

Visual search in barn owls: From feature to conjunction search

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Summary

Visual search is the process of searching for something interesting in a cluttered environment. It is well studied in humans, but not in non-primate species. This study provides a comprehensive overview of visual search in barn owls using a novel methodology: the OwlCam. The OwlCam is a tiny, lightweight camera that can be mounted onto the head of barn owls to record first person videos from these birds. Due to the very limited eye movements of barn owls this provides an easy method of gaze tracking with only one camera in these birds which is not possible in most other species. Six experiments to investigate overt visual search processes in barn owls are described. Experiment 1 investigates basic overt attentional processes in barn owls. The question was, whether barn owls are attracted to the same conspicuous stimuli as humans? This was shown by confronting barn owls with arrays of differently oriented stimuli containing one odd target among similar distracters. Barn owls were attracted to the odd stimulus, as humans are. Experiments 2 and 3 prove that barn owls have a pop-out effect. Pop-out is the ability of visual systems to detect and localize certain visual targets equally efficiently regardless of the complexity of visual distraction. This was tested by training the owls to search for a unique target in feature-search arrays. These feature searches contained several quantities of uniform distracters and one odd target, different from the distracters in either orientation (experiment 2) or intensity (experiment 3). The search time and number of saccades until the target was found did not change at different set sizes, showing that barn owls have a pop-out effect. Experiment 4 was similar to experiment 3 but with inverted target and distracters to test whether barn owls have search asymmetries. That may be the case, if a search task's difficulty changes when the target and distracters are inverted. The data showed that this was the case. Finally, experiment 5 and 6 were conjunction-search tasks. These are difficult search tasks, in which the target is a unique combination of two features, orientation and intensity, and the distracters are the other feature combinations. The owls could learn to do these tasks, and indeed it took them much longer to find the targets than in the simple feature searches, and search time depended on array size. Thus, this study shows that barn owls match human performance in several visual searches. Therefore, a pop-out effect or

complex visual searches do not require the elaborate cortical structure found in mammalian brains. Furthermore, this study shows that barn owls wearing OwlCams could be a model system to study visual search and overt attention in non-primate species.

Zusammenfassung

In meiner Studie untersuche ich das visuelle Suchverhalten von Schleiereulen mit Hilfe einer neu entwickelten Methodik, der OwlCam. Unter visueller Suche versteht man den Prozess, Interessantes in einer komplexen Umgebung zu suchen. Bei Menschen und Primaten ist die visuelle Suche Objekt intensiver Forschung, aber in anderen Tierarten ist nur wenig darüber bekannt. Deshalb untersuche ich die visuelle Suche bei Schleiereulen mittels der OwlCam, einer kleinen auf dem Kopf der Eule befestigten Mikrokamera. Aufgrund der fast nicht vorhandenen Augenbewegungen bei Schleiereulen, kann man mittels derer Kopfbewegungen ihren Blick per Kamera aufzeichnen. Mit 6 unterschiedlichen Versuchen beschreibe ich das visuelle Suchverhalten bei Schleiereulen. Das 1. Experiment befasst sich mit Grundlagen der visuellen Aufmerksamkeit. Sind die gleichen Objekte für Eulen von Bedeutung wie für Menschen? Dabei wurden Schleiereulen mit einem anders orientierten Ziel-Objekt unter ansonsten gleichen Distraktor-Objekten konfrontiert. Ähnlich zum Menschen ist das anders orientierte Objekt. In Experiment 2 und 3 wird bei Schleiereulen ein „Pop-out“ Effekt nachgewiesen. „Pop-out“ ist die Fähigkeit, bestimmte Objekte, unabhängig von der Anzahl anderer Objekte in einer Szene, sehr schnell zu finden. Hierzu wurden Eulen trainiert, ein Zielobjekt in einem „Feature-Suche“ Muster möglichst schnell zu fixieren. Unter einem Feature-Suche Muster versteht man ein Muster aus gleichen Objekten und einem Suchziel, das sich in einer Eigenschaft von den anderen Objekten unterscheidet. In Experiment 2 wurde ein anders orientiertes Suchziel und in Experiment 3 ein helleres Suchziel verwendet. Suchzeit und Anzahl der Sakkaden zur Fixation des Suchziels waren unabhängig von der Anzahl der Objekte im Suchmuster. Folglich haben Eulen einen „Pop-out“ Effekt. War das Suchziel dunkler als die Distraktoren, wie in Experiment 4, kam es zu einer Such-Asymmetrie, woraus sich schlussfolgern lässt, dass eine Ziel-Distraktor Kombination einfacher zu finden ist als die umgekehrte Kombination. In Experiment 5 und 6 wurden sogenannte „Conjunction-Suche“ Versuche durchgeführt. Das sind schwierige Suchaufgaben, da das Suchziel eine einzigartige Kombination aus 2 Eigenschaften, Helligkeit und Orientierung, ist. Die Distraktoren setzen sich aus den übrigen Kombinationen zusammen. Die Eulen konnten diese komplexe Aufgabe erlernen, allerdings brauchten sie länger, um das

Suchziel zu finden, als in den anderen Experimenten. Zudem nahm die Suchzeit mit Anzahl der Distraktoren zu.

Zusammenfassend zeigen meine Experimente, dass Schleiereulen ähnliches Suchverhalten wie Menschen zeigen. Somit sind Pop-out oder komplexe Suchaufgaben auch ohne kortikale Strukturen möglich. Des Weiteren zeige ich, dass Schleiereulen dank der OwlCam ein Model zur Untersuchung von visuellen Aufmerksamkeitsprozessen in nicht-Primaten sein können.

1 Introduction

Like in humans, in birds vision is the most important sense. Vision in barn owls (Jones et al. 2007; Harmening and Wagner 2011), has been studied in some detail (for instance: Schaeffel and Wagner 1996; Harmening et al. 2007a; Harmening et al. 2009; Orłowski et al. 2012). The results showed, for example, what barn owls are able to perceive based on basic properties such as spatial resolution, contrast sensitivity or even on more complex abilities like stereovision. However, we don't really know how barn owls cope with the information they perceive. How is the information integrated and structured? Barn owls are highly specialized nocturnal hunters, who need to find food, predators, or mates in a difficult environment. In searching for objects some informational cues may be more important than others. Since brains have only limited processing power, only the most important information can be processed in time. Considering the brain size, a smart selection process is even more important for survival in barn owls than in humans.

Decades of research on visual search have made it one of the best understood processes in primates (Eckstein 2011). We have two different search modes, fast parallel search and slow serial search (Treisman and Gelade 1980). In parallel search search time does not depend on the number of other objects present, the search target pops out. In serial search the search gets more difficult when more distracting items are present. However, we know only little about whether these findings can be transferred to other species. This is mostly due to the difficulty of training animals to conduct a task as complex as visual search and then to compare these findings to our knowledge on primates, specifically humans. Only a few experiments have been conducted with non-mammalians, among them pigeons, archer fish, and bees (Blough 1977; Spaethe et al. 2006; Mokeichev et al. 2010).

The aim of this thesis is to extend our knowledge on visual search processes to barn owls. I mimicked experimental procedures used in humans as close as possible to achieve that. I asked the following questions: Do barn owls show the same division between parallel and serial search? Can they be trained to do complex serial search experiments?

I chose barn owls as a model organism for non-primate visual search, because these birds lack eye movements, and, thus, their gaze can be tracked rather easily during experiments

with a head mounted camera – the OwlCam. The OwlCam allows to record an animal's first person view. This view does not only give insight about the completion of a search, but also about the search process itself. So far this was only possible in primates.

1.1 Visual search

Consider searching for a favorite pen on a desk. If the table is nearly empty, we will find the pen in no time, perhaps even without realizing the search process. However, if the table is cluttered with scientific publications, other pens, coffee mugs, and sweets, this task will be much more difficult. Probably, we will have inspected several locations and items on the table until we have found our pen. The second task is more difficult and time consuming than the first. But why is this so?

Visual search is the task of looking for something in a cluttered environment. In a typical visual search tasks, an observer searches for a target item among a varying number of distractor items. In complex scenes, it is impossible to process all the available information in time due to our limited brain power (Tsotsos1990). However, the visual system of most animals is well adapted to this fact; by a process called visual attention we serialize the scene analysis. At each point in time only a small subset of the visual field is analyzed. Then, attention shifts to other locations based on their conspicuity or the observers search goals. The visual search will continue until the search target is found or the search is abandoned.

The question raised at the beginning is the guiding question of visual search. Why are some searches easy, and some not? The common approach to study search processes is by comparing the search times (reaction times) of different search tasks. In these experiments, observers are asked to find a single target in a search array consisting of several distractors. Between experiments the set size, the number of items - and thus the number of distractors, is varied. One of the most striking findings is that reaction times in some searches are independent of set size, an effect called pop-out (Treisman and Gelade 1980). If reaction time is plotted against set size, these searches will have slopes of approximately zero. They are efficient searches (Wolfe and Horowitz 2004). However, in most searches this will not be the case; search time will increase linearly with set size. Therefore, the slope of the reaction time x set size function is a good measure of ranking search difficulty. This search dichotomy is explained in the feature integration theory of attention (Treisman and Gelade 1980): Searches

are divided in so called single and multiple feature (conjunction) searches, with a feature being an early visual property such as orientation or color. Single features are extracted preattentively while feature combinations require attention. The general assumption is that parallel, preattentive scanning occurs for each feature. If the target differs only in a specific feature it is detected immediately and pops out. If more information than a single feature difference is necessary to identify the target, if it is defined by a unique conjunction of several features than a process called feature binding is necessary for identification. This process requires serial attention and is limited to only one or a few items at a time (Treisman 1982). Parallel feature search and serial conjunction search have been used extensively in laboratory experiments on visual search.

The theory of visual attention proposed by Treisman and Gelade (1980) has been challenged and refined in the last decades (for instance: Wolfe 1994; Itti and Koch 2000; Hochstein and Ahissar 2002). Not all basic visual features allow for parallel searches and not all conjunction searches require serial search (for instance: Nakayama and Silverman 1986; Theeuwes 1994; Wolfe 2003). In fact, there seems to be no clear division between parallel (easy) and serial (difficult) searches based on the search slope (Wolfe 1998). The best descriptor for search difficulty seems to be a large perceived target – distractor difference makes search fast, while otherwise search will be slow (Duncan and Humphreys 1989). A black dot among white dots will pop-out, but this will not be the case if the distractors are dark grey. Many other effects also impact visual search performance: spatial layout of the search array (Sagi 1990; Nothdurft 2000), the distance between target and initial fixation point (Carrasco et al. 1995), or in certain instances learning (Kunar et al. 2007), to mention a few. However, there are exceptions to these findings, too. In some feature searches search time depends on which stimulus is the target (Treisman and Gormican 1988). For instance, an orange dot among red distractors is detected faster than a red dot among orange distractors – a phenomenon called search asymmetry (Wolfe 2001).

