distribution compared with the control distribution, suggesting that on average, target fixations were more numerous per trial. For example, Fig. 3*B* shows that in the control item was not fixated in ~36%/38% of the trials, whereas the target was not fixated in only 7%/13% of the trials. The same graphs also show that the control item was never fixated more than 6/5 times per trial, whereas the target was fixated much more frequently, as
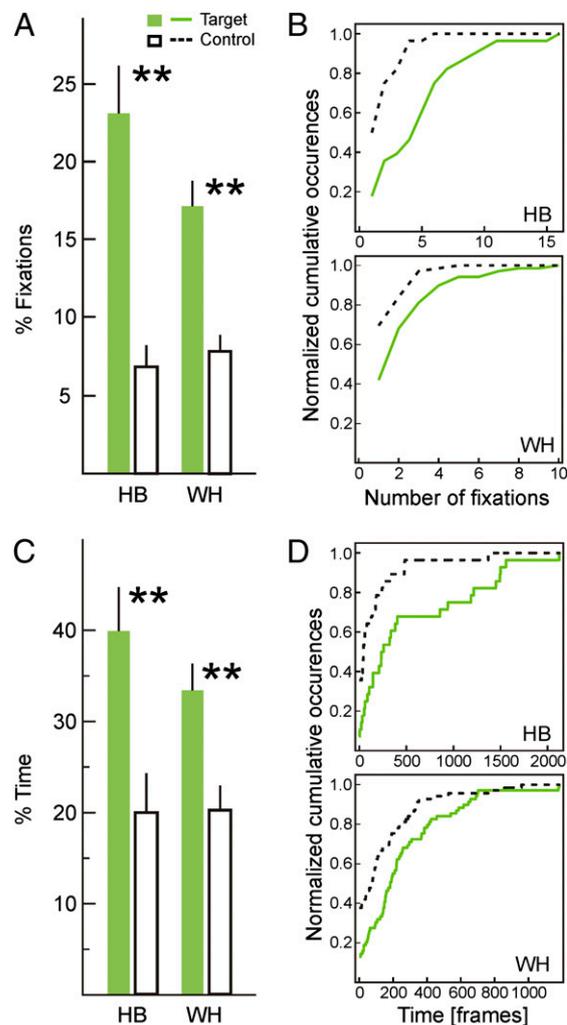
many as 16/10 times per trial. In summary, our analyses clearly show that the target exhibited increased saliency for both owls.

We aimed to confirm the significant difference of target selection for oriented objects in the time domain by computing the relative time spent on each of the frontal, target, and control fixations out of all scene fixations. The duration of each frontal, target, and control fixation was determined directly from the video recordings, accumulated by category, and divided by the total time spent on all three categories. The mean proportion of time spent on target items was 0.40/0.34 and that spent on control items was 0.20/0.22 (Fig. 3*C*), whereas the mean proportion of frontal viewing without fixation of either the target or the control bar was 0.40/0.34. Notably, the difference between target fixation time and control fixation time was highly significant for the in-

dividual trials as well. The average time per trial spent on target and control items yielded 548/254.17 frames on target items and 148.25/137.88 frames on control items, a highly significant difference ($P < 0.01/< 0.001$, Wilcoxon matched-pair signed-rank test). The difference in viewing time between target and control is also obvious in the cumulative probability plots, assembled in a way analogous to those shown in Fig. 3B. The curves reflecting the fixations at target are shifted to the right compared with the control curve (Fig. 3D). In >95% of all trials, the owls looked at the control for <500/400 frames, compared with 1,000/800 frames for the target. Overall, the owls fixated on the target bars more often and longer than on the control bars.

