



Interactions between top-down and bottom-up attention in barn owls (*Tyto alba*)

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Abstract

Selective attention, the prioritization of behaviorally relevant stimuli for behavioral control, is commonly divided into two processes: bottom-up, stimulus-driven selection and top-down, task-driven selection. Here, we tested two barn owls in a visual search task that examines attentional capture of the top-down task by bottom-up mechanisms. We trained barn owls to search for a vertical Gabor patch embedded in a circular array of differently oriented Gabor distractors (top-down guided search). To track the point of gaze, a lightweight wireless video camera was mounted on the owl's head. Three experiments were conducted in which the owls were tested in the following conditions: (1) five distractors; (2) nine distractors; (3) five distractors with one distractor surrounded by a red circle; or (4) five distractors with a brief sound at the initiation of the stimulus. Search times and number of head saccades to reach the target were measured and compared between the different conditions. It was found that search time and number of saccades to the target increased when the number of distractors was larger (condition 2) and when an additional irrelevant salient stimulus, auditory or visual, was added to the scene (conditions 3 and 4). These results demonstrate that in barn owls, bottom-up attention interacts with top-down attention to shape behavior in ways similar to human attentional capture. The findings suggest similar attentional principles in taxa that have been evolutionarily separated for 300 million years.

Keywords Animal behavior · Attentional capture · Birds · Saliency · Stimulus selection

Introduction

The ability to focus on a particular task while ignoring distractors is an important cognitive ability. However, salient sudden distractors may signal the necessity to abandon the task and orient to a new event. This balance between top-down (goal-driven) and bottom-up (stimulus-driven) attention is a critical factor for normal behavior, and its abnormal operation is related to attentional deficit disorders (Forster and Lavie 2016). Humans searching for a specific target perform worse if a salient, task-irrelevant, visual or auditory stimulus is present before or during the target presentation

(Pinto et al. 2013; Dalton and Hughes 2014). This cost in performance is attributed to the deleterious effects of bottom-up attention. The interpretation is that the focus of attention is automatically and unavoidably captured by salient stimuli, even when attentional resources are highly engaged in a top-down controlled task (Koelewijn et al. 2009). Attentional capture, as measured in humans, likely reflects an evolutionary balance between the need to focus attention on an important task at hand and the need to remain alert to sudden dangers or opportunities in the environment.

A common view in the field of attention is that bottom-up attentional mechanisms are primitive in evolution, while top-down attention is a high-level mechanism that involves the cortical system that has the ability to integrate sources of information with goals, memory and internal states (Pinto et al. 2013). An alternative view is that both types of attention, top-down and bottom-up, are widespread in the animal kingdom (de Bivort and van Swinderen 2016). The need to focus on a specific search task while resisting irrelevant distractors is common to all food foraging animals (Dukas and Kamil 2000).

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Here, we studied attentional capture in barn owls (*Tyto alba*). These birds rely on the rapid detection of small prey items in highly cluttered, dim and noisy environments, conditions that are challenging to any attentional system (O'Carroll and Warrant 2017). Birds are evolutionarily separated from mammals for over 300 million years (Kumar and Hedges 1998). Thus, barn owls provide an excellent case study to address the above questions regarding the evolution of top-down and bottom-up attentional processes. Barn owls have been shown to possess well-developed bottom-up attentional mechanisms, including cueing effects and pop-out perception (Johnen et al. 2001; Harmening et al. 2011; Orłowski et al. 2015). Yet, a systematic study of interactions between top-down and bottom-up attention has not been performed in barn owls.

To facilitate comparison, we tested barn owls in an attentional capture task commonly used in humans (Koelewijn et al. 2009; Matusz and Eimer 2011; Pinto et al. 2013). Owls were trained to detect a vertical Gabor patch among other, non-vertically oriented Gabor patches. In half of the trials, a task-irrelevant stimulus appeared (a red circle on the screen or a brief sound). Although the owls performed the task well both with and without the irrelevant stimuli, the time to reach the target as well as the number of head saccades to find the target increased when irrelevant stimuli appeared. These results are consistent with bottom-up attentional capture and are qualitatively similar to parallel results obtained in humans.

Materials and methods

Animals

Two adult barn owls (DO and DK), females of about one and a half years of age, were used in this study. The owls were hatched in captivity and hand-raised from the age of 1 week. Between training and experimental sessions, the owls were kept in flight aviaries equipped with perching spots and nesting boxes. All surgical procedures were performed under anesthesia. The owls were provided for in accordance with guidelines established by the NIH on the care and use of animals in research. All procedures complied with the guidelines and were confirmed by the Technion Institutional Animal Care and Use Committee.