When studying visual attention and visual search it is useful to distinguish between overt and covert search. If attentional shifts in a visual search experiment are accompanied by eye movements they are overt – visible. Attentional shifts may also occur covert – hidden. This may happen while a subject is fixating an object with its eyes, in other words, the eyes are

stationary. Many attentional tasks can be conducted covertly (Posner et al. 1980). Classical laboratory experiments use large, distinct stimuli that do not require foveation and thus have mostly bypassed the impact of eye movements on visual search. In these searches, enforced fixation preventing eye movements has usually no impact on the results (Klein and Farrell 1989). However, visual resolution is greatly reduced in the periphery of the visual field, only the small region covered by the fovea has high resolution (Wertheim 1894). Therefore, most real world searches require foveation and are coupled with eye movements, typically 3-4 per second. If fixation is not enforced, human observers will make saccadic eye movements during most search tasks (Findlay 1997). The number these are closely linked to reaction time (Zelinsky and Sheinberg 1997). Eye movements reflect the complexity of the search task, their amplitude increases and the duration of the fixations in between relatively decreases in easy search tasks compared to difficult searches (Vlaskamp et al. 2005). During a natural search for objects in the real world, we make eye movements to bring regions we need to inspect into the high resolution fovea and objects that we inspect may move to new locations after we have determined they are not the target.

1.1.1 Saliency

In our environment we are confronted with an overwhelming amount of information. Due to limited processing power of the brain it is not possible to compute everything in time (Tsotsos 1990). Yet, reacting and orienting in this environment appears to be nearly effortless. The human visual system, and that of many animals, is well adapted to such a task. Usually, only particular pieces of a visual scene are attended to (Goldsmith 1998). This selection process is based on visual salience. To us an object or a location is salient, if we perceive it to be different from its surroundings (Koch and Ullman 1985). Therefore, saliency strongly depends on context, the more different an object is, the higher is its saliency - *“this location is sufficiently different from its surroundings to be worthy of your attention”* (Itti 2007). Usually, the most salient location attracts our attention. It is important to understand that saliency is not a physical property of a stimulus but a subjective perception, and therefore, may be different from observer to observer – or species to species. A line of differing orientation may not be as salient to barn owls as it is to humans.

Koch and Ullman (1985) proposed the concept of a saliency map as a solution to the question of how saliency is computed in the brain. Their concept is dependent only on “bottom-up” factors, that is, entirely stimulus driven. This saliency map is a central topographical map that encodes stimulus conspicuity in the visual scene which is then used to determine the locus of next attentional deployment. The saliency map received input from individual feature maps that derive of early stages of visual processing. Each feature map is tuned to a single feature, for instance orientation or luminance intensity. The feature maps are coded in parallel over the entire visual field (Treisman and Gelade 1980). In each feature map locations that differ for the specific feature are highlighted. These highlighted locations are integrated to a central saliency map: this saliency map then is a topographic representation of saliency, which is independent of the features (Koch and Ullman 1985; Nothdurft 2000). The contribution of a feature to the saliency map depends on the differences in these features (Itti and Koch 2001). That is, a feature map with only one outstanding location has more impact than one with many active locations.

The final selection mechanism is quite simple: Attention is drawn towards the most active location in the saliency map by a Winner-takes-all mechanism. Then attention is retracted from that location by an inhibition of return mechanism and the location with the next highest saliency is selected (Posner and Cohen 1984; Klein 1988; Itti and Koch 2000). This process then continues until the target is found or the search is abandoned.

However, this pure bottom-up deployment of attention is only true in the absence of a particular task. All mentioned stages can be modified by “top-down” factors (Desimone and Duncan 1995; Niebur and Koch 1996). Top-down factors take into account the internal state of the observer, such as motivation or knowledge about the scene context (Neider and Zelinsky 2006). For instance, a search task for a specific feature may lead the observer to ignore highly salient locations (though some salient stimuli cannot be ignored (Theeuwes 1994b)) or put more emphasis on that one feature than on others. According to the popular model of visual search, guided search, top-down factors change the saliency in a scene to prioritize items that share features with the search target (Cave and Wolfe 1990).

Effects of visual attention are found in many areas in the primate brain, in areas from the pulvinar in the thalamus to cortical areas such as the posterior parietal cortex (Wright &

Ward 2008). Since many feature maps are located in specific brain areas, the same has often been assumed for a central saliency map. Many candidates for the location of a saliency map have been proposed, among them the primary visual cortex (Li 2002), medial temporal cortex (Treue and Cesar Martinez-Trujillo 2006), left interparietal area (Kusunoki et al. 2000) and the frontal eye fields (Bichot et al. 1996). Interestingly, some of these maps seem to be modulated by top-down factors with differing strengths. While the frontal eye field integrates bottom-up and top-down signals, the saliency map in the lateral interparietal area has only bottom-up influences. It seems obvious, that there is not only one saliency map; apparently, there are many. Probably, their impact on the next attentional deployment differs depending on the task.

1.2 Barn owl vision

1.2.1 Visual capacities of barn owls

Barn owls are nocturnal predators. They are highly specialized to hunt in darkness with several adaptations that differentiate them from diurnal raptors. Among these are the exceptional sound localization capabilities (Payne 1971; Knudsen and Konishi 1979), special feather designs for silent flight (Bachmann et al. 2007), and large frontally oriented eyes with high quality optics (Harmening et al. 2007b). The eyes occupy approximately 50% of the cranial volume which is typical for birds. While the basic optical eye structure is similar to that of mammals, barn owl eyes are shaped tubular. That is, a concave intermediate segment is elongated along the anteroposterior axis, thus forming a tube before connecting to the posterior segment. This increases the retinal image compared to a round, globose eye of similar weight. While their eyes appear to be frontally oriented, the optical axes have been observed to diverge by 62° (Harmening and Wagner 2011). However the location of their area centralis – the location of highest resolution in the retinae due to photoreceptor and ganglion cell density - is shifted to the temporal retina. This leads to parallel visual axes despite of the eyes' differing orientation, typical in owls and raptorial birds. Owls have a rod dominated retina with a rod – cone ration of 30:3 (Oehme 1964), especially their fovea consists almost only of rods (Fite 1973). While this arrangement leads to low visual acuity – based on

measurement method between 3.5 - 8.4 cycles / degree (Wathey and Pettigrew 1989; Ghim and Hodos 2006; Harmening et al. 2009) it maximizes sensitivity at low light levels leading only to a small drop in acuity at low light levels (Orlowski et al. 2012). Due to the frontal facing eyes, owls have a small visual field compared to other birds ($\sim 200^\circ$ in tawny owls compared to $\sim 316^\circ$ in pigeons (Martin 1984)) but a large binocular field of view (46° in barn owls compared to 22.5° in pigeons (Martin 1984; Knudsen and Knudsen 1989)). One of the implications of the large binocular overlap is that barn owls are the only known non-mammalian species able to use stereovision for depth estimation (van der Willigen and van Opstal 2000; van der Willigen et al. 2002). Stereovision is based on the neural comparison of the retinal activity of the shared binocular field for each eye. Birds share the split visual pathway known from mammals. Retinal efferents either project to the optic tectum, the avian homologue of the superior colliculus or to the thalamus (Karten 1969, Revzin and Karten 1966). The tectal pathway includes the nucleus rotundus and the ectostriatum and seems to be especially dominant in laterally eyed birds such as the pigeon. The thalamic pathway projecting to the visual wulst, the avian homologue to the primary visual cortex, is important for binocular birds, that is diurnal raptors or owls (Pettigrew and Konishi 1976; Wagner and Frost 1993).

1.2.2 Active Vision

Due to their tubular eye shape, the eye movements of barn owls are limited to 2° (Steinbach and Money 1973). This is compensated by a flexible neck, possibly allowing head rotations more than 270° (Bowmans, Krings and Wagner, unpublished). These head rotations are remarkably fast, up to $900^\circ/\text{s}$, similar to human eye motions (du Lac and Knudsen 1990). Three types of barn owl head movements were described (Ohayon et al. 2006): Fixations, head translations, and head rotations. Fixations are periods of no head movements, translations are movements along a straight line, while head rotations are combined with translations. These simple movements are combined to form the complex movement patterns involved in predation (Fux and Eilam 2009). Another typical head movement are the peering movements, small recurring translations along a horizontal axis, which are assumed to be involved in distance estimation (van der Willigen et al. 2002).

In a novel attempt Ohayon et al. (2008) used a head mounted camera, the OwlCam, to study overt attention in these birds. Due to the near immovability of the owls' eyes the camera could record first person videos from the owls' point of view. In this study the authors could show that barn owls consistently aligned objects of interest to a specific location in the video frame, a location they called "functional fovea". In a recent study it was shown with ophthalmoscopy that this fixation spot indeed aligns with the retinal area centralis (Hazan et al. 2015). The results of Ohayon et al. (2008) further showed that free viewing barn owls are attracted to salient locations when confronted with natural scenes – though not always to the most salient location. There are several studies investigating the neural substrate of attentional behavior in barn owls. Most tectal neurons are bimodal for auditory and visual information (Reches and Gutfreund 2008; Reches et al. 2010). It is assumed that tectal neurons are involved in stimulus selection and gaze orientation (du Lac and Knudsen 1990; Mysore et al. 2011). Moreover, Zahar et al. (2012) reported pop-out capacity of owl tectal cells, though this was found for motion only – and not for other modalities such as orientation. Therefore, and due to the fact that numerous candidates for a saliency map have been found in primates, it is also possible that the thalamofugal pathway is involved in saliency computing. Considering that the visual wulst is the substrate for complex percepts such as illusory contours and binocular disparities this seems likely (Wagner and Frost 1993; Nieder and Wagner 2001a).

1.3 Organization of the thesis

The main goal of this thesis is to extend research about visual search to a non-mammalian species, the barn owl. This first chapter has introduced basic concepts such as visual attention, saliency, and visual search with consideration of eye movements. Moreover, the visual system of birds and barn owls has been described to the extent necessary for this study. The second chapter will give a short overview of the used methods: The animal subjects used in the experiments, the OwlCam itself, and the stimuli and basic experimental procedure. More details on the specific methods will be described prior to the presentation of the results of the specific experiments.

The third chapter will contain the main part of the thesis, the 6 experiments conducted in the course of this thesis. The experiments will be split in three parts, reflecting the order in which

they were – or will be – published. The first study contains experiment 1 and investigates overt attention in barn owls. Barn owls were confronted with arrays of oriented stimuli to test whether they show similar saliency effects like humans do. Study two and three describe visual search tasks in which the owls were trained to search for a specific target. In the second study barn owls were confronted with orientation (experiment 2) and intensity (experiment 3) feature search arrays, which are known to have a pop-out effect in human perception. The third study consisted of three more difficult visual searches, experiments 4-6. Experiment 4 was similar to experiment 3 but with inverted target and distracters to test whether barn owls have search asymmetries. Experiment 5 and 6 were conjunction search tasks. Here, the question was not only whether the barn owls show the same effects as humans do in these searches, but also whether barn owls can do these searches at all.