Whether or not the target bar was more salient than other items also may be reflected in how *fast* it drew the owl's view. We counted the number of saccades from the onset of a stimulus (lights switched on) until the target or control item was first looked at. For example, in the trial shown in Fig. 2B, the owl first hit the target with its fifth saccade, whereas it hit the control with its third saccade. When all data were averaged, the mean number of saccades until the target was looked at was 3.92/3.17, and that until the control was looked at was 15.5/5.93 (Fig. 4A). Although both differences were statistically significant ($P = 0.0022/0.0129$), the distribution of the number of saccades until first hit was positively skewed for both target and control items; that is, there were generally more observations below the arithmetical average. Specifically, in 67% of all cases, owl HB looked at the target item after one (i.e., the first fixation was at the target; $n = 7$), two ($n = 6$), or three ($n = 4$) saccades, suggesting that the median numbers of saccades might be more informative than the averages in this case. Indeed, the median number of saccades until the target item was first looked at was 1.5/2, compared with 8.5/4 for the control item. The difference between the target and control conditions was highly significant for owl HB and significant for owl WH ($P < 0.01$; $n = 17/P = 0.014$; $n = 38$, Wilcoxon matched-pair signed-

rank test). The faster gazing toward the target than toward the control also becomes obvious in the cumulative probability plots for both owls shown in Fig. 4B. The curves reflecting the number of saccades to the target are shifted to the left compared with the control curves. In other words, the target is reached with the first saccade in 25%/19% of the trials, compared with 0%/7% for the control. Likewise, after 10 saccades, the target was reached in 86%/84% of the trials, whereas the control was reached in only 36%/49%. These last values indicate that the control was not reached at all in a considerable number of trials. In summary, our data show that the target was reached after a lower number of saccades compared with the control bar.

During the training phase, both artificial objects and food items were scattered on the floor (*Materials and Methods*). Because food items should be the most salient visual objects presented in an experimental room, it is interesting to examine how they drew the owls' attention compared with our oriented targets and distracters. On repeating the foregoing analysis, the mean number of saccades to food was 2.5/3.17, compared with the median number of saccades of 3/3 (Fig. 4A). No significant differences were found compared with the mean number of saccades to our differently oriented target ($P = 0.73/0.59$). Thus, the most salient visual items that we observed at all times—food items—were looked at after the same number of saccades as the target item that was defined by a different orientation.

Discussion

Our study of visual search in barn owls demonstrates that the free-viewing animals looked longer, more often, and earlier at differently oriented targets than at a control item, in a manner resembling visual search in humans. The expression of orientation saliency in visual search, demonstrated here in a bird species, raises intriguing questions and has important implications regarding the neural machinery that might be responsible for the observed behavior, the evolutionary relationship between birds and primates, and the role of orientation-based saliency in efficient visual information processing.

The predatory barn owl, with its specialization for hunting in low-light conditions (30) needs to catch approximately two food items (mainly mice) each day to survive and more than 20 a day to feed its offspring. The selective pressure on these birds is especially high if weather conditions are unfavorable due to rain or snow. Indeed, in central Europe, ~60% of barn owl yearlings do not survive their first winter (31). Under such high selective pressure, it would be to the animal's advantage to exploit every possible cue available to find its prey. Indeed, barn owls are known to be effective hunters (32), and thus exploiting even minute visual cues is likely to be an intrinsic part of their visual behavior.

The evolution of different forms of saliency may be related to the high selective pressure experienced by this bird. The orientation saliency reported here could help the owl detect prey more easily and more quickly. Pigeons are able to group bars of similar orientation and discriminate the resulting figure from bars with a different orientation (4). Pigeons also can detect odd objects in a scene and even discriminate letters and faces (5, 7). Thus, birds seem to have the neural machinery necessary for complex scene analysis.

