Visual search in barn owls: Task difficulty and saccadic behavior

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How do we find what we are looking for? A target can be in plain view, but it may be detected only after extensive search. During a search we make directed attentional deployments like saccades to segment the scene until we detect the target. Depending on difficulty, the search may be fast with few attentional deployments or slow with many, shorter deployments. Here we study visual search in barn owls by tracking their overt attentional deployments—that is, their head movements—with a camera. We conducted a low-contrast feature search, a high-contrast orientation conjunction search, and a low-contrast orientation conjunction search, each with set sizes varying from 16 to 64 items. The barn owls were able to learn all of these tasks and showed serial search behavior. In a subsequent step, we analyzed how search behavior of owls changes with search complexity. We compared the search mechanisms in these three serial searches with results from pop-out searches our group had reported earlier. Saccade amplitude shortened and fixation duration increased in difficult searches. Also, in conjunction search saccades were guided toward items with shared target features. These data suggest that during visual search, barn owls utilize mechanisms similar to those that humans use.

Introduction

Effective vision depends on the ability to segregate important information from an often-cluttered scene—for example, the search for a target in a background containing many other items, the *distracters*. Humans and animals achieve effective vision by a variety of so-called *(visual) search modes*. Since most of the research has been conducted with humans, in the following we shall dwell on results from human cognitive psychology to explain the general principles of visual search, before we turn to solutions found in the animal kingdom and especially our experimental animal, the barn owl (*Tyto furcata pratincola*).

A typical visual-search task is to detect the target amongst distracters as fast as possible. This is not easy, because the visual environment usually contains more information than can be processed in a reasonable time (Tsotsos, 1990). This problem is mitigated by attentional processes, which select a small subset of the scene to be processed at a given time—usually the contents of the high-resolution fovea (Eckstein, 2011; Goldsmith, 1998). Thus, visual search is closely linked to attention. The speed of a search depends on the conspicuity of the target. This conspicuity is called *saliency* (Wolfe & Horowitz, 2004). Target saliency depends on the perceived differences between the target and the distracters as well as between the target and the background (Nothdurft, 2015). If saliency is high, we can detect a target almost instantly—it pops out; search time does not depend on the number of distracters. Classically, this search mode is called *parallel* (Treisman & Gelade, 1980). If, however, the difference from the distracters decreases or the distracters get more heterogeneous, search becomes more difficult (Duncan & Humphreys, 1989). In such situations, the target is found by serially inspecting the scene. This increases search time. The slope of the function that relates search time to set size (target plus number of distracters) is a means to describe the difficulty of a search (Treisman & Gelade, 1980; Wolfe, 2016). In humans, easy, parallel searches have search slopes of

nearly zero (Wolfe & Horowitz, 2004). This is usually the case if a target is defined by a single feature, such as orientation. In most other cases, searches are serial. In particular, in conjunction search the target consists of a unique combination of the two features, which decreases target saliency compared to single-feature searches. However, not all conjunction searches are serial searches (Theeuwes & Kooi, 1994); in a similar way, some feature searches have quite steep slopes (Treisman & Gormican, 1988; Wolfe & Horowitz, 2004). One reason for this is that attention may be restricted to items sharing any features with the search target, or to a specific feature only (Shen & Paré, 2006).

In addition to the different search modes and their characterization by search time, an interesting question is how the search is performed by the subjects from a mechanistic point of view. This question may be tackled by tracking eye movements. In this way, we get insights into overt search mechanisms by analyzing saccades and fixations during searching. Human studies show a decrease in average saccade amplitude and an increase in fixation duration with increasing search complexity (Vlaskamp, Over, & Hooge, 2005), likely due to increasing top-down guidance—that is, behavioral goals (Stritzke, Trommershäuser, & Gegenfurtner, 2009).

In recent years, knowledge about visual search and its underlying neural mechanisms has extended from primates (Balan, Oristaglio, Schneider, & Gottlieb, 2008; Bichot & Schall, 1999; Chelazzi, Miller, Duncan, & Desimone, 1993; Ipata, Gee, Gottlieb, Bisley, & Goldberg, 2006) to nonprimate species. For instance, visual search has been studied in rats (Botly & De Rosa, 2012), pigeons (Blough, 1979), archerfish (Ben-Tov, Donchin, Ben-Shahar, & Segev, 2015; Rischawy & Schuster, 2013), and barn owls (Harmening, Orlowski, Ben-Shahar, & Wagner, 2011; Ohayon, Harmening, Wagner, & Rivlin, 2008; Orlowski et al., 2015). In our experiments with barn owls, employing a paradigm of overt attention, we have already shown that barn owls are attracted to salient locations as assessed with a bottom-up computational model (Itti & Koch, 2001; Ohayon et al., 2008). In a free-viewing task with elongated items, one of which (the target) was differently oriented from the others (the distracters), naïve barn owls fixated the target faster, longer, and more often than a randomly chosen distracter (Harmening et al., 2011). When barn owls were explicitly trained to search for the target, we could demonstrate a pop-out effect—that is, their search time was largely independent of set size in two feature searches for luminance contrast and for orientation (Orlowski et al., 2015).

In the following, we build upon these findings and examine how barn owls perform in searches that have been shown to be more difficult in humans: a low-luminance-contrast feature search and two conjunction searches. We first demonstrate that barn owls can learn these tasks and that the tasks are indeed more difficult for barn owls as well than are the simpler feature searches we studied before. Furthermore, we show that the overt search mechanisms employed by the barn owls are strikingly similar to ours.