In the final chapter the findings will be discussed. Is barn owl visual search similar to human visual search? What is known from other species and how does barn owl visual search fit to these findings? Finally, this thesis will finish with an outlook on open questions and further research opportunities in barn owl visual search.

1.4 Statement of originality

The work contained in this thesis has not been previously submitted for a degree or diploma at any higher education institution. To the best of my knowledge and belief, the thesis contains no material previously published or written by another person except where due references are made.

.....

.....

Place and date

Signature

2. Methods

This chapter will provide a brief overview of the different stimuli and the experimental procedures. More detailed descriptions of the individual experiments are found in the following chapters focusing on the specific experiments. Briefly, owls wearing an OwlCam were confronted with several feature and conjunction arrays. In the first experiment the birds were observing a feature array without a direct search task, while in the other 5 experiments the barn owls were trained to search for a specific target in the array. I analyzed, among others, search time and the number of saccades until the target was fixated for the first time. These parameters characterized the difficulty of these search tasks for barn owls.

2.1 Animal subjects

The experiments described here were conducted with two American barn owls, *Tyto furcata pratincola* (subjects WH and HB), from the breeding colony of the Department of Zoology at RWTH Aachen University. Both animals were hand raised and tame. Before they started doing experiments with the OwlCam they had conducted experiments in a similar free-flight-setting before (Hausmann et al. 2008). Experiments were conducted under a permit issued by the Landespräsidium für Natur, Umwelt und Verbraucherschutz Nordrhein Westfalen, Recklinghausen, Germany. During the experiments the owl's body weight was kept at about 90 percent of their free-feeding weight (420g and 480g). The birds were rewarded pieces of chicken meat during the experiments and were fed with additional chicken meat after an experiment to maintain body weight irrespective of behavioral performance. The owls participated in experiments 5 – 6 days a week, approximately 2 hours a day, and were fed in their aviaries when no experiment was conducted. To supplement their diet they were fed with mice every second week. No attempt was made to reverse their nocturnal cycle. Both owls had a small aluminum head post fixed to their skull, 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)). Three other owls also participated in the study (subjects HA, VA, and TE). HA and VA died due to illness before enough data could be collected, while owl TE was unable to learn the task.

2.2 The OwlCam

The studies described in this work are based on data recorded with the OwlCam. The OwlCam is a lightweight microcamera combined with a video broadcasting board, cast into a customized frame of dental cement (**Fig. 2-1**). 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 metaloxide semiconductor active pixel sensor (purchased from <http://www.microcameras.com>, site no longer available) 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 × 8 × 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. I have good experience with the considerably lower 3.7 V delivered by a single lithium polymer cell if the converter is discarded. 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. 2-1c**). 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 were then covered with a fluid rubber coating (PlastiDip) to prevent current leakage and to improve durability. Power connectors were custom made from spare cascable IC pins (**Fig. 2-1a** and **b**). The antenna of the broadcast unit was cut to an arbitrary length, because the transmission range is relatively small and antenna length is not critical. The entire setup was cast into dental cement (Paladur, Heraeus) to fix the physical layout of the camera and also to provide the custom made mounting socket. The mounting socket slides onto a small metal plate implanted into the owl's forehead (for surgery see above). The camera's field of view must be realigned 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. The weight of the setup without batteries is 3 g. A lithium-polymer rechargeable battery (LiPo; Tenenergy) 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. 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. 2-1b**). 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.

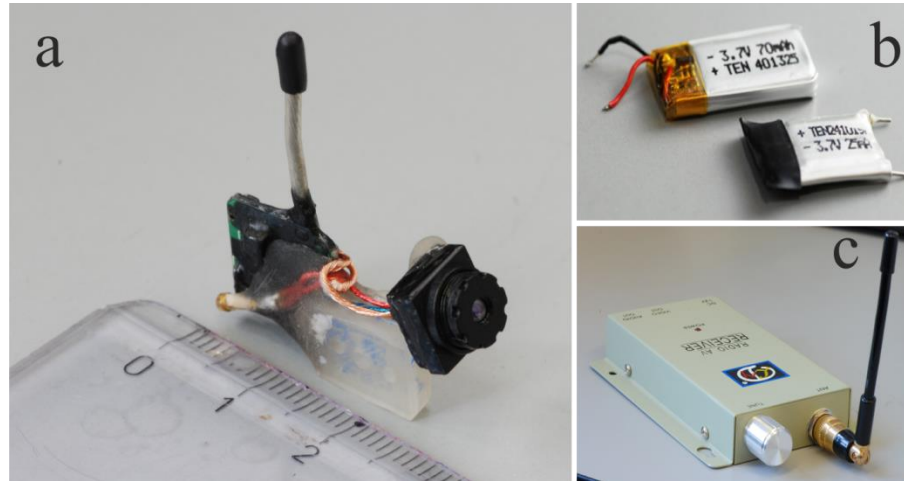


Figure 2-1: The OwlCam. See text for explanation. (a) Overview of the OwlCam setup. The setup is light, small, rigid, and easy to handle. (b) Rechargeable LiPo batteries serve as the power source. (c) 900-MHz tunable receiver.

2.3 Setup and stimuli

Six different experiments were conducted for this thesis. The stimuli consisted always of rectangular search arrays containing one unique target among several distracters. In the first experiment the owls were tested without a direct task. This was done to test for general saliency effects. They could observe the stimuli and the target at their own volition. The stimulus was an orientation feature search array with 25 items. That is, all items were rectangular bars, with the target oriented 45° from the owl's point of view. All items were slightly jittered in position and orientation. Prior to experiments 2 – 6 the owls were trained to search for the respective target. These experiments were conducted with 5 different set sizes: 16, 25, 36, 49, and 64 items. Experiment 2 was an orientation feature search experiment, too. However, the array was less jittered than in experiment 1. Experiments 3 and 4 were intensity feature searches. The items were round discs; in experiment 3 the target was brighter than the distracters; in experiment 4 it was darker. Experiment 5 and 6 were conjunction search experiments. There the target was a unique combination of intensity and

orientation (in 5: bright target, 45° orientation, in 6: dark target, 0° orientation) while the distractors were the remaining combinations in randomized proportions. Figure 2-1 shows examples of each stimulus.

The basic setup was identical for all experiments. The owls were unrestrained and wore the OwlCam. The owls' fixation spot in the video feed was determined using a calibration method explained in detail in chapter 3.3. Prior to each experiment the birds were placed on a perch fixed to a wall of a rectangular room. From there they could observe the search array displayed at the room's floor. However, between experiments, the experimental room was changed twice and the setup was modified. The changes are presented here briefly, and in more detail in chapter 3 and 4. Initially, cardboard stimuli were used. Before each trial a curtain was lowered in front of the owls' perch while the cardboard items were rearranged. Then the curtain was retracted and light was switched on to initiate a trial. For Experiment 2, 3, and part of experiment 5 were conducted in a second room, but with the same experimental setup. Experiments 4, the other part of 5, and 6 were conducted in a third room. In experiments 4 and 6 the stimuli were projected on the ground by a projector, thus the curtain was no longer used. So, the experiments are numbered thematically and not in temporal order.

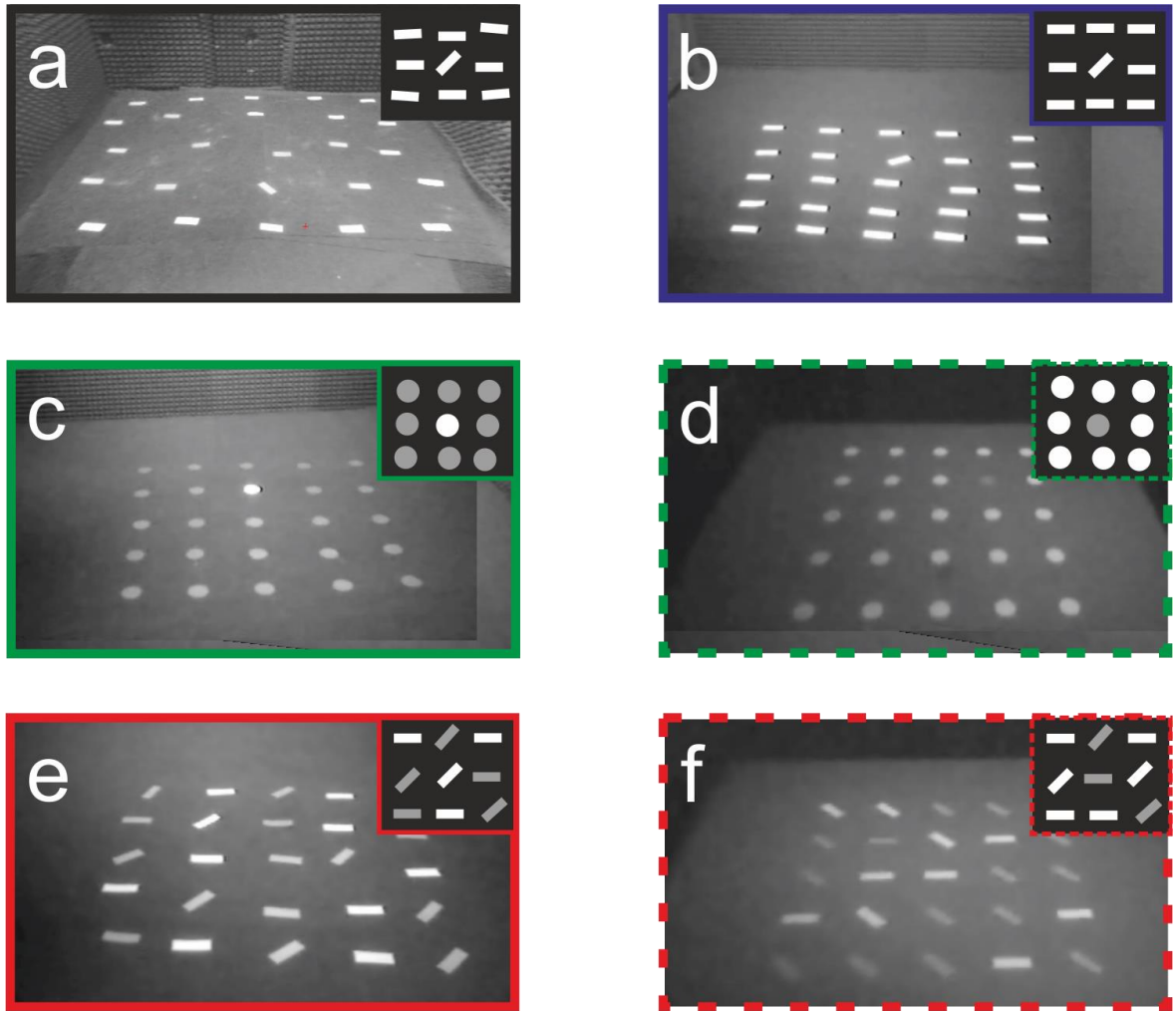


Figure 2-2: Overview of the stimuli. Shown in each subset is a panoramic construction from an OwlCam video with a search array of 25 items. A schematic of the same stimulus type featuring the target in the center is shown in the top right of each panoramic. Overall luminance differences between the videos are due to different camera angles and battery charge. **a)** Orientation stimulus used in experiment 1 (chapter 3); **b)** Orientation, experiment 2; **c)** Intensity positive (both chapter 4); **d)** intensity(-); **e)** conjunction; **f)** conjunction2 (all chapter 5).