Stimuli and experimental setup

The visual stimuli were computed in MATLAB using the Psych Toolbox extensions (Brainard 1997) and were displayed on an LCD screen (17-in. 1280/1024 pixels at a refresh rate of 76 Hz, NEC MultiSync LCD1770VX, NEC Company, Tokyo, Japan).

The owls were placed on a perch in a darkened room with the computer screen facing upwards, about 25 cm below eye level. This range allowed the owl to pick food from the screen without getting off the perch (see Fig. 1a for the experimental setup). To track the owl's gaze, a lightweight wireless video camera (Owl-Cam, 30 frames per second, $\sim 60^\circ$ view angle) was mounted on the owl's head (Fig. 1b, c). The camera was self-assembled from a miniature micro-camera combined with a video broadcasting chip (900 MHz) and a rechargeable lithium-polymer battery. The Owl-Cam was attached to the head using a 3D printed device that was affixed to a base unit glued to the skull with dental cement (weight together with mounting device was about 10.5 g). The attachment device maintained a fixed and reproducible relationship between the Owl-Cam and the head. For additional details on the camera assembly, see Hazan et al. (2015). Since barn owls lack substantial eye movements, a head-fixed camera can provide a reliable estimation of the owl's gaze position (Ohayon et al. 2008). Initially, the position of the gaze center (functional fovea) on the headcam video frame was calibrated for each owl by allowing the owl to fixate on multiple salient targets on the screen and registering the average position of targets on the video frame. This resulted in a heat map of target fixations (Fig. 1d). The pixel having the highest probability of fixating on a target was considered the point of gaze for further analysis. For additional details of the calibration process and method validation, see Harmening et al. (2011) and Hazan et al. (2015).

Behavioral tasks

In all experiments, the owl initiated a trial by fixating on a red spot at the center of the screen. This was followed by disappearance of the fixation spot and the display of a target embedded in a distractor array. The target and distractors were high-contrast Gabor patches (spatial resolution of about 0.44 cycles per degree for a viewing distance of 25 cm) presented on a uniform middle range gray background. The target was always vertically oriented while the distractors were randomly oriented in five possible orientations: 40° , 50° , 60° , 70° or 80° . Target and distractors were organized in a circle around the initial fixation point at a radius of 7 cm (288 pixels) from the center (see Fig. 2a and Online Resource 1). The target was positioned either to the left or to the right from the initial fixation point.

The owls were rewarded for fixating on the target patch and occasionally for initiating trials. Rewards were small chunks of chicken meat positioned manually onto the glass covering the screen at about the target position and then, either given to the owl above the screen or letting the owl pick the food from the screen. After rewarding, the display turned gray until the next trial was manually initiated