Methods

All experiments were conducted with two American barn owls (subjects WH and HB), taken from the breeding colony of the Department of Zoology at RWTH Aachen University. Both animals were hand raised and tame. Experiments were conducted under a permit issued by the Landespräsidium für Natur, Umwelt und Verbraucherschutz Nordrhein Westfalen, Recklinghausen, Germany. During experiments the owls' body weight was kept at about 90 percent of their free-feeding weight (420 and 480 g). The birds were rewarded with pieces of chicken meat. After an experiment, they were fed with additional chicken meat to maintain body weight irrespective of behavioral performance. The owls participated in experiments 5–6 days a week, approximately 2 hours per day, and were fed in their aviaries when no experiment was conducted. No attempt was made to reverse their nocturnal cycle. Both owls had a small brass head post fixed to their skulls, to which the OwlCam could be affixed during experiments. This head post was put on the skull under anesthesia before the experiments started (for details of the anesthesia, see Vonderschen and Wagner, 2009).

Setup and experimental procedure

The experimental procedures and the basic setup were mostly unchanged from Orlowski et al. (2015). Briefly: We tracked overt attention of barn owls by recording first-person-view videos via the head-mounted OwlCam in three different experiments. The tracking of head movements is adequate for studying gaze in these birds, because eye movements are very small (Steinbach & Money, 1973). In these experiments the birds were confronted with rectangular arrays of 16, 25, 36, 49, or 64 items placed on the ground, containing a unique target item and several distracters.

The size of the experimental chamber was $545 \times 405 \times 265$ cm (length, width, height). Its walls were coated with pyramidal foam for sound attenuation. The owls were placed on a perch near the shorter wall at 200 cm height. Between experimental trials, an opaque retractable curtain was lowered in front of the perch to

block the animal's view. All items were cut from cardboard and placed on a dark-gray background. Experiment 1 (e1) was a luminance-contrast feature search. There were two types of items, the unique target and the single class of distracters. The items were circles of 5 cm radius, with the target being gray (low background contrast) and the distracters white (high background contrast). Experiments e2 and e3 were conjunction searches. These consisted of four sets of rectangular bar-like items measuring 15×5 cm: the unique target and three distracter classes each containing about 33% of all array items. In e2 the target was white and oriented at 45°. The distracters were either gray and oriented at 45°, white and oriented at 0°, or gray and oriented at 0°. Since the white target had a high contrast compared with the background, we shall refer to this task as *high-contrast conjunction search*. Experiment e3 was designed to be a more difficult conjunction search using the same item categories as in e2 with the following exception: The target was gray and oriented at 0°, and the third distracter class was white and oriented at 45°. Since the gray target had a low contrast compared with the background, we shall refer to this task as *low-contrast conjunction search*. To avoid edge effects, the target item never appeared at the borders of the arrays. Interitem distance was kept constant at 15 cm except for a small positional jitter. Thus, the visual angle subtended by the array as seen from the resting position of the owl changed from an average of $30° \times 15°$ with 16 items to $55° \times 30°$ with 64 items.

Prior to each experiment, the owls were trained for at least a month to search for the respective target item by placing food items onto it. Each single trial was conducted as follows: The owl was placed on the perch behind the curtain. Then the array was arranged on the ground by the experimenter. The curtain was retracted in darkness. After a short interval (5–10 s), the experimenter started the trial by switching on the light again. No cue was provided prior to stimulus onset, and the owls were not trained to fixate a specific location. The owls were completely unrestrained and could behave as they pleased during a trial, with individual trials lasting up to 3 min or until the owls flew from the perch. If the owls flew toward the target, they would get a food reward. The behavior of the owl was video-recorded for later analysis, one video for each trial. In the following, we shall use "number of videos" and "number of trials" interchangeably. Up to 15 trials per day were performed in this way with each owl; three or four of these were reinforcement trials, with food placed on the target item to keep the owl under stimulus control. Overall, the experimentation period for the three experiments lasted 129 days for 940 trials, not counting training (between 1 and 3 months for each experiment) and reinforcement trials.

Video and data analysis

The videos were analyzed with a custom-written semiautomated MATLAB program described in detail by Orlowski et al. (2015). Briefly, each video was segregated into fixations and saccades. Single fixations were stitched together to create a panoramic view of the scene from the owl's vantage point. 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, we created global scan paths to analyze. In separate calibration experiments we determined each owl's functional fixation spot in the OwlCam's field of view, an approximately 1° wide area corresponding to the owl's "foveal region" (Hazan, Kra, Yarin, Wagner, & Gutfreund, 2015). Each fixation was then classified according to the content of the owl's fixation spot. We first discriminated between inside fixations (array visible) and outside fixations (array not visible). An inside fixation was termed a *target fixation* if the fixation spot touched the target item; otherwise, it was an *array fixation*. An array fixation was termed a *distracter fixation* if the fixation spot touched a distracter item. This discrimination allowed us to calculate the ratio of target fixations to inside fixations and to judge whether the owls fixated the target above chance level. Chance level was calculated as 1 divided by the set size. Note that this calculation is an upper bound for—or conservative measure of—chance level, because it assumes that all inside fixations are either target fixations or distracter fixations, and that no fixations occurred between items or outside the array (but with the array visible). The analysis tools allowed for extraction of the time course, the spatial position of each fixation, and the content of the owl's fixation spot.

This information was used to analyze the first 60 s of each video to study the owl's viewing behavior with respect to several criteria (Figure 1). To measure saliency and training success we looked at the proportion of fixations directed at the target. To determine search difficulty of the experiments we measured search time, error rate, and number of saccades until the target was first fixated. These data were then compared to the pop-out experiments from a previous publication (Orlowski et al., 2015). Finally, we investigated the search mechanisms to understand how owls search for a target. For that, we looked at fixation durations, saccade amplitudes, and the sequence of fixations in each trial.