3 Overt attention towards oriented objects in barn owls

This work was already published in PNAS in 2011 (Harmening et al., 2011). . The text of this publication is slightly edited here to conform to the style of this thesis.

Julius Orłowski was involved in designing this study, together with Wolf Harmening, Ohad Ben-Shahar, and Hermann Wagner. Wolf Harmening build the OwlCam. Julius Orłowski and Wolf Harmening performed the research; the actual experiments were conducted by Julius Orłowski, while Wolf Harmening trained the owls to wear the OwlCam. Wolf Harmening, Julius Orłowski, Ohad Ben-Shahar analyzed the data. The manuscript was written by Wolf Harmening, Ohad Ben-Shahar, and Hermann Wagner.

3.1 Introduction

In his now-classic experiments, Yarbush (1967) 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 (Mazer and Gallant 2003; Einhäuser et al. 2006) and even in birds (Blough 1977; Cook et al. 1996; Ohayon et al. 2008; Dittrich et al. 2010). 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 Wolfe and Horowitz 2004; Krummenacher et al. 2010). The selective nature of the visual system perhaps is best expressed in what has been termed “visual search” (Wolfe 1994; Hochstein and Ahissar 2002). 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) (Treisman and Gelade 1980). Studies in which the target differs from the distracters in one visual feature are referred to as feature search (Hochstein and Ahissar 2002). 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 (Treisman and Gelade 1980). Although much is known about the properties and the neural networks involved in visual search in humans and primates (Treisman and Gelade 1980; Lee et al. 2002; Hochstein and Ahissar 2002; Hegdé and Felleman 2003; Nothdurft et al. 2009), knowledge of this process (especially its neural substrate) in non-primate 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 (Blough 1977; Cook et al. 1996) and recent orientation-saliency behavior found in archer fish (Mokeichev et al. 2010). I choose to study visual search in free-viewing barn owls, which 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 (Ohayon et al. 2008). Second, barn owls are known to make conspicuous peering movements (Ohayon et al. 2006) and can also covertly shift attention toward interesting targets (Johnen et al. 2001), meaning that their vision is likely to incorporate attention mechanisms. Third, much is known about barn owls' visual system (Pettigrew and Konishi 1976; Liu and Pettigrew 2003), and the neural circuits underlying visual perception in this species have been studied in some detail (Nieder and Wagner 1999; Harmening et al. 2007a; Reches and Gutfreund 2008; Harmening et al. 2009; Zahar et al. 2009; Mysore et al. 2010). With this in mind, I asked whether barn owls exhibit similar visual search behavior as humans. The data presented here indeed show such similarities.

3.2 Materials and methods

3.2.1 Animals

The experimental animals were two adult American barn owls (*T. furcata pratincola*; subjects WH and HB) that were taken from the breeding stock of the Department of Zoology at Rheinisch-Westfaelische Technische Hochschule Aachen. The birds were hand-raised and tame. The wingspan of barn owls is 1.1 m (Bachmann et al. 2007). 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 anesthesia 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.

3.2.2 Experimental Setup and Procedure

Experiments and training were performed in a large room (4.2 m long $\times$ 3.2 m wide $\times$ 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. 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.

3.2.2 OwlCam and Video Analysis

During all experimental and training sessions, the owls carried a head-mounted lightweight wireless camera device, the OwlCam. 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. 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 non-motion (Ohayon et al. 2008). 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 (Ohayon et al. 2008). In brief, during calibration, interesting bright targets scattered on a dark floor were presented (**Fig. 3-1b**). 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. 3-1c**). 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 my 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 (Steinbach and Money 1973; du Lac and Knudsen 1990). 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 my 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 (D'Angelo 2010). 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.

3.3 Results

In my barn owl experiments, the setup and procedures were chosen to resemble the classical visual search studies performed with humans (Yarbus 1967; Treisman 1982), 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. 3-1A**). In a typical experimental trial (**Fig. 3-1B**), 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. I 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 (Oehme 1964; Wathey and Pettigrew 1989), 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. This yields the "functional fixation point" of the owl in camera-frame coordinates, which serves as a reference frame for all of my reported data.

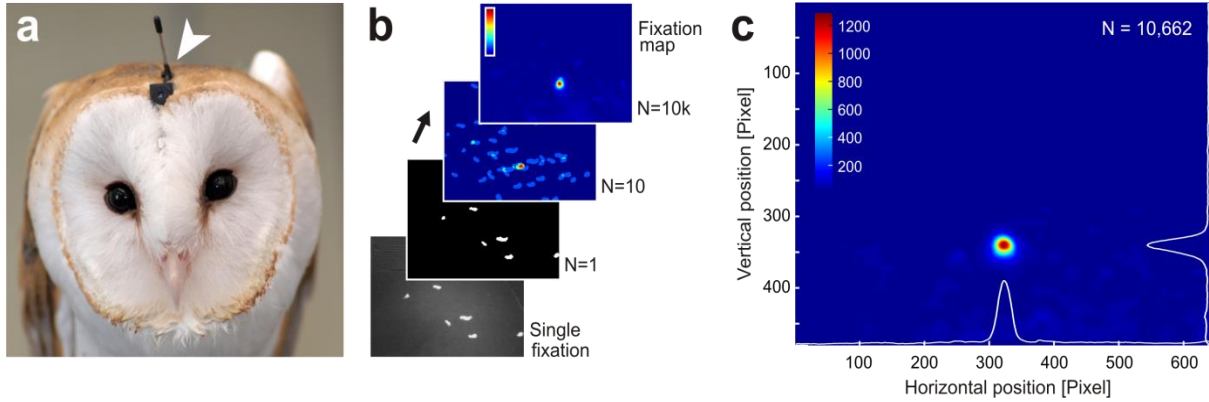


Figure 3-1: Calibration of the OwlCam. (a) OwlCam (indicated by the white arrow) attached to the head of a barn owl. Only the antenna and the frontal part of the camera unit are visible. The total weight of the setup, including the battery, is 5.5 g. (b) Fixation spot calibration procedure. Single fixation 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 my 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).

As discussed in Materials and Methods, both of my owl subjects were found to have a similar fixation spot of $\sim 2.3^\circ$ of visual angle and steep flanks. In the OwlCam image plane, this amounts to a disk of 25 pixels in diameter, which was used in all of my subsequent analyses. In the visual search experiment, the room contained 25 oriented bars scattered on the floor in a 5×5 jittered configuration (**Fig. 3-2**). 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 already fixated earlier. In a total of 97 experimental trials, ~ 120 minutes (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 I

present all results using the notation “HB/WH.” In 28 / 69 experimental trials, a total of 45 / 75 minutes (82,090 / 135,219 frames) of video material was recorded. The average length of each trial was 97.7 / 65.3 seconds (2,931.8 / 1,959.7 frames). The experimental video material was separated into segments of image motion and non-motion (Ohayon et al. 2006), corresponding to the phases of head movement (saccades) and non-movement (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 seconds. The average duration of a saccade was 0.35/0.28 seconds. Because of the static nature of fixation segments, only one frame was used to represent the content of each fixation. For my analysis, I 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. 3-2**):

- 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.

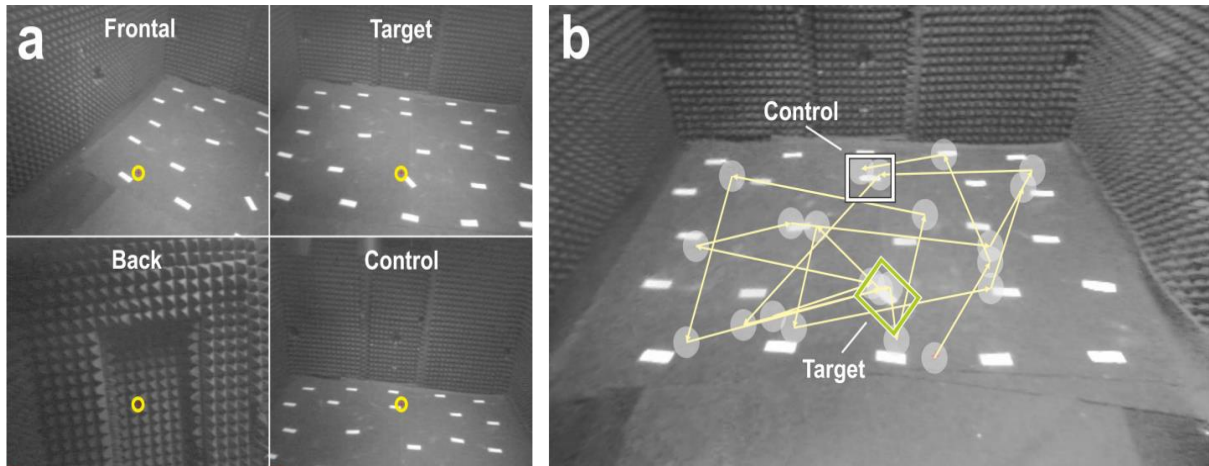


Figure 3-2: Classes of fixations (a) The fixation classes were determined by the content of the frame in the fixation spot (marked by the yellow circle) and away from it. In target fixation, the owl was looking toward the stimulus array, and the target item (in this case, rotated by 45° compared with 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.

For simplicity of presentation, I also designate all non-back 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 my 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, I 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. 3-2a**). 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, I also counted the number of fixations for each category in each trial. For example, in the trial shown in **Fig. 3-2b**, the owl looked at the target three times, whereas the fixation spot appeared at the control item two times.

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, I also plotted the data as cumulative probability distributions (**Fig. 3-3b**). 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, Figure 3-3b 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, the

analyses clearly show that the target exhibited increased saliency for both owls. I 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. 3-3c**), 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 individual 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 Figure **3-3b**. The curves reflecting the fixations at target are shifted to the right compared with the control curve (**Fig. 3-3d**). 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. I 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. 3-2b**, 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. 3-3e**). 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. 3-3f**. 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, my 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 the 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. 3-3e**). No significant differences were found compared with the mean number of saccades to the differently oriented target ($P = 0.73$ / 0.59). Thus, the most salient visual items that I 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.