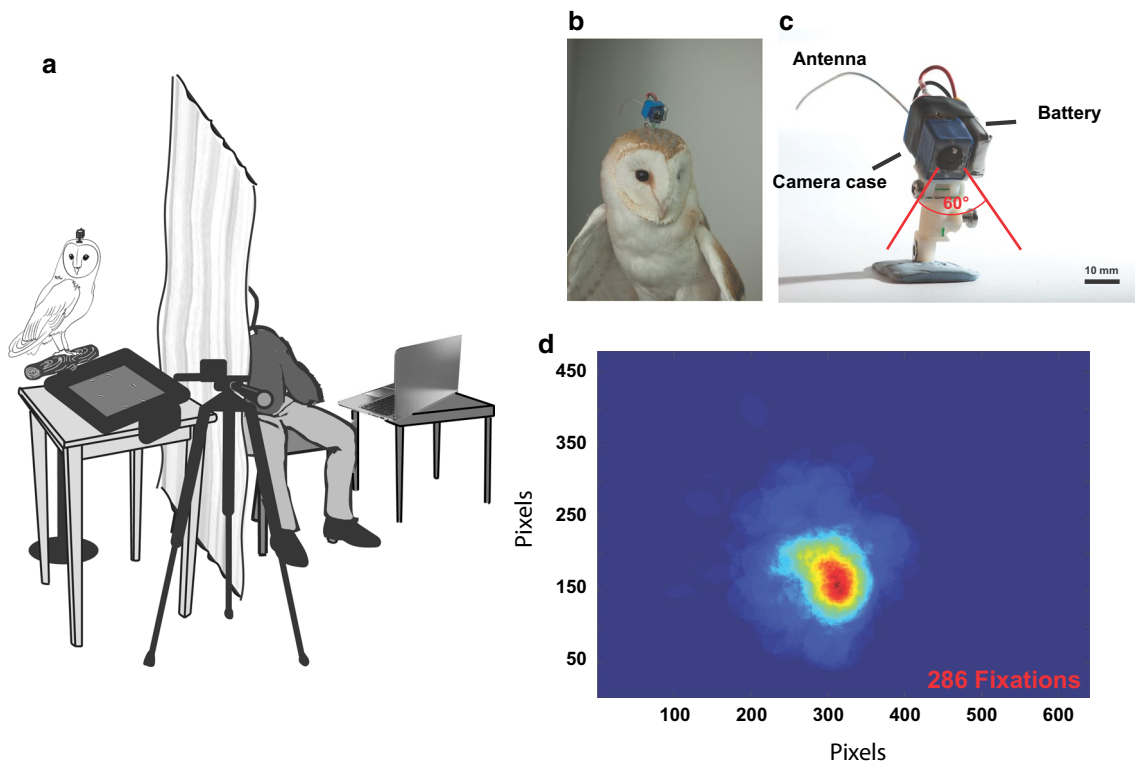


Fig. 1 The experimental setup and Owl-Cam. **a** An illustration of the behavioral setup. **b** The Owl-Cam mounted on an owl's head. **c** A close view of the Owl-Cam with the attachment unit. **d** A heat map

showing the rate of fixation points on the video frame during a single session (286 fixation in this example). A single peak is clearly distinguishable defined as the functional fovea

by the experimenter (inter-trial intervals were typically in the range of a few seconds). If no fixation was achieved after 30 s, the display turned gray and no reward was given. See a video example of an owl performing the task in Online Resource 1. The position of the experimenter close to the animal, behind a curtain (Fig. 1), is not likely to bias the performance of the owls because the experimenter is not aware of the computer-generated signal until it is initiated by the owl's fixation, leaving very little time for any possible behavioral cueing.

Three experiments were performed (Fig. 2a). In experiment 1, the stimuli included the target with either five or nine distractors. In experiment 2, the target appeared with five distractors, either without additional stimuli or with a red circle (pen width of 2 or 10 pixels) surrounding one of the distractors. The position of the encircled distractor was chosen randomly every trial. In experiment 3, the target appeared with five distractors, either without additional stimuli or together with a brief sound. The sound was a 500 ms duration Gaussian noise initiated at the onset of the trial. The sound (about 70 dB SPL) was emitted from a speaker positioned behind the computer screen. Owls performed normally 20–50 trials a day. In each experiment, at least 100 trials were collected from each owl in five successive days.

Data analysis

Owl-Cam data were analyzed frame-by-frame using a custom-made MATLAB GUI. Typically, owl search behavior consists of stable fixation periods for 0.3–4 s durations terminated by rapid head movements to a new fixation point (Hazan et al. 2015). A fixation was considered on target if the border of the target Gabor appeared inside a circular area (80 pixels diameter) surrounding the functional fovea and was maintained there for at least 10 consecutive frames. The relatively large fixation window was chosen to account for the relatively large area centralis of barn owls (Wathey and Pettigrew 1989), and to encompass variations in fixation on a target that may arise from differences in distance and gaze angle to screen plane. For training, we used a stricter criterion for a fixation of 50 pixels diameter around the functional fovea. In each trial, the time from stimulus onset to first gaze on the target (search time ST) and number of head saccades (HS) to reach the target were registered. A trial was considered a failure if the owl did not fixate on the target during the 30 s of stimulus display.

In the search time analysis, we discarded trials with search times slower than three times the standard deviation of that test. This led to the exclusion of 4 and 4.2% of the trials for DO and DK, respectively. The datasets generated