Unless stated otherwise, we used the following statistical analyses available as functions in MATLAB: Data groups were analyzed using the Kruskal–Wallis test to test for significant difference. In the case of significance, we employed a Bonferroni post hoc adjustment to compensate for multiple comparisons.
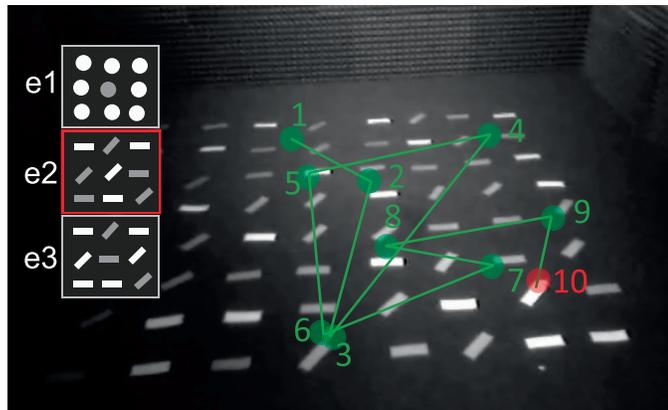
Figure 1. Fixations and gaze path of a single conjunction search trial of e2. Fixations are numbered and superposed on a fixation image from the owl's point of view taken from OwlCam video. The target is detected with the last fixation displayed here (Fixation 10). Inset shows sketches of the stimuli for e1 through e3 (note that the targets are always in center of the sketches).

To test for individual differences between two data sets we used the Wilcoxon signed-rank test.

Results

Data overview

The three sets of experiments on visual search of barn owls reported here extend the findings of pop-out perception in barn owls reported earlier by our group (Orlowski et al., 2015). These new experiments are considered more difficult for human subjects than the experiments we previously reported; we assumed that this would also be the case for barn owls. The experiments were a low-luminance-contrast feature search (target gray and distracters white, e1) and two luminance-orientation-conjunction searches. In the first conjunction search, the target was high-contrast white and slanted 45° (e2). In the second conjunction search, the target was low-contrast gray and not slanted (e3). The background was dark gray in all cases. We recorded a total of 940 videos across the three experiments.

An example of a fixation sequence

A typical trial of e2 is visualized in Figure 1. After the lights were switched on, the owl oriented itself toward the array. The first fixation in which the array was visible in the video was used as starting fixation (Fixation 1 in Figure 1). The behavior of the owl was analyzed for 1 min after this initial fixation, or shorter
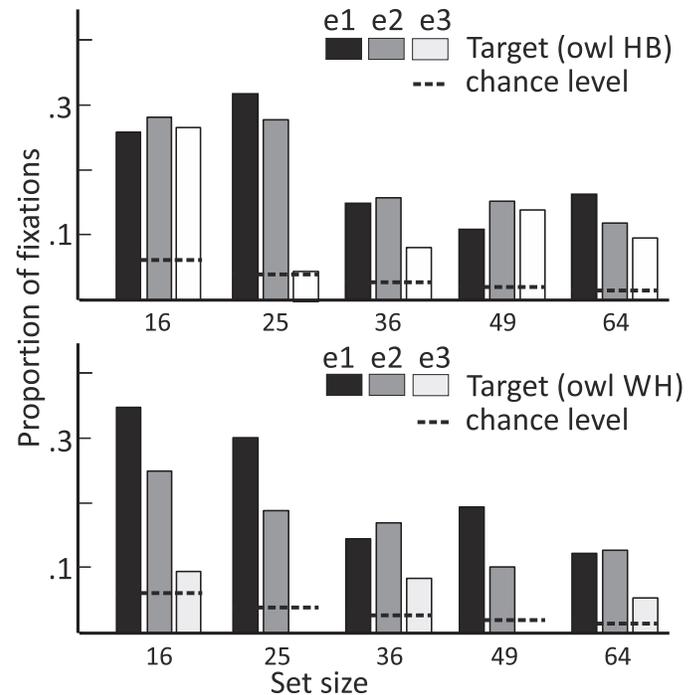

Figure 2. Proportion of fixations. The proportion of target fixation was calculated as the ratio of target fixations to inside fixations. The black dashed line shows the expected proportion of fixations on a random item for each array size, calculated as 1/set size. Data from owl HB are based on 1,634/3,487/1,737 (e1/e2/e3) fixations in 118/221/141 videos; data from owl WH are from 994/2,015/2,261 fixations in 136/217/107 videos.

if the owl stopped the trial by flying from its perch. During the trial, the owl searched by sequentially inspecting several items (1–10 in Figure 1). Note that in this trial, no outside fixations occurred. Fixation duration and saccade amplitude could differ from each gaze shift to the next. For example, the path from Fixation 1 to Fixation 2 is shorter than the path from Fixation 3 to Fixation 4 (Figure 1). If the target was fixated (10 in Figure 1), the owl could either fly toward the target or continue inspecting the array and possibly return to fixate the target at some later point in time. In any case, the first target fixation was used to calculate search time and number of saccades until target detection. Thus, in the search sequence shown in Figure 1, the number of saccades until target detection was nine.

Fixation analysis: Barn owls can do conjunction search

We analyzed the fixations to find out whether the owls could successfully detect the target in the arrays (Figure 2). The results of e1 are based on the analysis of 254 videos. Over the course of approximately 3.5 months, owl WH participated in 136 single experiments with each set size consisting of at least 21 (maximum

32) videos. Owl HB took part in 118 trials, ranging from 20 to 26 videos per set size, conducted over approximately 1.5 months of experimentation. To measure target saliency as perceived by the owls, the proportion of target fixations compared to inside fixations was analyzed. This ratio decreased in both owls from 0.27/0.35 (owl HB/owl WH; this denomination is kept throughout the following) at set size 16 to 0.16/0.13 at set size 64 (Figure 2). Even though these ratios are much lower at set size 64, they are still far above chance level (1/set size)—that is, above 0.06 (set size 16) or 0.02 (set size 64).