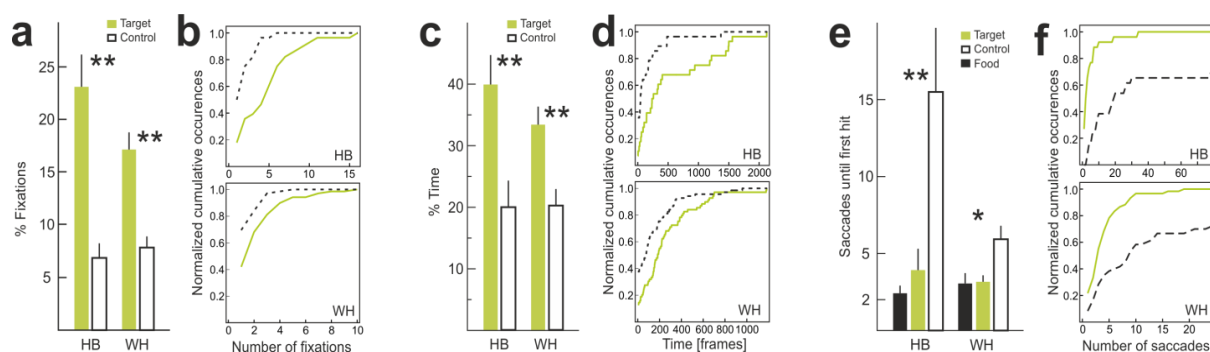


Figure 3-3: Target advantage over control in terms of number and total fixation time. (a) Mean proportion of fixations on target (green, filled) and control items (white, open) out of all frontal fixations for both owl subjects (HB and WH). The difference between target and control conditions

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. **(e)** 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. **(f)** 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.

4 Visual Pop-out in barn owls: Human like behavior in the avian brain

This is an edited version of a manuscript which is ready for submission

Author contributions:

Julius Orłowski designed the research, together with Yoram Gutfreund, Ohad Ben-Shahar, and Hermann Wagner. Wolf Harmening built the OwlCam. Julius Orłowski, Christian Beißel and Friederike Rohn performed the research; experiment 2 was conducted by Christian Beißel for his bachelor's thesis, experiment 3 was conducted by Friederike Rohn for her bachelor's thesis. The data was analyzed by Christian Beißel, Friederike Rohn, and Julius Orłowski. The manuscript was written by Julius Orłowski, Ohad Ben-Shahar, and Hermann Wagner.

4.1 Introduction

Attentional selection of salient or task-relevant information (Yarbus 1967; Tsotsos 1990) helps to focus sensory processing. For example, animals and humans direct their gaze towards conspicuous objects during visual search. In standard visual search tasks in the laboratory observers are asked to search for a target item in a scene containing also other items, the distractors. Such a task may be classified as easy/parallel or difficult/serial (Wolfe and Horowitz 2004). In easy search tasks search time and the number of fixations until the target is found do not depend on the total number of items present, a phenomenon referred to as parallel search or *pop-out* (Treisman and Gelade 1980; Wolfe 1994; Zelinsky and Sheinberg 1997). Pop-out may thus be regarded as a very effective search strategy. Targets tend to pop out if they are distinctly different from the distractors in at least one feature such as color, motion, or orientation. In difficult search tasks, for instance, when the target is specified by a combination of features, search time and the number of fixations until the target is found increase linearly with the number of items in a display (Treisman and Gelade 1980; Williams et al. 1997). Here, serial focusing of attention on single items or a group of items at a time is required until the target is found. Therefore, this case is often called *serial search*.

Since pop-out facilitates the detection of predator and prey, it should have evolved whenever the ecological conditions provided enough selection pressure and when enough brain capacity was available. Indeed, pop-out is present in humans and primates (Treisman and Gelade 1980; Hochstein and Ahissar 2002; Wolfe and Horowitz 2004; Nothdurft et al. 2009). By contrast, less is known about it in non-primate animals. It is already known that free flying bees are able to find a target among differently colored objects, but as set size increases so does their search time (Spaethe et al. 2006). Archer fish are able to shoot at targets displayed on screens based on saliency and are able to match human performance in a serial search task (Mokeichev et al. 2010; Rischawy and Schuster 2013). Barn owls fixate at an odd target faster, longer, and more often than a randomly chosen distractor item (Harmening et al. 2011). These findings demonstrate capabilities of visual search in different species, but are not sufficient to demonstrate a pop-out. The only non-mammalian species for which pop-out has been demonstrated are the rat (Botly and De Rosa 2012), the pigeon (Blough 1977; Allan and Blough 1989) and the zebra fish (Proulx et al. 2014), but this already indicates that a cortex is not necessary for the implementation of pop-out sensitivity. Moreover, Zahar et al. (2012) reported pop-out capacity of owl tectal cells, though this was found for motion rather than static pictorial cues such as orientation or luminance. Since more information is needed both at the behavioral and neural levels, it is especially interesting to examine non-primate species in more depth to find out what types of visual-search strategies are present, whether these species have evolved pop-out sensitivity, and how this sensitivity is implemented in the brain.

The barn owl is an excellent model system for such studies. This species is a keen hunter that uses both the auditory and visual systems to locate prey (Harmening and Wagner 2011; Orłowski et al. 2012; Wagner et al. 2012). It possesses stereopsis (Willigen et al. 1998) and motion parallax (van der Willigen et al. 2002) that both help to unmask camouflaged objects. Crossmodal attentional advantage also has been demonstrated (Hausmann et al. 2008). Furthermore, a big advantage of using the barn owl for such studies is that their gaze may easily be tracked by monitoring head movements (Masino and Knudsen 1990; Ohayon et al. 2006). This is possible because barn owl eye movements are limited to less than 2 degrees (Steinbach and Money 1973). One way to monitor these head movements is a head-mounted camera, known as the OwlCam (Ohayon et al. 2008). The scenes recorded by the OwlCam

offer a unique first person view from the owl's perspective and facilitate analysis of its visual decisions during visual search (or other) tasks.

Instead of measuring reaction times as commonly done in humans (Treisman and Gelade 1980; Duncan and Humphreys 1989; Wolfe 1998), the findings by Harmening et al. (2011) were based on measures more suited for the free-viewing situation, in particular on the number of saccades and the time it takes the owl to fixate the odd target. Using similar types of measures, in the following I report a series of feature-search experiments designed to examine pop-out capacity in barn owls. I report that both search time and the number of saccades until the target was fixated remain largely independent of the number of distractors in a search task where target orientation was used as a feature and in a search task where intensity was the feature that discriminated the target from the distractors. I interpret the data to suggest that barn owls can exhibit pop-out during visual search.

4.2 Methods

4.2.1 Animal subjects

Two American barn owls, *Tyto furcata pratincola* (subjects WH and HB), from the breeding colony of the Department of Zoology at RWTH Aachen University were used for the experiments. 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 the experiments the owl's body weight was kept at about 90 percent of their free-feeding weight (420 g and 480 g). They were rewarded pieces of chicken meat during the experiments and were fed with additional chicken meat after an experiment to maintain body weight irrespective of behavioral performance. The owls participated in experiments 5 – 6 days a week, approximately 2 hours a 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 aluminum head post fixed to their skull, 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)).

4.2.2 Setup and experimental sequence

Experimental procedures and the basic setup followed Harmening et al. (2011). I recorded first-person-view videos from barn owls wearing the head mounted OwlCam. The birds were confronted with arrays of items that were organized on the floor of the experimental chamber. All arrays contained one odd item (the target) among several similar items (the distractors). In the orientation-feature search (experiment 2) the items were rectangular bars made from white cardboard and measured 15 x 5 cm. The target was slanted 45° compared to the prevalent distractor orientation. In the intensity search (experiment 3) the items were round discs 5 cm in radius. Here, the target was cut from white cardboard, while the distractors were grey. Arrays in both types of stimuli were rectangular in size and could contain 16, 25, 36, 49, or 64 items. The size of the experimental chamber was 545 x 405 x 265 cm and its walls were coated with pyramidal foam to provide sound attenuation. The owl's perch was placed 200 cm above the floor close to the smaller wall. From there the owls could observe the arrays placed on the floor. Between experimental trials an opaque retractable curtain was lowered in front of the perch to block the animal's view. The target item was placed at a random *internal* location in the array (i.e., targets were never placed at the outer ring of the arrays to avoid margin effects). Inter-item distance on the floor was kept constant at 15 cm except for a small positional jitter. Thus, after perspective projection, the retinal image of the arrays varied from an average of 30° x 15° in 4x4 = 16 item arrays to 55° x 30° in 8x8 = 64 item arrays.

Prior to the experiments the owls were trained to search for the target item. In this training phase that lasted up to a month food items were placed on the target to make the owls fixate it as fast as possible. Trials were conducted using the following procedure: First, the owl was placed on the perch with its view blocked by the curtain while the experimenter arranged the stimulus array on the floor. Then the experimenter left the room, retracted the curtain, and switched the light on, thereby starting a trial. The owl would then start searching for the target. A trial was terminated either after the owl flew from the perch to fetch a target or after it looked around freely for a maximum amount of time -- three minutes in orientation trials and one minute in intensity trials. Up to 15 trials per day were performed; approximately 20% (3-4) of these trials were reinforcement trials with food placed on the target bar to keep the owl motivated for the duration of the experimental session. These reinforcement trials

were excluded from analysis. Overall, experimentation period lasted 71 days for a total of 980 trials.

4.2.3 OwlCam calibration

During all experiments the owls were wearing the OwlCam, a lightweight wireless microcamera specifically designed to be worn by barn owls without restricting their head movements (Harmening et al. 2011). The OwlCam's digital video signal was stored at 30 frames per second in a 640*480 pixel video format. The videos were segregated into fixations (static video segments) and saccades (video segments showing significant motion) using a custom written algorithm. Due to the barn owls' lack of eye movements (Steinbach and Money 1973) and the fixed relation of the OwlCam to the gaze of the barn owl, a 'first person' representation of the owl's field of view was obtained. However, the location of the owls' 'functional fixation spot', i.e., its region of visual attention in camera coordinates, had to be obtained. For that I followed Ohayon et al. (2008) and Harmening et al. (2011) and in a preliminary step presented the owls with few (3-5) interesting items (food items or food item dummies) on the floor of the experimental room. To detect the food item the owls would repeatedly fixate at them. By design, these food items were much brighter than the floor such that the video frames containing fixations could be converted into a binary black-and white image leaving white only the location of the targets marked. These frames (5336 fixation frames in owl HB, 6579 fixation frames in owl WH) were then overlaid and the quantitative occurrence of items in camera coordinates was determined. This resulted in a circular area where most of the fixations occurred, which is the fixation spot (**Fig. 4-1a**). The center of the fixation spot of owl HB was located at camera coordinate 334 x 315 (in pixels, horizontal, vertical) and was 2.17° wide, while owl WH's fixation spot was at 344 x 319 and was 2.51° wide.