In primates, orientation-based saliency is facilitated by certain neural circuitries, particularly those creating orientation selectivity (33, 34). Long-range lateral connections found in the primary visual cortex (35, 36) have been shown to be important as well (37). Orientation sensitivity in the barn owl's visual Wulst is very similar to that seen in the visual cortex (19, 20). The function of the horizontal long-range connections in mammals may be accomplished in birds through the interconnectivity of many telencephalic nuclei (see ref. 38 for a review). Moreover, within the visual Wulst, organizational complexity increases as with increasing latency of neuronal responses, indicating a hierarchy
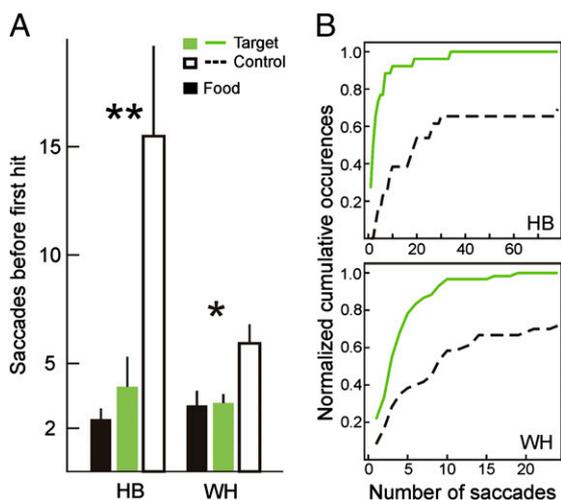
Fig. 4. Target advantage over control in terms of the number of saccades before first hit. (*A*) Mean number of saccades until target (green, filled) and control (white, open) were first looked at. Black bars indicate the mean number of saccades until food items were looked at in training. The differences between target and control conditions were highly significant for owl HB (**$P < 0.0001$, Wilcoxon matched-pair signed-rank test), and significant for owl WH (*$P = 0.014$, Wilcoxon matched-pair signed-rank test). Error bars are SEM. (*B*) Normalized cumulative occurrences of saccades until the target (green line) and the control (dashed line) were first looked at plotted against the number of saccades. Both owls looked at the target much faster, thereby causing a left shift in the cumulative plot. Note that in many trials, the owls never looked at the control item, and thus its curve does not converge to the 1.0 asymptote.

of processing (39). Furthermore, attentional mechanisms were found in the barn owl in cross-modal experiments that successfully used spatial attention to modulate sound localization (18). Cross-modal competition in barn owls also was found to occur in intermediate and deep layers of the optic tectum, a structure known to be involved in gaze control and attention (21).

The fact that two such distant species as humans and barn owls, whose brain structures are substantially different, exhibit similar visual search characteristics has profound implications. In this sense, our research is similar to a recent study on archer fish, which have been shown to exhibit orientation-based saliency similar to humans (16). Unlike Mokeichev et al. (16), however, who explored orientation-based saliency using a rapid forced choice procedure, our experiment was based on free-viewing visual search, reminiscent of the conditions under which this behavior is tested in humans. In both cases, bottom-up mechanisms are likely to play the main role in the observed behavior (although the effects of top-down influence, and of some implicit unspecified task, cannot be excluded), and in both cases the behavioral similarities in the reported findings suggest that visual processes, such as orientation-based visual search, may not necessarily require the elaborate cortical structures typically seen in humans. Unveiling the neural mechanisms that facilitate these processes in animals like the barn owl may provide important insight into saliency processing in other organisms as well.

In humans, classical visual search experiments are also used to discriminate between preattentive, pop-out, parallel processes and serial attentive processes by measuring how target detection time varies with the number of distracters. Pop-out also has been demonstrated in pigeons (40). Owing to the slower response time of the owls in our free-viewing paradigm, the difficulty in specifying a specific task, and the indirect way in which the subjects' responses must be measured, exploring true pop-out in barn owls is more challenging. However, comparing our visual search results for the differently oriented targets and the food items reveals that the both were looked at after approximately the same number of head saccades. This comparable performance to the "most desirable" target may indicate a perceptual popping-out of the differently oriented target against the distracter array, which draws the animal's attention equally effectively and may serve as a first indication of the existence of the pop-out effect in barn owls. To confirm this hypothesis and the equivalence of visual behavior between barn owls and humans in general will require an extensive and more challenging examination of visual search in barn owls. This will be done by confronting the animals with search stimuli presented on a monitor and by recording from brain structures putatively involved in visual search (21). Such experiments may shed light on whether theories hypothesized for human visual search (10, 11, 13) can model this visual process in the barn owl as well, or whether nature has found a different solution. Regardless of how this question is resolved, however, the fact that species as distant as humans and barn owls exhibit striking similarities in a fundamental visual behavior like orientation-based visual search suggests that orientation saliency has computational optimality in a wide variety of contexts and provides a universal building block for efficient visual information processing.