In e2 the owls performed a total of 438 trials (HB: 221 trials, 39–52 trials per set size; WH: 217 trials, 38–50 trials per set size), recorded over the course of approximately 2 months each. The ratio of target fixations to all array fixations decreased, too. It was 0.29/0.25 at set size 16 and 0.12/0.13 at set size 64 (Figure 2).

A total of 248 videos were recorded in e3 (HB: 141 trials, 23–33 trials per set size; WH: 107 trials, 33–40 trials per set size). Owl HB conducted experiments at all five set sizes in about a month, while owl WH could only conduct trials at three set sizes—16, 36, and 64—in the span of 4 months (Figure 2). Again, the overall ratio of target fixations decreased from 0.27/0.10 at set size 16 to 0.10/0.05 at set size 64. Both owls fixated the target in e3 least often, with the exception of set size 49 for owl HB (Figure 2).

Target fixation rate was always quite high at small set sizes and decreased at larger set sizes. However, in all experiments and set sizes the target was fixated well above chance level. We concluded from these results that both owls were able to learn to find target objects of no direct behavioral relevance even in conjunction searches. However, the lengthy time period in which data was collected indicated that these tasks were difficult for the animals, especially for owl WH.

Search performance: Serial search in barn owls

The classic approach to measuring search performance is to determine the slope of the function of search time versus set size (Treisman & Gelade, 1980; Wolfe, 2016). While there is no clear threshold for transition between search modes, search slopes near zero are considered to be a sign of easy search tasks, and larger slopes of difficult tasks. In the following, we use search time to examine search difficulty, but we also track the number of saccades until the target is first fixated as a measure of separate overt attentional deployments during a search, and we calculated error rate. Search time, number of saccades, and error rates increased distinctively with set size in all three experiments and for both animals (Figure 3).

In e1, the two owls fixated the target on average across all set sizes after 3.38 ± 0.38 saccades (HB) and 2.57 ± 0.24 saccades (WH). In both animals the number of saccades until target detection increased from set size 16 (2.24 ± 0.55/1.37 ± 0.25) to set size 64 (4.75 ± 0.88/2.73 ± 0.41). Search time increased from 4.7 ± 1.7 s at set size 16 to 12.2 ± 2.6 s at set size 64 for owl HB, and from 5.1 ± 1.3 s to 8.8 ± 1.5 s for owl WH.

In e2, the target was fixated on average after 4.22 ± 0.39/4.15 ± 0.30 saccades, increasing from set size 16 to 64 (HB: 1.90 ± 0.20 to 6.35 ± 0.95; WH: 2.76 ± 0.35 to 5.32 ± 0.54). Search time increased from 3.0 ± 0.7 s/ 5.3s ± 0.9 s at set size 16 to 12.5 ± 2.0/10.3 ± 1.3 s at set size 64.

The slopes were largest in e3: The average saccade count was 5.02 ± 0.63/5.93 ± 0.54, increasing from 1.95 ± 0.35 to 9.89 ± 1.63 for owl HB and from 3.93 ± 0.56 to 8.89 ± 1.17 for owl WH. The same is evident for search time: HB's time increased from 3.3 ± 1.7 s at set size 16 to 20.1 ± 3.3 s at set size 64, and WH's from 11.4 ± 2.3 s to 25.0 ± 3.3 s for owl WH (Figure 3).

So, both number of saccades and search time showed similar effects: Small differences between experiments occurred for small set sizes, and the differences increased for larger set sizes. For example, it is clearly evident that target detection and fixation takes more time in e3 than in the other experiments at set size 64.

Search time is considered the main indicator of search performance (Treisman & Gelade, 1980). Another parameter of interest is error rate (Verghese, 2001). In human experiments, trials are usually split between two conditions: target-present trials with a target and target-absent trials with only distracters. Subjects decide between these two and sometimes make mistakes depending on search difficulty. Here, we tested the owls only in the target-present condition. However, the owls did not always complete the task; they sometimes aborted the search before fixating the target. We used the number of trials in which the target was not fixated at all as a proxy for target-absent trials and calculated the error rate from those trials. In e1, the target was not detected in 15.6%/15.8% of the trials at set size 16. With 64 items this rate was similar in HB, at 16.6%, while owl WH missed the target in more than half of the trials (53.1%). In e2 both owls showed an increase from 0%/11.4% at set size 16 to 29.6%/30.8% at set size 64. The outcome of e3 was similar to that of e2, but with a higher error rate: 18.5%/32% at 16 items and 37.5%/45.5% at 64.