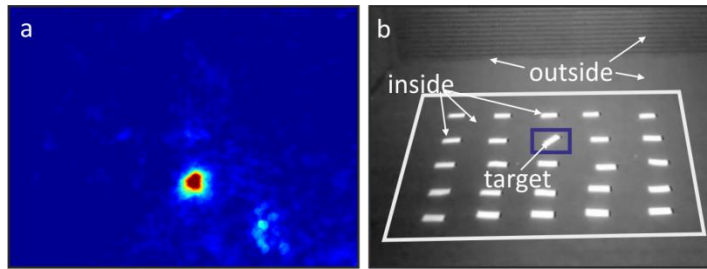


Figure 4-1: Functional fixation spot and classification of fixations. (a) The fixation map is a heat map with blue colors specifying locations of low target probability and red colors specifying regions of high target probability in the image. Assuming the bird has no reason to consistently fixate at "nothing", this map thus represents where in the image plane (or retina) the owl prefers to place targets (by proper head movements), a retinal position I consider as the "functional fovea" or "functional fixation spot". Shown here is the result for subject HB after applying the calibration procedure described in the text (also in Harmening et al. (2011)). Note the approximately circular shape. (b) Typical stimulus scene, containing a 25-item orientation feature-search array on the floor. Note the single target among 24 distractors. Scriptures mark the three content-categories for classification used in this study. Fixations are classified as 'target' if they intersect the target (marked by blue box), 'inside' if the fixation spot is not in the target area but inside the array area, and 'outside' if the fixation spot lies outside the stimulus array. Note that the inside category includes fixations on distractors or anywhere between items in the stimulus array.

4.2.4 Video Analysis

OwlCam videos were several (0.06-3) minutes long and contained numerous (1-140) fixations per trial. Since processing these videos for visual search characteristics required accurate and laborious operations, I helped to develop a video analysis software that provided fully automatic analysis of various aspects of the data. Implemented in Matlab, the system is also equipped with a graphical user interface (GUI) and semi-automatic tools allowing verification and modification of the results by a human inspector (if needed). In the following I describe this system.

Overview: Given an OwlCam video of a trial, it was segregated into fixations (video segments with no or negligible motion) and saccades (video segments with significant rapid motion). All fixations were classified either as “*inside*”, “*outside*” or, in the rare cases where their content could not be identified due to noise, as “*noise*”. Representative frames from “*inside*” fixations were stitched together to create a panoramic view of the scene from the owls’ vantage point. Then, the fixation spot location of each fixation was mapped to this global panoramic view and the distance to the nearest array item was calculated. Using this

information a scan path was generated and each '*inside*' fixation was classified as '*target*' or not (**Fig. 4-1b**) and the distance to the target was calculated. Adding the duration of each fixation and the time that elapsed between them, the system stored all scan path information and exported the data to Microsoft Excel for further analysis. Note that all this process was done completely automatically. Once tabulated, the owls' viewing behavior was then studied with respect to several criteria. In particular, I examined the relative and absolute number of fixations directed onto certain items (say, the target) or regions of interests, and the search time and number of head saccades performed until the items were first looked at.

Following the overview above, the pipeline of video analysis operations may be described as fixation, registration and room stitching, room analysis, and scan path computation. Each stage in this pipeline was designed as a "plug-and-play" module, allowing easy extensions for future and different experiments. The rest of this section describes these stages of the orientation-based visual search experiment that is one of the two foci of this chapter.

Preliminary video cropping: Note that the owls were not trained to fixate a certain location to initiate a trial. The camera was switched on after the trainer had left the room and had switched on the light. At this time the owls were still typically (in about 80% of the cases) fixating the door where the trainer had left the room or at other locations. These fixations suggest that the owl was not paying attention to the stimulus. Only when the owl fixated the stimulus for the first time was it clear that it was aware of the specific stimulus pattern. Therefore, I chose the first fixation on the stimulus as the onset of the trial and thus of the analysis. The analysis process below was applied on these cropped videos.

Fixation extraction: The raw OwlCam video was divided into frame segments of image motion (saccades) and non-motion (fixations) following the approach described in Ohayon et al (2008). First, each frame was divided into non-overlapping blocks of size 60x60 pixels. The histogram of the edges was calculated in each block and compared to the histogram of the same block in the previous frame. Once changes in histograms surpassed a given threshold, the corresponding frame was labeled as "saccade". In all other cases the frame was labeled as "fixation". The video was subsequently divided into continuous segments of saccade and fixation frames. The middle frame of each fixation segment was then extracted and used for further analysis as the representative frame of that fixation. Each such frame

was binarized using a unique luminance threshold set for each video by the experimenter (adaptive thresholding) in order to isolate and segment out the visual objects it contains.

Registration and room stitching: In order to obtain the scan path of the owl over the stimulus, a global panoramic map of the experimental room was needed, a representation that could be obtained after calculating the projection matrices between different fixations (represented by their middle frame as aforesaid). Given the number of trials and amount of raw data, a manual approach of the sort used in Harmening et al. 2011 was unrealistic and an improved automatic approach was required. Unfortunately, however, the nature of the stimulus precluded the use of standard approaches that are based on extracting and matching features (see Zitova & Flusser (2003) for a review). In particular, the high similarity between many objects in the image causes a degenerated feature extraction and matching process (since most of the extracted descriptors are the same), effectively prohibiting successful registration with such a standard approach.

To overcome such difficulties, instead of using local features for the registration task, I use an estimation of a global transformation between the fixations. The registration algorithm starts by choosing a fixation that contains a maximum number of the visual objects (henceforth denoted the *central frame*). Then global transformations between each fixation and the central frame were estimated using the Fourier-Mellin transform (Srinivasa Reddy and Chatterji 1996). The Fourier-Mellin was a particularly appealing choice for my task since its resulting spectrum is invariant under rotation, translation, and scale of the input and its computational complexity is low, allowing the use of modest computing power (e.g., a standard laptop) for processing the data. The transformation begins with a Fast Fourier Transform (FFT) that is converted to log-polar coordinates and represents scale and rotation differences as vertical and horizontal (i.e., translational) offsets that can be measured. A second FFT (known as the Mellin transform) gives a transform-space image that is invariant to translation, rotation and scale. The cross correlation between the log-polar FFT of the images provides the desired global transformation. Unfortunately, the degenerate nature of the images results in several candidates for this transformation and the best candidate is consequently chosen by evaluating the quality of the implied registrations. This is done by measuring the amount of overlap between visual objects in the two fixations and preferring

the registration that maximized it (see **Fig. 4-2**). More formally, the application maximizes the following measure

$$Q = \frac{\#pixels(Visual\ objects\ in\ the\ central\ frame \cap Visual\ objects\ in\ fixation\ i)}{\#pixels(Visual\ objects\ in\ the\ central\ frame \cup Visual\ objects\ in\ fixation\ i)} .$$

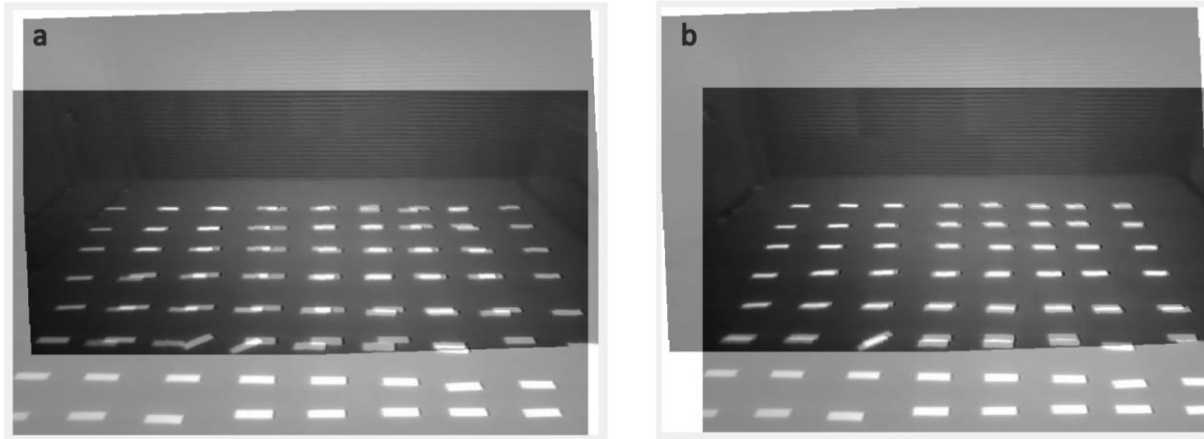


Figure 4-2: Fourier- Mellin registration. The best two results when using Fourier- Mellin registration: The cross correlation values in the log-polar FFT domain of these two examples (a and b) are quite close to each other. The degree of overlap between objects is different, though, allowing picking the right one as the better registration.

Once the best transformation between the central frame and the current fixation is computed, it also provides correspondence between visual objects in the two frames. Thus, the registration was even further improved by seeking the perspective transformation that optimally aligns the centers of mass of the corresponding visual objects of the two frames.

Room analysis: The first step when analyzing the experimental room is to observe the visual objects in it. A binary mask is created by thresholding each of the fixation frames (and the global panoramic image of the room). Each connected component in this mask is a visual object candidate. Using standard tools available in Matlab (regionprops function), each candidate is then analyzed for a set of properties such as its list of pixels, its size and location, its center of mass, and its orientation. Too small (in my case less than 50 pixels) or too big (more than 500 pixels) connected components are marked as noise and excluded from further analysis. Since the room light sources were sometimes visible (and were bright in appearance similar to the bars) I also excluded visual objects that are too far from the mean

location of all objects (more than 400 pixels). Once only stimulus objects are left, their properties are used to classify each of them as "target" or "distractor". Finally, the target and distractors are numbered according to their location in the experimental grid using the coordinates of their center of mass (see **Fig 4-3**).

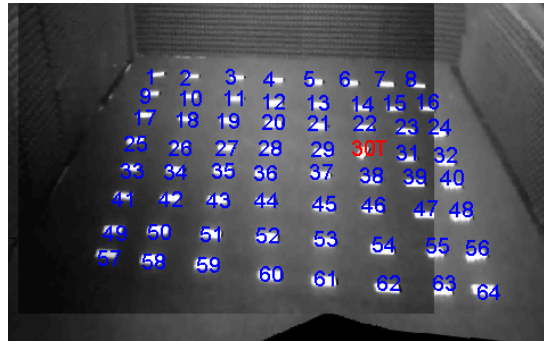


Figure 4-3: Numbered global map. The detected visual object in the global experimental map automatically numbered according to their position. The target is marked with red T. This snapshot taken directly from the OwlCamAnalysis main tool.

Scan path computation: Once the panoramic map is computed and fixation spots are transformed to it (using the registration matrices of each fixation), a full scan path can be created by connecting the transformed fixation spots according to their temporal ordering. The system does so automatically and generates a visualization of the sort shown in Figure 4-4a. In addition, all scan path information is tabulated and presented to the experimenter as shown in Figure 4-4b. This interactive table allows click-and-view operations for reviewing, verifying, and (if needed) correcting pieces of data before exporting it to Excel format.