Materials and Methods

Animals. The experimental animals were two adult American barn owls (*T. alba pratincola*; subjects WH and HB) that were taken from the breeding stock of the Department of Zoology at Rheinisch-Westfälische Technische Hochschule Aachen. The birds were hand-raised and tame. The wingspan of barn owls is ~1.1 m (41). During the phase of experimentation, the owls' body weight was maintained at ~90% of their free feeding weight (~415 g and 470 g). Water was given ad libitum, and food (dead chicken) was given only in the experimental room or as a reward directly after an experiment. Training and experiments were performed on five or six days per week. For each owl, a small aluminum headpost, to which the OwlCam was later attached (see below), had been fixed to the skull on the forehead under an-

esthesia at an earlier time. Care and treatment of the owls was carried out in accordance with the guidelines for animal experimentation as approved by local authorities (Landespräsidium für Natur, Umwelt und Verbraucherschutz Nordrhein Westfalen, Recklinghausen, Germany) and in compliance with the National Institutes of Health's guideline for the use and care of laboratory animals.

Experimental Setup and Procedure. Experiments and training were performed in a large room (4.2 m long × 3.2 m wide × 3.2 m high), in which the owls were allowed to move and fly freely. Moderate illumination was provided by ceiling-mounted tungsten lights that were switchable from outside. To achieve sound attenuation, the walls, ceiling, and floor were covered with planar and pyramidal foam. A wooden perch placed 1.75 m above the floor close to one short wall of the room served as a resting post just before and in between experiments. A retractable curtain made from thick black cardboard was placed in front of the perching position, such that the animals' view to the floor could be blocked until the experiment was started. The owls were trained to fly toward food items presented on the floor and to return to the perch after a successful strike, with the captured prey as a reward. During training, flights normally occurred after the experimenter left the room. Training trials also were interleaved irregularly between experimental trials at a ratio of about 1:5, to ensure high motivation and active viewing behavior of the owls in experiments, where no specific task was given.

Between experimental trials, the following procedure was performed. The curtain was moved into place to block the owl's view of the floor. The experimenter then entered the room and placed 24 distracter items on the floor to cover the virtual intersections of a sparsely arranged and randomly jittered 5 × 5 orthogonal grid (Fig. 2). The visual items were identical rectangular bar-like shapes (150 × 50 mm) cut from thick yellow cardboard. One additional item, defined as the target item, was differently oriented and slanted by 45° relative to the dominant orientation of the distracters. The target item was placed quasi-randomly and counterbalanced in one out of nine possible positions at the area of a concentrically arranged 3 × 3 grid. In this way, the target item never appeared at the immediate edge of the whole stimulus array, and possible margin confounds were avoided. The experimenter left the room, lights were switched off, and the curtain was retracted to allow a free view onto the stimulus array. The beginning of a trial was defined as the time when the lights were switched back on and the owl started to visually inspect the room. The owl was allowed to look around freely for a maximum of 3 min, after which the trial ended. Usually, the owls would fly toward one of the visual items after a shorter period of inspection and, upon entrance of the experimenter, retreat to the perching position. Approximately 5–15 consecutive trials were performed with one owl per day.

OwlCam and Video Analysis. During all experimental and training sessions, the owls carried a head-mounted lightweight wireless camera device, the OwlCam (*SI Materials and Methods*). The OwlCam consisted of a miniature complementary metal-oxide semiconductor active-pixel sensor and optics unit, a 900-MHz video broadcasting unit, a rechargeable lithium-polymer battery, and a custom-built attachment unit (Fig. S1). While maintaining high rigidity at a total weight of 5.5 g, the OwlCam delivered a black-and-white video signal at 30 frames per second with an effective vertical resolution of ~380 scan lines. The video signal was digitalized online and stored in a 640 × 480 pixel video format for further processing.