To summarize these results, number of saccades, search time, and error rate all increased with set size, indicating that the owls employed a serial search mode in e1 through e3. Also, these three factors differed between experiments, increasing from e1 to e3—with the exception of owl WH's error rate in e1.
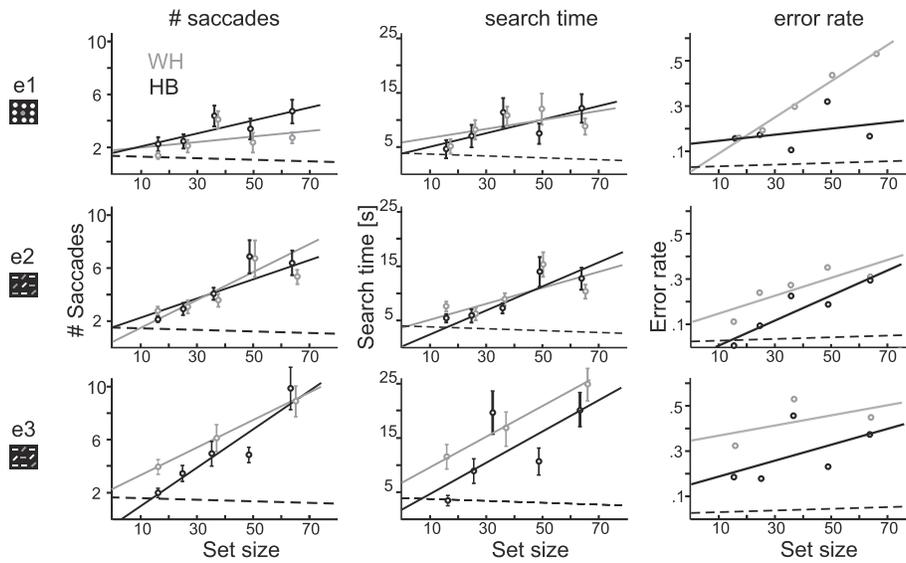
Figure 3. Search performance. The left column shows the number of saccades until target detection, the middle column the search time until detection, and the right column the error rate, all as a function of set size. The insets at the left side show a scheme of each stimulus type, with the target in the center. The upper row shows results from e1 (254 videos), the second row e2 (438 videos), and the bottom row e3 (248 videos). The dots are the average over all trials for each set size (21–52 trials per set size), error bars denote standard error of the mean, and lines are the linear best fits to the data for each owl. These are, for saccades, e1 (HB): $y = 0.05x + 1.73$, $R^2 = 0.84$; e1 (WH): $y = 0.02x + 1.76$, $R^2 = 0.39$; e2 (HB): $y = 0.11x + 0.42$, $R^2 = 0.93$; e2 (WH): $y = 0.07x + 1.53$, $R^2 = 0.83$; e3 (HB): $y = 0.15x + 0.55$, $R^2 = 0.93$; e3 (WH): $y = 0.10x + 2.30$, $R^2 = 1.00$. For search time, they are e1 (HB): $y = 0.12x + 4.30$, $R^2 = 0.72$; e1 (WH): $y = 0.08x + 5.76$, $R^2 = 0.60$; e2 (HB): $y = 0.22x + 0.00$, $R^2 = 0.92$; e2 (WH): $y = 0.15x + 3.57$, $R^2 = 0.73$; e3 (HB): $y = 0.29x + 1.70$, $R^2 = 0.76$; e3 (WH): $y = 0.28x + 6.65$, $R^2 = 1.00$. For error rate, they are e1 (HB): $y = 0.001x + 0.13$, $R^2 = 0.32$; e1 (WH): $y = 0.008x + 0.01$, $R^2 = 0.99$; e2 (HB): $y = 0.005x - 0.05$, $R^2 = 0.92$; e2 (WH): $y = 0.004x + 0.11$, $R^2 = 0.83$; e3 (HB): $y = 0.003x + 0.17$, $R^2 = 0.5$; e3 (WH): $y = 0.002x + 0.35$, $R^2 = 0.55$. The dashed line shows results conducted with the same owls from a pop-out search (high luminance-contrast search) as previously published (Orlowski et al., 2015). All functions have a distinct slope, which increases from e1 to e3, indicating an increase in search difficulty from e1 to e3.

Comparison of the new and earlier data

To provide a broader context of owl visual-search performance we directly compared the outcomes of e1 through e3 with data from Orlowski et al. (2015; see our Figure 4). There, two pop-out experiments were conducted: a high-contrast feature search (i.e., target white, distracters gray, and background dark gray; p1) and an orientation feature search (p2). All five experiments were conducted in the same setup, with the same animals and the same overall contrast conditions. Data from both owls were combined for the comparison, and data for search time and saccade number were plotted as a function of set size, resulting in one function each. The resulting functions for saccades were

p1: $y = -0.00x + 1.72$
p2: $y = 0.01x + 3.24$
e1: $y = 0.04x + 1.61$
e2: $y = 0.09x + 0.96$
e3: $y = 0.12x + 0.86$.

For search time they were

p1: $y = -0.01x + 3.75$
p2: $y = 0.01x + 8.08$
e1: $y = 0.11x + 4.59$
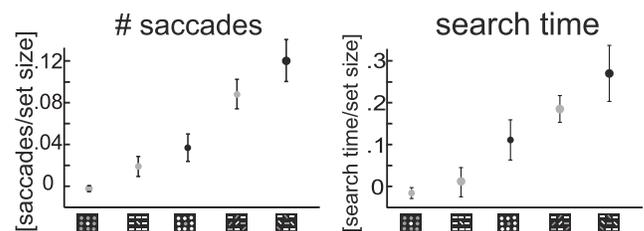e2: $y = 0.19x + 1.67$
e3: $y = 0.27x + 3.69$.

Figure 4. Search slopes. Data from e1 through e3 and two feature searches p1 and p2 (see Orlowski et al., 2015). Search slopes are for the five experiments, combined for both animals. Dots are the slopes, error bars are standard deviations (created with the MATLAB tool Aoctool). Sketches are in the following order: p1, p2, e1, e2, e3. Targets are in the center of the sketches.

The slopes increased from p1 (saccades [S]: 0.00; search time [ST]: −0.01) and p2 (S: 0.01; ST: 0.01) to e1 (S: 0.04; ST: 0.11), e2 (S: 0.09; ST: 0.19), and e3 (S: 0.12; ST: 0.27) for both measures. In other words, search slopes were close to zero in the two pop-out experiments, while they nearly doubled from e1 to e2 and tripled from e1 to e3.

We also compared the data sets with respect to error rate. For this comparison we used only the largest set size (64), because possible effects are expected to be most visible there. In p1, the average error rate at set size 64 was 3.8%, while in p2 it was 24.6%. The corresponding values for the new experiments were 34.9% in e1, 30.2% in e2, and 41.5% in e3. Thus, the average error rates in the serial search tasks were higher than those in the parallel search tasks.