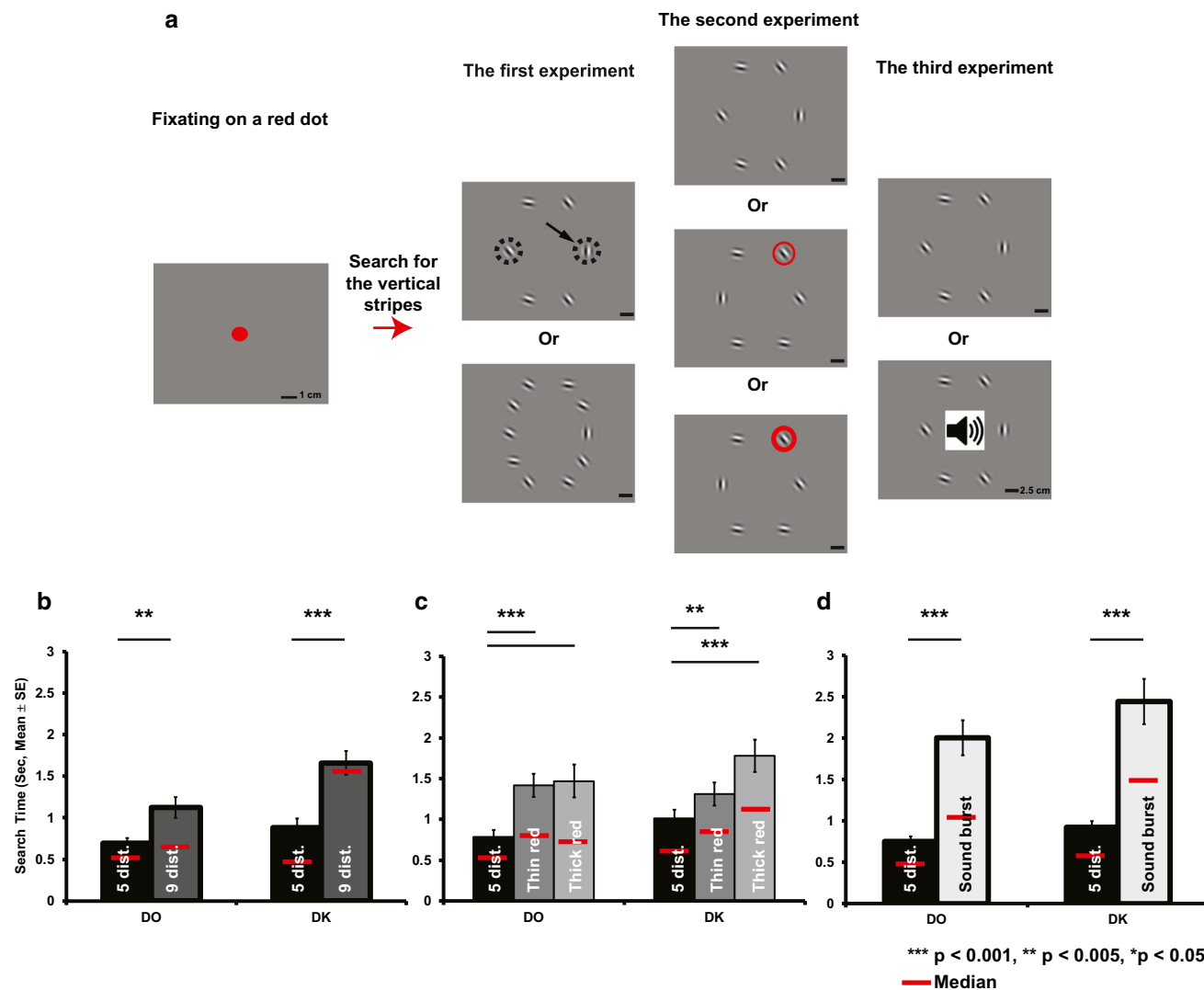


Fig. 2 Examples of the experimental conditions (top panel) and corresponding average search times (bottom panel). **a** An illustration of the experimental conditions. The owl initiates a trial by fixating at the red dot at the center of the screen, and then the dot disappears and a circular array of Gabor patches appears. A vertically oriented Gabor (the target, designated by an arrow in the upper left panel) was always in one of two sides of the initial fixation dot. The dotted outlines surrounding the target and control locations in the stimulus display for the first experiment depicts the two possible choice locations and is

and analyzed during the current study are available in Online Resource 2.

Results

Following trial initiation (fixation of a red dot), the barn owls typically scanned the computer screen and the surrounding room with abrupt head movements (Online Resource 1). We observed only two cases in owl DO (out of 675 trials for DO

only presented for illustrative purposes. **b** The average search times compared between a target with five additional elements and a target with nine additional elements. **c** The average search times compared between search trials without a circle, with an additional thin circle and with an additional thick circle. **d** The average search times compared between search trials without a sound and search trials with a sound. The red bars indicate the median values. The error bars designate S.E.M

and 730 trials for DK) in which the owl did not gaze at the target during the 30 s allowed for the test. Thus, the success rate for this task was almost 100%, hence performance was measured as search times (time to first fixation on target) and number of head saccades to fixate on the target. In the first experiment, we also registered fixations on the Gabor patch opposite the target, which served as a control. In marked contrast to fixations on the target, owls DO and DK gazed at the control patch in only 10 out of 104 and 8 out of 129 trials, respectively.

Average search time of a target with five distractors (basic configuration) was between 0.7 and 0.9 s (Fig. 2b–d, black columns). These relatively short STs indicate that the owls were well trained and motivated to perform the task. However, in all three experiments and for both owls, the time to reach the target increased when additional distractors or cues were added to the scene. Figure 2b–d summarizes the average search times for all three experiments. The two owls reached the target on average faster with five distractors compared to when the target appeared on-screen together with nine distractors (Fig. 2b; Mann–Whitney *U* test, $p < 0.002$, $r = 0.27$, $n = 129$ for DO and $p < 0.001$, $r = 0.42$, $n = 104$ for DK). The two owls reached the target faster when the target appeared with five distractors compared to when it appeared with five distractors of which one was encircled by a red circle (Fig. 2c; Mann–Whitney *U* test; $p < 0.001$, $r = 0.37$, $n = 127$ [line width of 2 pixels] and $p < 0.001$, $r = 0.396$, $n = 124$ [line width of 10 pixels] for DO; $p = 0.006$, $r = 0.243$, $n = 130$ [line width of 2 pixels] and $p < 0.001$, $r = 0.32$, $n = 135$ [line width of 10 pixels] for DK). Although both owls showed an increased mean search time when the line width of the circle was larger, the effect was not significant (Mann–Whitney *U* test, $p = 0.82$ and $p = 0.216$ for DO and DK, respectively). The two owls reached the target faster when it appeared with five distractors compared to when it appeared with an additional task-irrelevant sound at the beginning of the trial (Fig. 2d; Mann–Whitney *U* test, $p < 0.001$, $r = 0.335$, $n = 161$ for DO and $p < 0.001$, $r = 0.369$, $n = 196$ DK).