Using a custom-written algorithm, the raw video material was later divided into frame segments of image motion and nonmotion (6). Segments of consecutive frames in which no image motion occurred were defined as fixation intervals, and the middle frame of each interval was extracted and used as the fixation frame representing the whole interval. All subsequent processing steps were based on these fixation frames.

Each OwlCam was calibrated with respect to the relative geometric arrangement of camera field of view and the owl's gaze, to localize the owl's "functional fixation point" in camera frame coordinates (*Results*). In several calibration trials, a fixation map was constructed for each owl and OwlCam pair separately. Note that fixation maps are valid only for a specific owl–OwlCam pair, because of idiosyncratic differences of the owls' head post position, camera layout, and prealignment procedure. Based on this map, a single fixation spot relative to the camera frame coordinates was revealed, as described in detail elsewhere (6). In brief, during calibration, interesting bright targets scattered on a dark floor were presented (Fig. 1*B*). The owl typically scanned the environment by fixating one target and then making a saccade to another target, and so on. As more individual fixation frames were overlaid and averaged, a distinct circular-shaped fixation spot emerged for each owl (Fig. 1*C*). The resultant fixation map reflects the probability to encounter a bright target in camera frame coordinates. The fixation spot

itself indicates the image coordinates at which the owl would observe a bright target most often. Such a bright spot did indeed occur in the fixation map of each owl, at camera coordinates (335,322) for owl HB and (322,339) for owl WH. The diameter of the fixation spot was calculated as the mean width of the probability function at half height and was 26.71 pixels for owl HB and 22.41 pixels for WH (corresponding to 2.5° and 2.1° of visual angle, respectively). In quantitative terms, calibration targets appeared within the fixation spot in 94% ($n = 9,804$) of all fixations for owl HB and in 96% ($n = 10,662$) of all fixations for owl WH. Once determined, the fixation spot of each owl–OwlCam pair was used in the analysis of all video data. Note that the size of the fixation spot does not necessarily represent the actual size of the animal's retinal area of preferred fixation, because it is linked to the size of the calibration targets used. However, the calibration targets were set to have similar size as the bar objects used in our main experiments. After calibration, the fixation spot could be marked in each recorded fixation frame of the main experimental trials to serve as an estimate of where the owl was looking relative to the camera coordinates. This conclusion is possible with the barn owl, which virtually lacks eye movements (42, 43). Thus, the view of a properly aligned and fixed head camera is in register with the animal's gaze at all times.

Given the fixed relationship between the OwlCam and the owl's gaze, the individual fixation frames collected during our experimental trials were ego-centered and perspective-limited representations of the owl's view at a given time. To study the owls' viewing behavior as a consequence of the global visual stimulus, the complete visual scene had to be taken into account. However, to a good approximation, the fixation frames could be considered limited-view images of the same exterior setting observed from a specific vantage point at different viewing angles, resulting from the owl's head movements while keeping its body relatively fixed. Thus, a full-scene reconstruction was achieved by spatial transformation and alignment of the individual fixation frames to build a panoramic view of the entire scene as would be observed by a wide-angle observer at the vantage point (44). By mapping the coordinates of the spatially transformed loci of fixations in each single fixation frame to the corresponding coordinates in the full-scene panoramic image, global scan paths were created and analyzed. The owls' viewing behavior was then studied with respect to three main criteria: (*i*) relative and absolute gaze time spent at a specific location, (*ii*) relative and absolute number of fixations directed onto such locations, and (*iii*) number of head saccades performed until the locations were first looked at.