To conclude, of the five experiments the high-contrast feature search (p1) had the lowest saccade number, search slope, and error rate. If the target and distracters swapped their feature properties (e1), the search turned into a serial search with higher saccade number and error rate, especially at large set sizes. Orientation feature search (p2) resulted in nearly no search slope, but the average saccade number and the error rate were much higher than in p1. The first conjunction search (e2) was constructed from the target features of p1 and p2, with the target having a high contrast. Search slope, saccade number, and error rate increased compared with respect to p1 and e1. The second conjunction search (e3) was constructed from p2 and e1; it contained a low-contrast target. This further increased the value of all factors compared to e2, making it the most difficult search.

How is the search conducted?

We have shown so far how barn owls perform in five different search tasks: two pop-out searches and three serial searches. The OwlCam's gaze tracking allowed us to go beyond immediate measures and investigate the visual behavior of the animals during the two different search modes. We specifically asked two questions: (a) Which items or locations did the birds inspect during visual search? (b) Was their gazing behavior influenced by search difficulty?

Since saccade amplitude is linked to array size, and since differences between the five searches manifest themselves mostly at large set sizes, the following will be based on the two largest set sizes—49 and 64 items—pooled together. We discriminated between search and nonsearch conditions to investigate whether the owls change their typical behavior during search. Search behavior consisted of all saccades and fixations before target detection. After the target was first fixated, the owls would often continue to inspect the scene; the saccades occurring after the target was first fixated were considered as typical, nonsearch, behavior. This comparison showed that saccade amplitude stayed at similar levels across search conditions compared to nonsearch situations in the same settings (Figure 5A). However, differences between the pop-out and serial searches occurred in the search phase. On average, saccades in pop-out conditions were larger than in serial searches (15.85° vs. 12.73°; $p < 0.00$, Wilcoxon signed-rank test). This was especially apparent in the final saccade before target detection (14.90° vs. 10.66; $p < 0.00$). When compared individually, both owls showed the same trend. However, on average in all search conditions, owl HB tended to make shorter saccades than owl WH (11.66° vs. 16.29°; $p < 0.00$, Figure 5B, 5C). Compared to the nonsearch situation, fixation durations during search decreased by nearly 50% (Figure 5D). Also, fixations in easy searches tended to last for a shorter time than those in difficult searches (1.27 s vs. 1.95 s; $p < 0.00$). In both cases, fixations were shortened if the target was detected during the fixation and the owl performed a saccade to the target (1.18 s vs. 1.77 s). Individually, owl HB's fixations were shorter on average than WH's (1.54 s vs. 1.99 s; $p < 0.00$). Both were about half the duration in the easiest search task (p1: 0.88 s/1.20 s) compared to the most difficult search task (e3: 2.00 s/2.14 s; Figure 5E, 5F). The difference was not so clear for the other experiments, specifically for owl WH. However, it has to be noted that, regarding fixation duration and saccade amplitude, experiment p2 for owl WH is more in line with the serial searches than with e1. For owl HB there were also similar differences between p1 and p2; however, p2 was shorter in duration and larger in amplitude than the serial searches.

Feature guidance

Four sets of items were used in the conjunction search experiments (e2 and e3): the unique target and three distracter classes each containing about 33% of all array items. Of these, two classes shared one feature and one class shared no features with the target. We analyzed which item the owls fixated after the first saccade in each experiment to see whether barn owls are guided by the target's features. In e2, both owls seemed to ignore the unshared-feature distracter type. Only 15%/18% of the saccades were directed at these items (Figure 6). Comparing luminance-sharing and orientation-sharing items, no difference between the classes was evident. This was different in e3: Here, the two owls used different strategies for their initial fixations. Both avoided the no-shared-feature distracters, but they were attracted to different distracter types. Owl HB preferentially
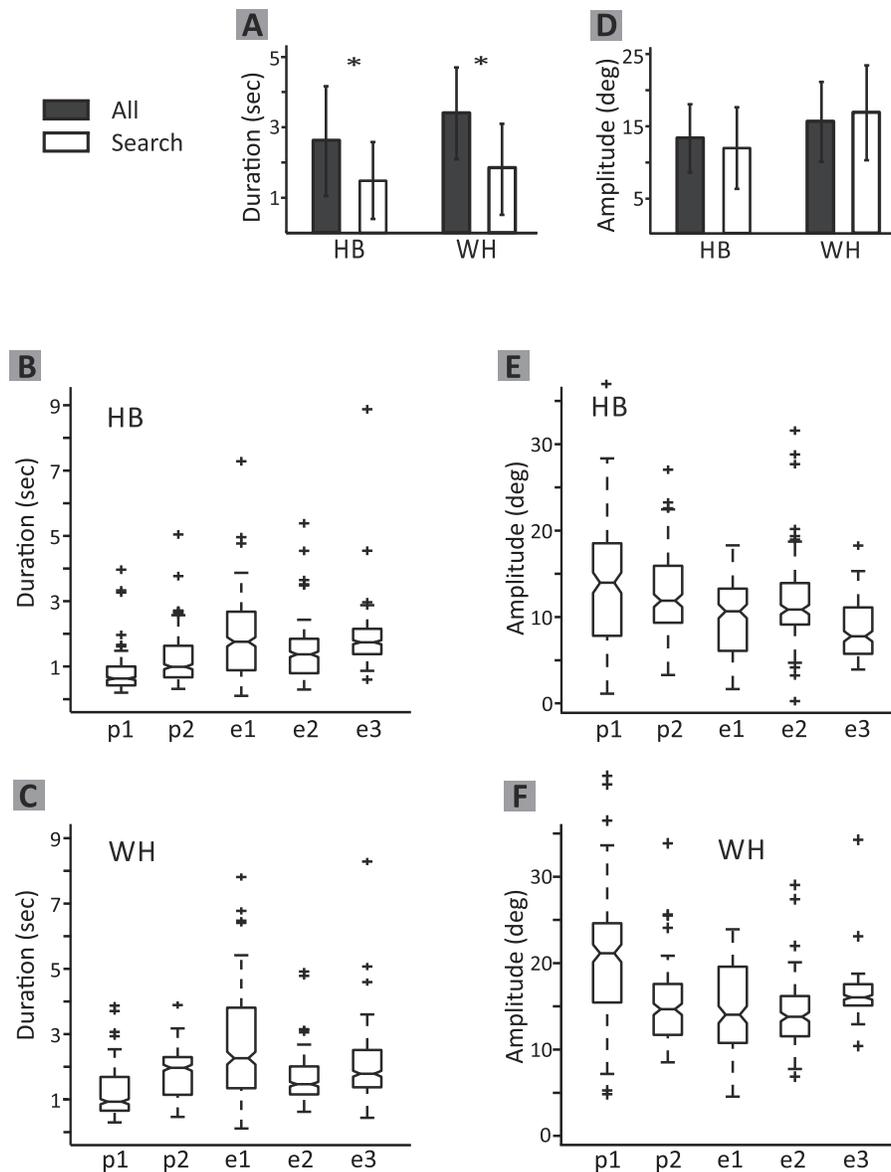
Figure 5. Search behavior of two barn owls at large set sizes (49 and 64 items). Left column shows fixation duration, right column shows saccade amplitude. The different experiments were: high luminance contrast (p1), orientation (p2), low luminance contrast (e1), high luminance-contrast conjunction (e2), and low luminance-contrast conjunction (e3). (A) Differences between fixation durations while searching (all fixations before the first target fixation) and durations of all fixations made during experiments (including search fixations) pooled for all experiments. (B–C) Fixation duration box plots for each experiment for owl HB (B) and owl WH (C). (D) Differences between search amplitudes and all saccade amplitudes pooled for all experiments. (E–F) Saccade amplitude box plots for each experiment for owl HB (E) and owl WH (F). Significant differences between compartments in (A) and (D) as judged by Wilcoxon signed-rank tests ($p < 0.05$) are indicated by asterisks. Significant differences in (B, C, E, F) as judged by the Kruskal–Wallis test ($p < 0.05$): (B) p1 from p2, e1, e2, e3; p2 from e1, e3; (C) p1 from p2, e1, e2, e3; (E) p1 from e3; p2 from e3; (F) p1 from e1, e2.