The same irrelevant cues for attentional capture were repeated over several days. Therefore, it is possible that their perceived saliency was reduced over time due to habituation. If so, we expect a reduction in the capture effect in the later

trials. To examine whether performance changes with time, we compared the average ST measured in the first half of the trials with the average ST in the second half. In the basic configuration of five distractors, search times were not significantly different between the first and second half of the experiments (Fig. 3a, b, black solid lines; Mann–Whitney *U* test, $p = 0.72$, $n = 219$ for DO and $p = 0.99$, $n = 229$ for DK). When a red circle as an irrelevant cue was displayed, STs on average decreased between the first and second half of the experiments. However, this was only significant in owl DK (Fig. 3b; Mann–Whitney *U* test, $p = 0.001$, $r = 0.3$, $n = 125$). In search trials where an irrelevant sound was used, average search times were significantly shorter in the second half compared to the first (Fig. 3a, b, Mann–Whitney *U* test, $p = 0.026$, $r = 0.255$, $n = 76$ for DO and $p = 0.005$, $r = 0.3$, $n = 89$ for DK). Thus, the increase in ST resulting from an irrelevant cue tended to be larger at the beginning of the experiments, suggesting the owls were learning to ignore the salient irrelevant cue. The presence of an irrelevant red circle maintained a significant increase in search times even when only trials from the second half of the experiment were considered (Mann–Whitney *U* test, $p < 0.001$, $r = 0.41$, $n = 170$ for DO and $p = 0.012$, $r = 0.19$, $n = 180$ for DK). The presentation of a sound source maintained a significant effect at the second half of the experiment in owl DK (Mann–Whitney *U* test, $p = 0.007$, $r = 0.21$, $n = 161$) but not in owl DO ($p = 0.07$, $r = 0.15$, $n = 144$). We do not know if further testing would have eliminated the capture effect or maintain it at a steady-state level.

Since eye movements in barn owls are limited up to 3°, they scan the environment with abrupt head movements called head saccades as an analogy to eye saccades (du Lac and Knudsen 1990). The number of head saccades (HS)

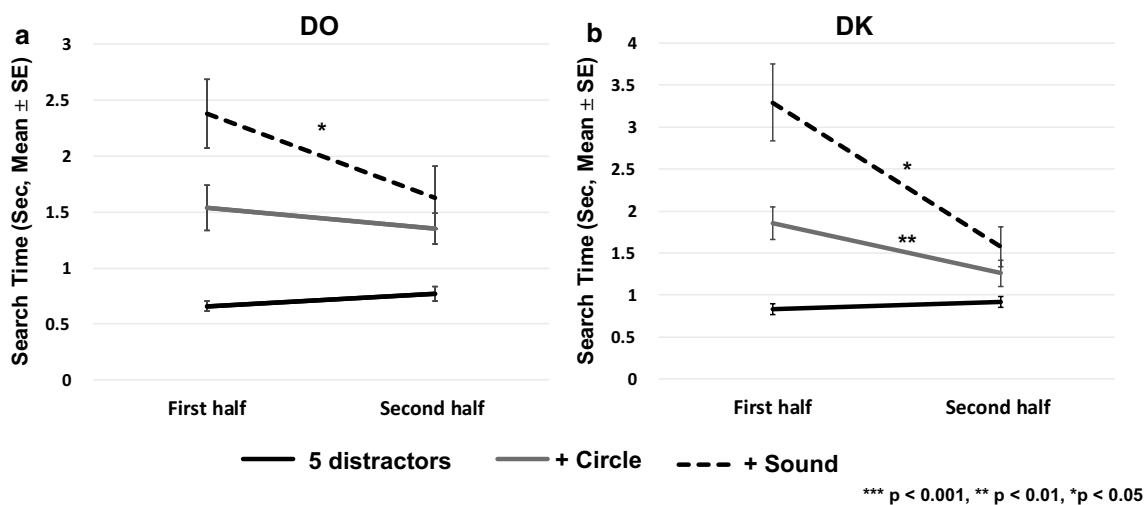


Fig. 3 The average search times in the first and second half of the three experiments for the five distractor, additional circle, and additional sound condition, respectively, for each experiment. **a** Results for owl DO. **b** Results for owl DK. The error bars designate S.E.M