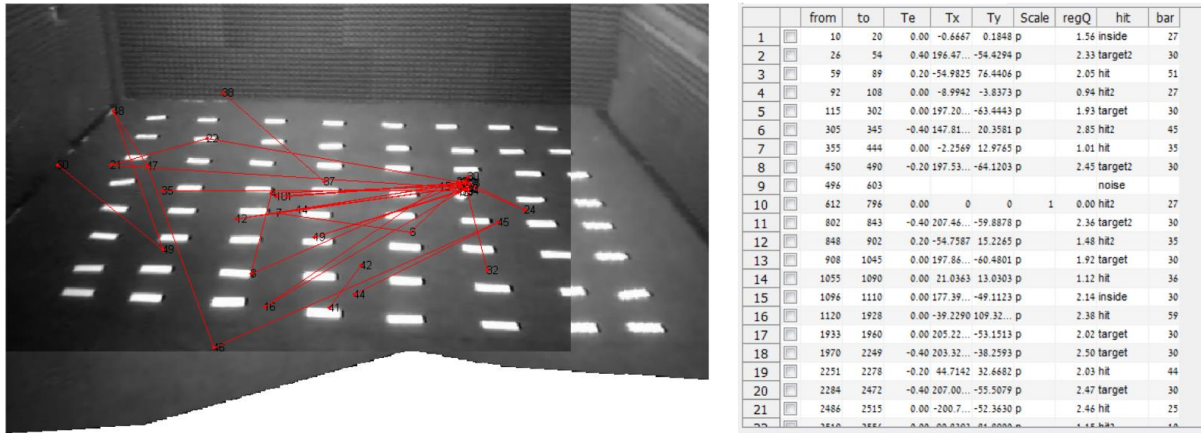


Figure 4-4: The two outputs of the OwlCamAnalysis system. (a) A visual depiction of the scan path on the global panorama map. (b) A tabular organization of the extracted data organized by fixations. All fixations are ordered by rows and each row holds information such as the fixation's starting and ending frame/time, the transformation parameters relative to the central image, a quality measure of the registration, the fixation description (inside/outside/noise, target/distractor, etc...) and the number of the visual object (target or distractor) that the fixation spot landed on (if applicable).

Supervised verification and interactive adjustments: As mentioned above, the system is equipped with a GUI that allows verification and modification of the automatic results by a human inspector. This was needed because occasionally the algorithm would make decisions that are not completely compatible with a human observer, e.g., when deciding what counts as a fixation or what may be the visually optimal transformation that aligns a fixation to the central frame). To that end the user was presented with a display as shown in Figure 4-5. The main controls are located at the left side of the screen (load movie, load fixation map, stitch the room, analyze, etc...). The right hand side of the screen provides the interactive output table and a dialog box with a log of the system's operations. The center of the screen presents a fixation frame (registered or non-registered) and the global panoramic map (if available at the time of presentation). Note how the fixation spot is marked in both panels. Below these panels a graph of frame affinity measure is shown, including the segmentation into fixational video segments (green horizontal bars). The current viewed fixation is marked on this graph with a red vertical line. Navigation between frames or fixations can be made by using the navigation bar between these two panels or by clicking the interactive table on the right.

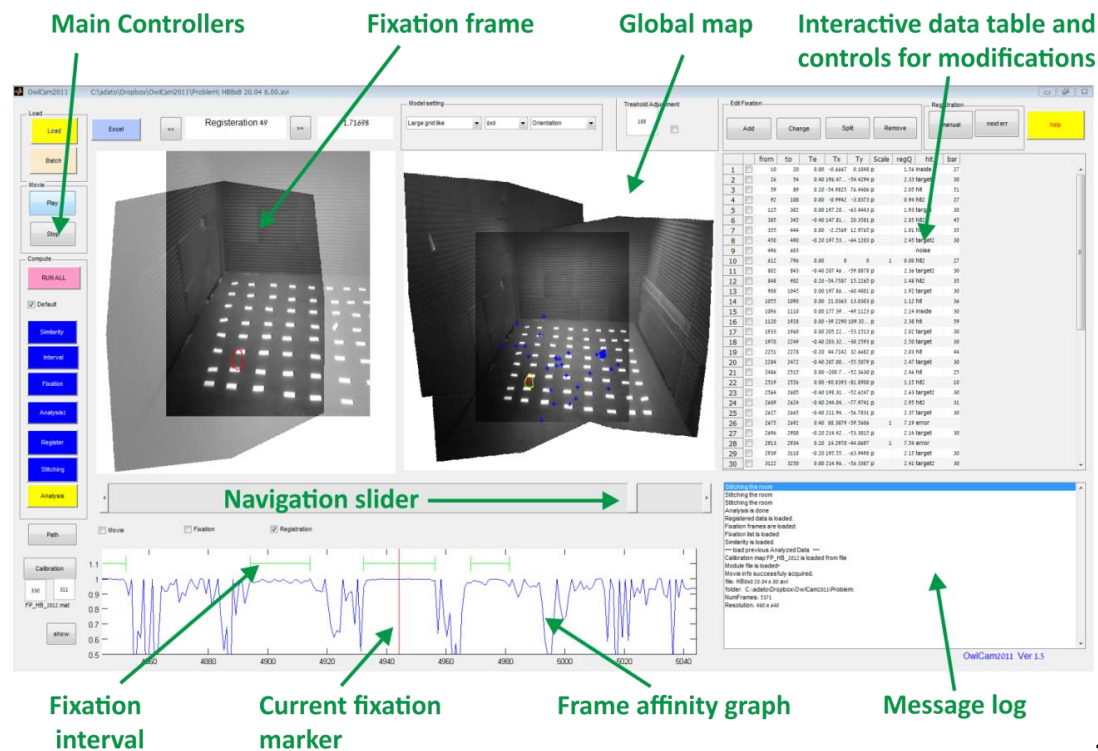


Figure 4-5: The main GUI of the OwlCamAnalysis system. See text for details.

The GUI just described allows the user to review and if needed modify almost all computation results made by the system. She/he can first modify fixation intervals (add, delete, change, merge, and split) if needed. After stitching, the registration is displayed in the main panels along with the registration quality. The user can then modify the frame classification (inside/outside/noise) or adjust the transformation parameters of each fixation interval interactively by opening additional dialogs using the buttons above the table. This process can continue until the visual result is satisfactory. At this point, all information (essentially, the one shown in the interactive table on the right hand side of the GUI) can be exported to file for statistical analysis.

4.2.5 Data Analysis

Unless otherwise declared I 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 significant differences I used “Tukey's least significant difference procedure” (which is not conservative and thus most likely showing significant differences)

as post hoc analysis to determine which data points differed from the group. To compare slopes and to check whether they deviated from a zero slope I used an ANOCOVA covariance analysis.

4.3 Results

After training (see Methods), my two owl subjects HB and WH performed visual search trials for more than 40 days for each experiment. The results in this section, first for orientation (experiment 2) and then for intensity-based targets (experiment 3), are reported by the individual subject (using a HB/WH notation) and later pooled over subjects when applicable. In all cases I report mean performance and the standard error of the mean.

For each subject, the data collected included at least 40 trials per experiment (not including reinforcement trials) and set size (16, 25, 36, 49, 64). This accumulated to 243 minutes (=27472 seconds = 824170 frames) of OwlCam video for owl HB and 233 minutes (=11806 seconds = 354195 frames) for owl WH in experiment 2. In experiment 3 the respective numbers were 147 minutes (=8830 seconds = 264600 frames) and 148 min (=8820 seconds = 264600 frames). For experiment 2 I recorded a total number of 241/233 trials. The owls terminated 189 / 228 trials by flying from the perch. The average duration of a trial was 114.7 / 47.7 seconds, during which a new fixation was selected every 2.6 / 3.4 seconds. In most cases, the owls did not stop scanning immediately after first detecting the target but returned to the target's location after a few fixations. On average, the owls made 43.9 ± 29.9 / 14.1 ± 12.3 fixations during a trial (i.e., in each video). For experiment 3 I recorded 230 / 231 videos, 231 / 155 of these were terminated by flying. Here, there is a shorter average trial duration of 38.2 / 38.3 seconds with a new fixation selected after 4.1/3.8 seconds. On average 9.3 ± 0.43 / 9.7 ± 0.47 fixations were made per trial.

Once fixations were collected, they were categorized as '*outside*', '*inside*', and '*target*' hits (**Fig. 4-6**) as discussed in the Methods. In both experiments only a small part of all fixations were outside of the array area (2.2 - 27.2%). Most of the remaining fixations were 'inside'. Of these, a large portion was also on the target. While the overall proportion of distractor fixations was higher than the proportion of target fixations, this comparison does not reveal

much. Instead, the target fixation has to be set in relation to the expected mean fixations on a random item. Ideally, these expected proportions range from 6.25 % (set size 16) to 1.56% (set size 64). However, because there were 'inside' fixations that were neither on the target nor on a distractor, these numbers are upper bounds and conservative estimates of the expectations. Nevertheless, using this criterion, the observed proportions of target fixations were much higher than the expectations (**Fig. 4-6**). It is also obvious that the proportions of target fixations were higher in experiment 3 than in experiment 2 in both owls. The range was between 29.5% (owl WH) and 36.7% (owl HB) in experiment 2. The proportions of target fixations in experiment 3 did not depend on the set size (**Fig. 4-6**). In experiment 2 the minimum proportion of target fixations was 6.9% (owl WH) while the maximum proportion of target fixations was 20.7% (owl HB). Here, the proportion of target fixations depended on set size. All in all, approximately twice as many fixations were on the target in intensity-search trials than in orientation-search trials.

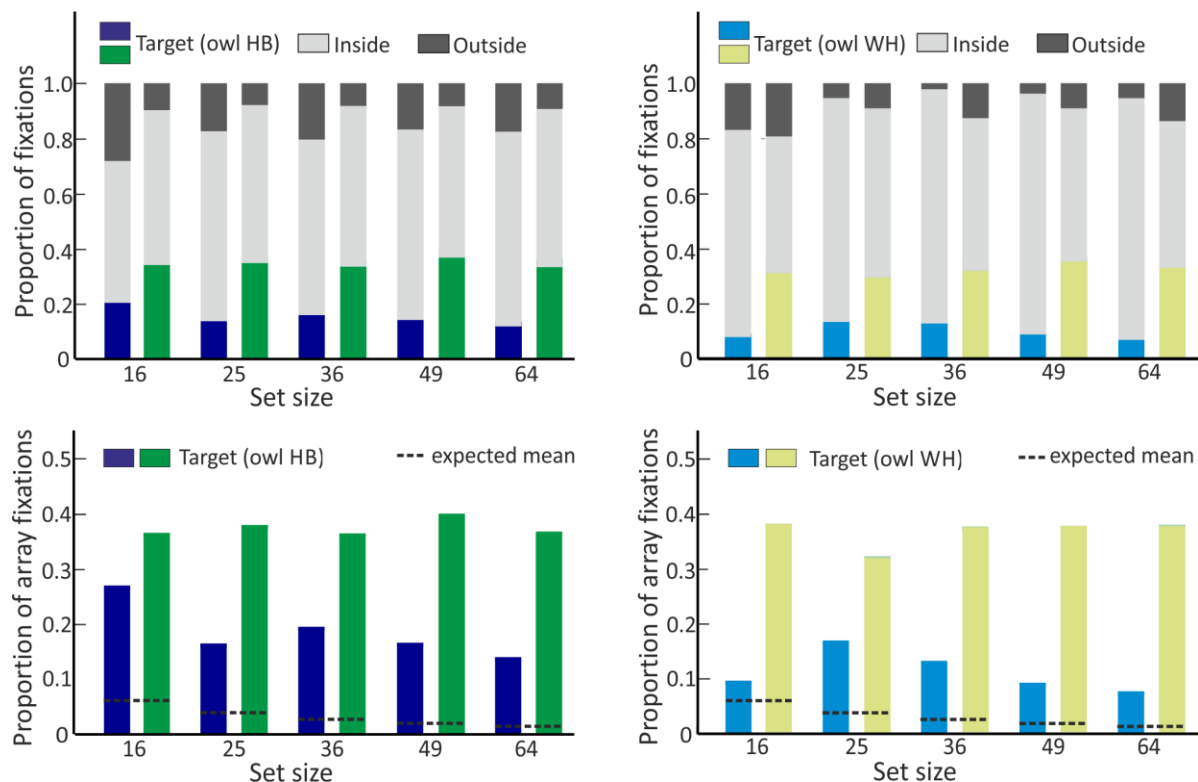


Figure 4-6: Upper row: Proportion of fixations during experiments for each set size and owl. Orientation-feature search is color coded blue (owl HB)/lightblue (owl WH); intensity-feature search is coded green / pale green. Lower row: Ratio of target fixations with outside fixations discounted. The black dashed line shows the expected proportion of fixations on a random item for each array

size. Data from owl HB is based on 10557/2151 (orientation/intensity) fixations in 241/255 videos, data from owl WH is from 3245/2293 fixations in 233/251 videos.