looked at items sharing target luminance, while owl WH was guided to items sharing the target's orientation. Despite these differences, it was clear that in both experiments the owls preferred to look at target features, while ignoring the uninformative distracter type that did not share any features with the target.

Discussion

Building on the finding that barn owls are attracted by the saliency of visual items (Harmening et al., 2011) and have a pop-out effect for two features (orientation and luminance contrast; Orlowski et al., 2015), we attempted to characterize barn-owl visual-search be-
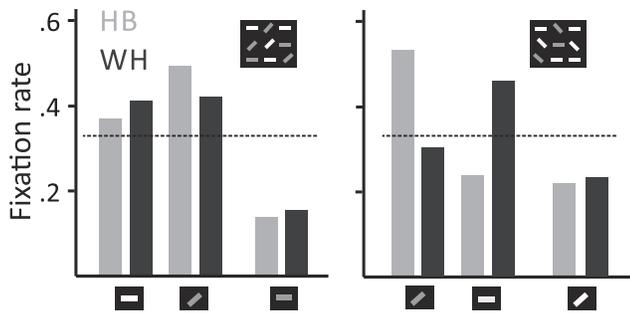
Figure 6. Search guidance in conjunction search. Plotted is the ratio of distracter classes fixated after the first saccade in each trial. Left figure is for e2 (white slanted target), right figure is for e3 (gray horizontal target). Icons show the fixated item class. Dashed line is the chance level. Both owls avoid the distracters that share no features with the target.

havior in complex search tasks and compare the latter behavior to the behavior observed in the easy search tasks. When we switched target and distracter luminance in the luminance task, the owls switched from a pop-out search mode (white target among gray distracters) to a serial search mode (gray target among white distracters). In other words, search time and number of saccades increased with set size in the latter but not the former condition. The two conjunction searches were conducted in a serial manner by the owls as well. We also analyzed the dependence of the mechanisms of the visual-search behavior on visual complexity and compared those to human or primate data. In the following, we shall first discuss the performance of the barn owls in our search tasks and compare it to data from other species. Then we discuss search mechanisms, namely fixations and saccades.

Performance in visual-search tasks

The first finding was that barn owls can learn to do conjunction search tasks with static items. However, the long training time of up to 2 months showed that this was a very difficult task for the owls. This is also reflected in the long time needed for data collection, which was about twice as long for the serial search tasks as for the pop-out search tasks. This was in stark contrast to the previous experiments on orientation saliency, in which the owls fixated odd items in feature arrays without prior training.

To further analyze search performance we analyzed three factors: search time, saccade number, and error rate. All three showed quite similar results. We already knew that barn owls have a pop-out effect for luminance contrast (target high contrast, distractor low contrast; p1) and orientation (p2). Of these, luminance contrast was the easier task, and average search time

was much lower than in the orientation search task. Search time per item increased from below 10 ms to 190 ms when these two features (luminance and orientation) were combined in a conjunction search (e2; see Figure 4). This suggests again a large increase in search difficulty.

In e1, target and distracter luminance were swapped compared to p1. While throughput was without a delay, if the target was brighter than the distracters it took the owls 110 ms/item to search for the target when the contrast was swapped, resulting in a search asymmetry as also observed in humans (Treisman & Gormican, 1988). In reference to human data, this result was not unexpected, since target–background saliency decreased even though target–distracter discrimination saliency remained similar (Braun, 1994; Nothdurft, 2015).