performed before reaching the target was measured. Average HS to reach the target followed the same trend as STs. The owls performed on average more HS to reach the target when the number of distractors increased from five to nine (Fig. 4a; Mann–Whitney U test, $p = 0.005$, $r = 0.245$, $n = 129$ for DO; $p < 0.001$, $r = 0.39$, $n = 104$ for DK). The owls performed on average more HS to reach the target when a red circle appeared (Fig. 4b; Mann–Whitney U test, $p = 0.003$, $r = 0.264$, $n = 127$ [line of 2 pixels] and $p = 0.009$, $r = 0.236$, $n = 124$ [line width of 10 pixels] for DO; $p = 0.3$, $r = 0$, $n = 130$ [line width of 2 pixels] and $p = 0.002$, $r = 0.271$, $n = 135$ [line width of 10 pixels] for DK, respectively). The average number of HS increased when a sound was played together with trial initiation (Fig. 4c; Mann–Whitney Test, $p < 0.001$, $r = 0.288$, $n = 196$ for DK and $p < 0.001$, $r = 0.365$, $n = 161$ for DO).

The cumulative distributions of head saccades to reach the target are shown in Fig. 4d. In the basic configuration

with five distractors, owl DO made a single saccade to the target in 83% of the trials and owl DK in 70% of the trials (Fig. 4d, black curve). When additional distractors (a red circle or a sound) were added, the percentage of reaching the target on the first saccade decreased (Fig. 4d). It can be seen from the cumulative distributions that the curves for the experiments with more distractors or with additional task-irrelevant stimuli are shifted to the right compared to the curve for the trials with just five distractors alone. However, under all conditions, the target was eventually reached after 10 HS at the most.

The relatively good agreement between the number of head saccades to reach the target and the STs suggests that the average fixation period is relatively similar under the different conditions. To examine this, we measured the reaction times by taking into consideration only those trials in which the target was reached in the first saccade. In the basic configuration, without additional distractors, the average time