1. Yarbus AL (1967) *Eye Movements and Vision* (Plenum, New York).
2. Einhäuser W, Kruse W, Hoffmann K-P, König P (2006) Differences of monkey and human overt attention under natural conditions. *Vision Res* 46:1194–1209.
3. Mazer JA, Gallant JL (2003) Goal-related activity in V4 during free viewing visual search: Evidence for a ventral stream visual salience map. *Neuron* 40:1241–1250.
4. Cook RG, Cavoto KK, Cavoto BR (1996) Mechanisms of multidimensional grouping, fusion, and search in avian texture discrimination. *Anim Learn Behav* 24:150–167.
5. Blough DS (1977) Visual search in the pigeon: Hunt and peck method. *Science* 196:1013–1014.
6. Ohayon S, Harmening WM, Wagner H, Rivlin E (2008) Through a barn owl's eyes: Interactions between scene content and visual attention. *Biol Cybern* 98:115–132.
7. Dittrich L, Rose J, Buschmann J-UF, Bourdonnais M, Güntürkün O (2010) Peck tracking: A method for localizing critical features within complex pictures for pigeons. *Anim Cogn* 13:133–143.
8. Krummenacher J, Müller HJ, Deubel H, Wolfe JM, Humphreys GW (2010) Editorial: Visual search and selective attention. *Vision Res* 50:1301–1303.
9. Wolfe JM, Horowitz TS (2004) What attributes guide the deployment of visual attention and how do they do it? *Nat Rev Neurosci* 5:495–501.
10. Wolfe JM (1994) A revised model of visual search. *Psychon Bull Rev* 1:202–238.
11. Hochstein S, Ahissar M (2002) View from the top: Hierarchies and reverse hierarchies in the visual system. *Neuron* 36:791–804.
12. Treisman AM, Gelade G (1980) A feature-integration theory of attention. *Cognit Psychol* 12:97–136.
13. Lee TS, Yang CF, Romero RD, Mumford D (2002) Neural activity in early visual cortex reflects behavioral experience and higher-order perceptual saliency. *Nat Neurosci* 5:589–597.
14. Hegdé J, Felleman DJ (2003) How selective are V1 cells for pop-out stimuli? *J Neurosci* 23:9968–9980.
15. Nothdurft H-C, Pigarev IN, Kastner S (2009) Overt and covert visual search in primates: Reaction times and gaze shift strategies. *J Integr Neurosci* 8:137–174.
16. Mokeichev A, Segev R, Ben-Shahar O (2010) Orientation saliency without visual cortex and target selection in archer fish. *Proc Natl Acad Sci USA* 107:16726–16731.
17. Ohayon S, van der Willigen RF, Wagner H, Katsman I, Rivlin E (2006) On the barn owl's visual pre-attack behavior, I: Structure of head movements and motion patterns. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 192:927–940.
18. Johnen A, Wagner H, Gaese BH (2001) Spatial attention modulates sound localization in barn owls. *J Neurophysiol* 85:1009–1012.
19. Liu GB, Pettigrew JD (2003) Orientation mosaic in barn owl's visual Wulst revealed by optical imaging: Comparison with cat and monkey striate and extra-striate areas. *Brain Res* 961:153–158.
20. Pettigrew JD, Konishi M (1976) Neurons selective for orientation and binocular disparity in the visual Wulst of the barn owl (*Tyto alba*). *Science* 193:675–678.
21. Mysore SP, Asadollahi A, Knudsen EI (2010) Global inhibition and stimulus competition in the owl optic tectum. *J Neurosci* 30:1727–1738.
22. Reches A, Gutfreund Y (2008) Stimulus-specific adaptations in the gaze control system of the barn owl. *J Neurosci* 28:1523–1533.