When, according to human data, the task was made even more difficult (e3), average search time further increased to 270 ms/item. This suggests that the difficulty for the owls resembled the difficulty observed in human experiments. The increase in search difficulty from e1 to e3 was also evident in the proxy we used for error rate. Thus, both search time and error rate in owls resemble those in human visual search (Scialfa & Joffe, 1998; Shen & Paré, 2006).

There are, of course, some differences between the behavior of the barn owls and of humans. Search time in our experiments was much longer than that observed in human experiments (Wolfe, 1998; Wolfe, Palmer, & Horowitz, 2010). Such a difference is also visible in other, nonprimate animal experiments on visual search—for instance, in rats, zebrafish, or archerfish (Botly & De Rosa, 2012; Proulx, Parker, Tahir, & Brennan, 2014; Rischawy & Schuster, 2013), but interestingly not in pigeons (Blough, 1979). These differences may be due to setup limitations in adapting a visual-search experiment to fit a nonprimate animal, or to lower performance of the animals in these tasks— perhaps due to lower computational power. For example, when Rischawy & Schuster (2013) conducted the same visual-search experiments on archerfish and humans, humans performed much better. However, when the human subjects were distracted by asking them to solve calculations during the search, performance was more similar. Moreover, visual-search experiments with small children or infants have demonstrated that response time, error rate, and search slopes decrease with age (Donnelly et al., 2007; Trick & Enns, 1998). For instance, the search slope of 24-month-old infants in a conjunction search experiment was similar to that of our owls in e3 (Gerhardstein & Rovee-Collier, 2002). The visual system of barn owls is different from the primate system in several ways. Resolution and contrast sensitivity are much lower (Harmening, Nikolay, Orlowski, & Wagner, 2009;

Orlowski, Harmening, & Wagner, 2012). The fovea of barn owls is much less developed and is rod dominated (Oehme, 1964; Wathey & Pettigrew, 1989). In our experiments, we made sure that our stimuli were well within the visible range of barn owls. Although we realize that it is difficult to assess the owls' performance quantitatively by comparing it to that of humans or even other animals, we were surprised by the many qualitative similarities that we observed in our experiments. Based on our findings we assume that the same basic features are salient to owls and humans if they are not restricted by visual thresholds—at least achromatically.

We also are aware that in some cases the birds failed to detect the target although they were looking at it (inattentional blindness), as is also seen in humans and nonhuman primates (Dias, Sajda, Dmochowski, & Parra, 2013; Mack & Rock, 1998). While we cannot exclude this possibility, we think such failures would not have affected our general conclusions. Our conclusion is based on the following observations: (a) The average durations of individual target fixations were much longer than those of average fixations (target: 5.0 s/6.3 s; all: 2.8 s/4.4 s). (b) The durations of fixations before target detection were much shorter than average fixations (all fixations, see Figure 5A). (c) The owls were only rewarded after successful flights toward the targets. Although these are indirect evidences, they all suggest that the owl indeed had detected the target while looking at it.

Head saccades and fixations in barn-owl search

Our methodology gives us a unique view to study visual behavior in a bird by tracking overt attention. In visual search, eye movements of primates are indeed guided by information about the sought-after target (Findlay, 1997; Findlay, Brown, & Gilchrist, 2001). This also held for the head movements of the owls studied here. By tracking overt attention we can not only analyze the result of the task—the search termination—but also see what happens during search by analyzing fixations and saccades. In all but the simplest searches, the number of fixations is tightly linked to search time (Motter & Belky, 1998; Williams, Reingold, Moscovitch, & Behrmann, 1997; Zelinsky & Sheinberg, 1997). In our experiments, barn owls showed a strong correlation between saccadic movements and search time as well, with the functions of saccades versus set size and search time versus set size both behaving similarly (Figure 4).

The gaze of barn owls was also guided by target information: In conjunction search, the first saccade was more often directed to distracters sharing features with the target than to distracters that had no shared

features. This saccadic selectivity is consistent with primate visual search and may be an indication of top-down search guidance (Findlay, 1997; Scialfa & Joffe, 1998; Shen & Paré, 2006).

Looking at saccade number, barn owls did not differ too much from primates, a finding we have reported previously (Orlowski et al., 2015). However, fixation durations, and therefore search time, were vastly longer, as search time is approximately equal to the product of average fixation duration and saccade number. In our experiments, barn owls had average fixation durations of 1.77 s for set sizes of 49 and 64, the two largest set sizes used. Compared to humans, barn owls appeared to need much more time to inspect the content in the fixation area. One speculation is that inspection took longer because receptor density is lower in the visual streak of barn owls than in the fovea of humans (Wathey & Pettigrew, 1989). The inspection duration also depended on task difficulty: 1.25 s on average in the parallel searches and 1.95 s in the serial searches. The increase in fixation duration and fixation number is a double adaptation to an increase in scene complexity: Longer fixations indicate that fewer items are inspected per time, and more fixations show that fewer items are inspected per fixation. The area, or visual span, inspected per fixation decreases. This is compensated by smaller saccade amplitudes. Saccade amplitudes decreased from the pop-out searches to the serial searches, although this trend from easy to difficult searches was not as pronounced as for fixation durations. So we conclude that barn owls adapt their overt search behavior temporally and spatially by adjusting fixation duration and saccade amplitude when search difficulty changes. Similar adaptations can be found in human overt search behavior: In free-viewing conditions, fixation numbers for human subjects increase similarly to search time when comparing easy to serial search (Williams et al., 1997; Zelinsky & Sheinberg, 1997). Fixation durations also increase with task difficulty (Moffitt, 1980; Vlaskamp & Hooge, 2006), while saccade amplitude decreases (Hooge, Over, van Wezel, & Frens, 2005; Jacobs, 1986).

In summary, although birds and mammals evolved independently for 300 million years, both use very similar mechanisms for visual search.

Keywords: head movement, visual search, overt attention, cognition, conjunction search, saccades

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