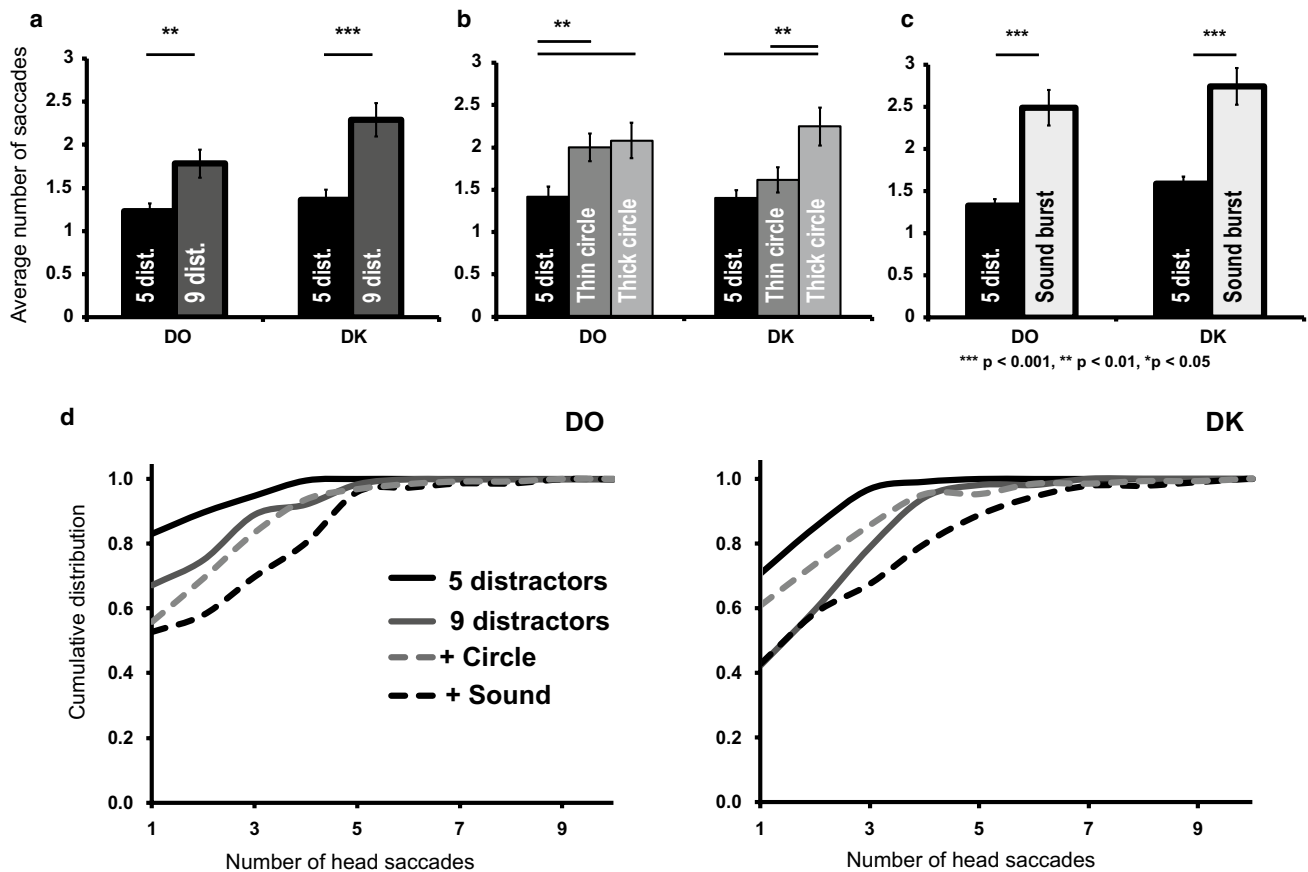


Fig. 4 Summary of number of head saccades until fixation on target. **a** The average number of saccades to reach the target compared between trials with five additional distractors and trials with nine additional distractors. **b** The average number of saccades to reach the target compared between trials without a circle, trials with a thin circle and trials with a thick circle. **c** The average number of saccades to reach the target compared between trials without a sound and trials

in which an additional sound was played. Error bars in a–c designate S.E.M. **d** The cumulative distribution of number of saccades to reach the target for five distractors (black solid curve), for nine distractors (gray solid curve), for five distractors + a circle (dashed gray curve) and for five distractors + a sound (black dashed curve). Left panel shows data from owl DO and right panel shows data from owl DK

to reach the target in only one saccade was 0.58 ± 0.44 s ($n = 162$) and 0.52 ± 0.26 s ($n = 176$) in owls DK and DO, respectively. With an additional irrelevant stimulus (visual or auditory), it took more time to reach the target with one saccade, 0.78 ± 0.55 s ($n = 114$) and 0.63 ± 0.34 s ($n = 111$) in owls DK and DO, respectively (Mann–Whitney U test, $p < 0.001$ and $p < 0.001$ in DK and DO). Thus, the attentional capture is manifested in more saccades as well as longer holding periods at the initiation of the trial.

Discussion

In this study, we tested whether typical attentional capture tasks in barn owls provide comparable results to those obtained in humans. We conducted three experiments: one involved an increase in the number of distractors; and two involved the addition of task-irrelevant cues, visual or auditory. The performance of human subjects in visual search tasks similar to those used here has been studied in great detail over the years (Theeuwes 1992; Awh et al. 2012; Lavie 2005; Pinto et al. 2013; Dalton and Hughes 2014). One typical example of visual search is to find a specific target (vertical Gabor) among distractors of different orientations. The general finding in humans is the existence of search slopes (Treisman and Gelade 1980), i.e., the more the number of distractors, the longer the detection time. The interpretation for such search slopes is debatable (Wolfe et al. 1989; Treisman and Sato 1990). However, a common notion is that they reflect the difficulty of the search task. The shallower the slope, the easier it is to separate the target from the distractors (Wolfe and Horowitz 2004). Our results show first that barn owls can readily learn and detect a task-relevant feature among distractors, and second, when doing so, they display significantly increasing search times with the increasing number of distractors (search slopes). In humans, search slopes vary between different searches. In some single-feature searches where the target differs by a single feature from a mostly homogeneous background, the search is efficient (i.e., pops-out), while in others, which are mostly conjunction searches where the target is defined by a combination of two features, they are difficult (Treisman and Gelade 1980). The current task is a single-feature task; however, the distractors are heterogenic. Such tasks are usually difficult in humans, demonstrating significant search slopes (Duncan and Humphreys 1989). In a recent study carried out on barn owls, it was shown that a visual search task to a single feature, orientation of a bar, as well as brightness tend to pop-out, whereas conjunction searches, for targets distinguished by a combination of orientation and brightness, showed slopes (Orlowski et al. 2015). Pigeons, as well, are more accurate and faster when searching for a target defined by a single-feature contrast compared to conjunction

of two features (Cook et al. 1996). Search slopes were found also in conjunction visual searches in archer fish (Ben-Tov et al. 2015) and in bees (Spaethe et al. 2006). The findings reported here add to this body of knowledge by showing a search slope in barn owls when searching for a target in a heterogenic population of distractors. Thus, the principle of set-size effect in various types of visual searches (Davis and Palmer 2004) seems to be conserved across species.