23. Zahar Y, Reches A, Gutfreund Y (2009) Multisensory enhancement in the optic tectum of the barn owl: Spike count and spike timing. *J Neurophysiol* 101:2380–2394.
24. Harmening WM, Göbbels K, Wagner H (2007) Vernier acuity in barn owls. *Vision Res* 47:1020–1026.
25. Harmening WM, Nikolay P, Orlowski J, Wagner H (2009) Spatial contrast sensitivity and grating acuity of barn owls. *J Vis* 9:1–12.
26. Nieder A, Wagner H (1999) Perception and neuronal coding of subjective contours in the owl. *Nat Neurosci* 2:660–663.
27. Wagner H, Frost B (1993) Disparity-sensitive cells in the owl have a characteristic disparity. *Nature* 364:796–798.
28. Wathey JC, Pettigrew JD (1989) Quantitative analysis of the retinal ganglion cell layer and optic nerve of the barn owl *Tyto alba*. *Brain Behav Evol* 33:279–292.
29. Oehme H (1964) Vergleichende untersuchungen an greifvogelaugen. *Z Morphol Oekol Tiere* 53:618–635.
30. van der Willigen RF, Harmening WM, Vossen S, Wagner H (2010) Disparity sensitivity in man and owl: Psychophysical evidence for equivalent perception of shape-from-stereo. *J Vis* 10:1–11.
31. Mebs T, Scherzinger W (2000) *Die Eulen Europas: Biologie, Kennzeichen, Bestände* (Franckh-Kosmos, Stuttgart).
32. Ilany A, Eilam D (2007) Wait before running for your life: Defensive tactics of spiny mice (*Acomys cahirinus*) in evading barn owl (*Tyto alba*) attack. *Behav Ecol Sociobiol* 62:923–933.
33. Supèr H, Spekreijse H, Lamme VA (2001) Two distinct modes of sensory processing observed in monkey primary visual cortex (V1). *Nat Neurosci* 4:304–310.
34. Kastner S, Nothdurft HC, Pigarev IN (1997) Neuronal correlates of pop-out in cat striate cortex. *Vision Res* 37:371–376.
35. Hubel DH, Wiesel TN (1977) Ferrier Lecture: Functional architecture of macaque monkey visual cortex. *Proc R Soc Lond B Biol Sci* 198:1–59.
36. Rockland KS, Lund JS (1982) Widespread periodic intrinsic connections in the tree shrew visual cortex. *Science* 215:1532–1534.
37. Ben-Shahar O, Zucker S (2004) Geometrical computations explain projection patterns of long-range horizontal connections in visual cortex. *Neural Comput* 16:445–476.
38. Jarvis ED, et al.; Avian Brain Nomenclature Consortium (2005) Avian brains and a new understanding of vertebrate brain evolution. *Nat Rev Neurosci* 6:151–159.
39. Nieder A, Wagner H (2001) Hierarchical processing of horizontal disparity information in the visual forebrain of behaving owls. *J Neurosci* 21:4514–4522.
40. Blough D (1992) *Cognitive Aspects of Stimulus Control*, eds Honig WK, Fetterman G (Psychology Press, Lawrence Erlbaum Associates, Inc., Hillsdale, NJ), p 456.
41. Bachmann T, et al. (2007) Morphometric characterisation of wing feathers of the barn owl *Tyto alba pratincola* and the pigeon *Columba livia*. *Front Zool* 4:23.
42. Steinbach MJ, Money KE (1973) Eye movements of the owl. *Vision Res* 13:889–891.
43. du Lac S, Knudsen EI (1990) Neural maps of head movement vector and speed in the optic tectum of the barn owl. *J Neurophysiol* 63:131–146.
44. D'Angelo P (2010) Hugin. Available at http://hugin.sourceforge.net/. Accessed March 16, 2010.

Supporting Information

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SI Materials and Methods

The OwlCam is a lightweight microcamera combined with a video broadcasting board, cast into a customized frame of dental cement (Fig. S1 *A–F*). Its small size and rigid physical properties allow its use in small animals (e.g., rats, mice, birds) to provide a genuine first-person view of the animal's visual field. The individual parts, detailed below, are all off-the-shelf. The total cost of one OwlCam unit is ~150 Euro.

The camera unit consists of a 1/4-inch complementary metal-oxide semiconductor active pixel sensor (purchased from http://www.microcameras.com) equipped with an objective lens and adjustable focus. The vertical resolution is ~380 lines, and the horizontal field of view is ~60°. The camera's outer dimensions are $8 \times 8 \times 10$ mm, and the weight without cables is 1 g. Power intake is specified at 7–12 V DC, 30 mA, but the camera operates at a lower voltage. The camera comes with a cable connector with built-in step-down converter to accommodate typical power supplies, such as a 9V battery. We have good experience with the considerablly lower 3.7 V delivered by a single lithium polymer cell if the converter is discarded. If low overall weight is a goal, all cable pieces can be unsoldered from the camera. The cable consists of three individual strands sheathed in a rubber coating. Although the coating can be discarded, the strands should be kept for later use, because the enameled copper wire type is light and relatively easy to solder (Fig. S1*A*).

The camera unit was wired to a 900-MHz video broadcasting board (transmitter), which can be easily obtained by dismantling a low-cost "spy camera" available at many online stores. Typically, these cameras also come with a receiver unit (Fig. S1*E*). If more than one camera is used with a single receiver, care must be taken to ensure that the receiver is either tunable or has shiftable discrete frequency settings. Usually, the broadcasting unit can transmit an audio signal as well if necessary. Video and power connections are made by soldering copper strands to the camera and transmitter board at a short distance. Solder contacts and the back surface of the camera and the transmitter are then covered with a fluid rubber coating (PlastiDip) to prevent current leakage and to improve durability. Power connectors can be custom made from spare cascadable IC pins (Fig. S1 *A and D*). The antenna of the broadcast unit is cut to an arbitrary length, because the transmission range is relatively small and antenna length is not critical.

The entire setup is cast into dental cement (Paladur, Heraeus) to fix the physical layout of the camera and also provide the custom-made mounting socket. The mounting socket slides onto a small metal plate implanted into the owl's forehead. The camera's field of view must be prealigned before casting. The dental cement and rubber coating increase the unit's overall rigidity and durability, making the OwlCam easy to handle, especially in difficult situations while equipping the animal (Fig. S1*B*). The weight of the setup without batteries is 3 g. A lithium-polymer rechargeable battery (LiPo; Tenergy) is used to power the OwlCam at 3.7 V. The battery is mounted to the OwlCam by taping it to the long side of the camera (Fig. S1*C*). The choice of battery capacity governs the total weight of the setup, with a 70-mAh cell weighing ~2.5 g and a 25-mAh cell weighing ~0.9 g (Fig. S1*D*). The lifetime of a fully charged 70-mAh LiPo battery is ~145 min of constant recording, and that of the 25-mAh battery is ~45 min.

One of our goals in this study was to miniaturize the original camera setup developed in an earlier work (1), as shown in Fig. S1*F*. The total weight of the original setup was 29 g, and some animals displayed a noticeable change in behavior (in particular, head shaking and forward inclination of the head) while wearing the device. No behavioral changes were observed with the new setup, and the same video quality and transmission range were obtained at a fraction of the original total weight. The latest prototype involves a custom-designed transmitter board and reduces weight by another 1 g. With the 25-mAh LiPo battery, this setup has a total weight of <3 g, all other things being equal (Fig. S1*C*).

1. Ohayon S, Harmening WM, Wagner H, Rivlin E (2008) Through a barn owl's eyes: Interactions between scene content and visual attention. *Biol Cybern* 98:115–132.

Fig. S1. OwlCam details. See text for explanation. (*A*) Overview of the setup. (*B*) The setup is light, small, rigid, and easy to handle. (*C*) The current setup (*Right*) next to a recent prototype. (*D*) Rechargeable LiPo batteries serve as the power source. (*E*) Low-cost 900-MHz tunable receiver. (*F*) Size comparison of the earlier model (*Left*) and the current model.

Movie S1. Sample video sequence recorded from an OwlCam during a single experimental trial. (The scan path from this trial is also shown in Fig. 2*B*.) The fixation spot location is denoted by a red circle overlay. Note the typical short sequences of image motion, which are a consequence of head saccades, and longer periods of frames without motion, which are fixations.

[Movie S1](#)