Another common way to probe attentional mechanisms is by measuring the visual capture effect of a salient task-irrelevant stimulus (Theeuwes et al. 2010). It is well documented that humans instructed to focus on a task are distracted by irrelevant stimuli. The cost in performance is known as attentional capture, which has been studied extensively in humans (Theeuwes et al. 2010; Liesefeld et al. 2017). Under laboratory conditions, capture effects are quantified by instructing subjects to perform a guided search task and measuring the increase in search time when a salient, bottom-up task-irrelevant cue is presented. The common finding in humans is that the capture effect increases with the saliency of the irrelevant stimulus and decreases with the perceptual demand of the task (Lavie 2005; Hickey et al. 2006).

Here, we performed a similar test in barn owls. We trained barn owls to search for a vertically oriented Gabor patch among distractors. Using this, we showed a significant increase in search times when an irrelevant visual cue was added to the display. The interpretation is that the owl's attention is inevitably allocated to the additional cue, resulting in an increase in time to find the target, i.e., attentional capture. Repetitions of the trials tended to reduce the attentional capture effect. This is unlikely to reflect improvement in task performance with time, because the STs did not improve in the control conditions (see Fig. 3 solid lines). Thus, these observations are in line with the notion that bottom-up saliency of irrelevant distractors are responsible for the capture effect (Theeuwes et al. 2010; Liesefeld et al. 2017). Visual attentional capture has been suggested previously in pigeons (Cook et al. 1997, 2012) further pointing to commonalities in the organization of visual search behaviors among species.

In our experiments, the target was positioned either left or right of the initial fixation point. The motivation for this design was to eliminate possible confounding effects from the biomechanical differences of sideways versus vertical head motions. Furthermore, by maintaining the target position along the horizontal line, we avoid complexities that may arise from possible differences in processing information from upper versus lower visual field (Fitzke et al. 1985). This, however, simplifies substantially the search task. In humans, a general finding is that attentional capture effects are enhanced when the search task is made simpler (Lavie 1995), an effect that is attributed to the allocation of attentional load (Lavie 2005). Search slopes, on the other hand,

are reduced in simpler tasks (Duncan and Humphreys 1989). In search paradigm where targets were limited to appear in pre-cued locations, as in ours, search slopes were reduced but not eliminated (Carrasco and Yeshurun 1998). It would be interesting to test in a future study more difficult searches in barn owls. The prediction would be that attentional capture effects will be reduced and search slopes increase.

An important question regarding attentional capture is to what extent can it be cross-modal (Hillyard et al. 2016). If attentional mechanisms are separated between modalities, we expect weaker attentional capture by cross-modal cues compared to the same modal cues. Although results in humans vary among different modalities and tasks (Matusz et al. 2015; Tellinghuisen and Nowak 2003; Berti 2013), a general finding is that a sudden or deviant auditory stimulus can capture visual attention (Koelewijn et al. 2009; Berti 2013; Hillyard et al. 2016). Here, we tested this question in experiment 3 where an irrelevant sound was presented in 50% of the trials. The results showed a significant increase in visual search time induced by the sound. Although it is necessary to study more tasks and a variety of cues, the results so far suggest that in barn owls, auditory capture of visual attention is comparable to visual capture of visual attention. Barn owls are nocturnal animals that rely on audition for hunting (Knudsen et al. 1979). It is possible that the contribution of auditory signals to attentional capture in this species is stronger compared to other species.

Over the years, a variety of animal species have been tested in laboratory tasks borrowed from human psychophysical attention studies. The accumulating result is that animals from far apart taxa ranging from insects, fish, birds and mammals show surprisingly similar attentional behaviors (Ingle 1975; Sareen et al. 2011; Zentall 2005; Bushnell and Strupp 2009; Mokeichev et al. 2010; Sridharan et al. 2014). Barn owls, for example, demonstrate cueing effects (Johnen et al. 2001), pop-out perception (Orlowski et al. 2015) and grouping effects (Nieder and Wagner 1999) reminiscent of human abilities. The current study adds an important demonstration to this list, namely, attentional capture by task-irrelevant distractors. Searching for Gabor patterns on a computer screen is highly artificial for an owl, yet the behavioral outcomes are qualitatively similar to that of humans. Thus, this result strengthens the notion that attentional behavior is conserved in evolution. Moreover, strong homologies across vertebrates can be found in brain structures supporting attentional behavior, with the optic tectum/superior colliculus as the main subcortical hub for stimulus selection (Krauzlis et al. 2004; Knudsen 2011; Gutfreund 2012). Thus, mechanisms of attention apparently have a common evolutionary origin. We speculate that organisms that can focus efficiently on behaviorally relevant targets while avoiding interference by irrelevant distractors are favored by evolution, giving rise to the sophisticated

memory- and context-dependent attentional mechanisms as we know them today.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

Human and animal rights This article does not contain any studies with human participants performed by any of the authors.

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