Recall that analysis of OwlCam videos started from the first fixation on the target array (see Methods). From this first fixation the owls started to look for the target by making saccades across the array (**Fig. 4-7a**). In the example with set size 16 (left in **Fig. 4-7a**), the recording started at an outer item. The bird then fixated an inner item, before it looked at the target. Thus, the '*target*' was first fixated with the second saccade. Likewise, the scan path shown in the middle panel starts at an inner item, and then passed through two inner items, before the owl turned to the target after the third saccade. A similar sequence as in the middle panel is shown in the right panel, despite an increase in set size from 36 to 64.

As mentioned before, the target bar was fixated much more frequently than each individual item. The analysis of cumulative probabilities (**Fig. 4-7b**) yields more information than the data presented in figure 4-6. For example, in both experiments the owls made at least one saccade to the target in most of the cases. The numbers range from 52% (set size 64, experiment 2, owl WH) to 100% (many set sizes, both experiments, owl HB or owl WH). The observed percentages were at least two times higher than the average numbers calculated from saccades towards all other items (compare the dotted with the solid lines in **Fig 4-7b**). However, it has to be noted that my analysis program (see Methods) could not detect all distractor-items in experiment 3 due to their lower contrast to the background in the videos. Therefore, the observed percentages might be slightly higher than shown in figure 4-7b. This analysis also demonstrated that especially owl WH fixated the target in more trials in the intensity-search task than in the orientation-search task (compare light green solid lines with light blue solid lines in **Fig. 4-7b**). Moreover, when comparing the normalized cumulative occurrences of saccades towards the '*target*' in both feature searches it is evident that the intensity-curves are shifted leftwards compared to the orientation curve. This means that the first fixation of the '*target*' occurred earlier in a fixations sequence in experiment 3 than in experiment 2. Specifically, in the orientation-search task the target was fixated already with the first saccade in 7% - 48% by owl HB and in 5% - 20% by owl WH. This percentage was much higher in intensity search with 67% - 75% for owl HB and 57% - 75% for owl WH. In other words, in more than half of all intensity search trials the target was fixated with the first

saccade. These data also indicates that the orientation-search task was more difficult for the owls than the intensity search task.

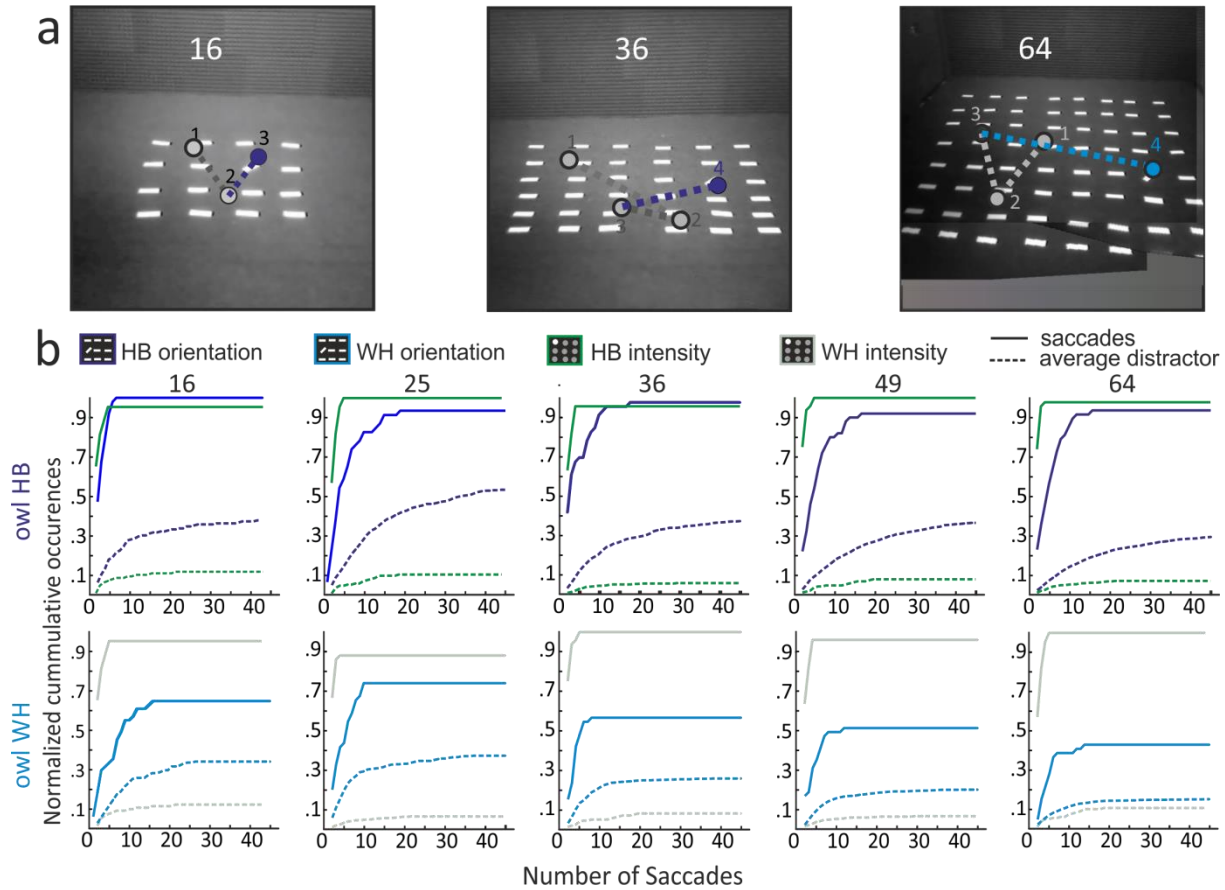


Figure 4-7: Panoramic scene reconstruction and cumulative occurrences. (a) Panoramic scene reconstruction of OwlCam videos showing scan paths and fixation-spot location until the first hit on the target in arrays containing 16, 36, and 64 items for orientation feature search. Overall luminance differences between the videos are due to different camera angles and battery charge. Fixations are numbered sequentially. Fixation spots are filled blue at target location, grey if they cover an 'inner item', and outlined otherwise. Dashed lines represent the scan paths. (b) Normalized cumulative occurrences of saccades until the target was hit first (owl HB: top, blue, owl WH: bottom, light blue lines) and the average of each of the inner items (light grey lines) were first looked at plotted as a function of the number of saccades for each array size. Orientation feature search is color coded blue (owl HB) and light blue (owl WH), intensity feature search is green (owl HB) and pale green (owl WH). Target saccades are solid lines; dashed lines are average distractor saccades. The target plot is shifted left and up from the distractors in each condition for both owls demonstrating that the owls look faster and in more trials at the target. This effect is stronger in the intensity feature search, though it is definitely present for orientation feature search, too.

When comparing the number of saccades at each set size no differences for owl WH in both experiments are evident (orientation: $p = 0.63$, intensity: $p = 0.46$). Owl HB exhibit the same behavior in general, except for one set size in each experiments, namely set size 16 for orientation search and set size 36 for intensity search (HB: $p = 0.00$, WH: $P = 0.04$) (**Fig. 4-8a**). On average across all set sizes, the two owls fixated the 'target' after nearly the same number of saccades: 3.72 ± 0.2 saccades for owl HB and 3.76 ± 0.17 saccades for owl WH in experiment 2, and 1.11 ± 0.07 saccades for owl HB and 1.83 ± 0.09 saccades for owl WH in experiment 3. In experiment 2, HB's number of saccades before the first target fixation increased slightly with set size (best linear fit: $y(HBsaccades) = 0.038x + 2.36$) (**Fig. 4-8a**), while for owl WH the slope was slightly negative ($y(Whsaccades) = -0.01x + 4.12$) (**Fig. 4-8a**). When pooled across subjects, the saccades versus set size function had a small, but significant increase with set size: $y(saccades) = 0.013x + 3.24$ (**Fig. 4-8c**, blue dashed line). The data from experiment 3 looks similar. However, this time the slope in the pooled data was slightly negative (-0.002 saccades / item; **Fig. 4-8c**, green dashed line). The pooled slope for orientation differs significantly from zero; the intensity slope does not ($p = 0.01$ / $p = 0.11$). Therefore, the slope for experiment 2 is significantly larger than for experiment 3.

So far I have analyzed the number of saccades it takes until the target is first fixated. The performance in visual search tasks is usually expressed by the reaction time (Treisman and Gelade 1980; Palmer 1995). Reaction time is typically measured by pressing a button measuring the latency of a saccade after the initiation of a trial. In analogy with these criteria I measured the time until first target hit after the owl had initiated a trial by looking inside the target array. In general, the search-time results closely resemble the findings with the number of saccade until the 'target' was first hit presented above. However, some differences seem worth mentioning. In experiment 2, Owl HB was usually faster in fixating the target, with average time to fixate the target being 6.88 ± 0.6 seconds. Owl WH fixated the 'target' after 11.07 ± 0.07 seconds. Again, set size HB16 differed significantly (HB: $p = 0.00$ / WH: $p = 0.60$). Owl HB's search time increased slightly with set size: $y(HBtime) = 0.087x + 3.64$, while owl WH's search time decreased: $y(Whtime) = -0.09x + 14.15$ (**Fig. 4-8d**). When pooled across subjects, average search time hardly changed ($y(time) = 0.012x + 8.08$). The

search independent overhead was 8.08 seconds. That corresponds nicely to the 3.24 saccadic overhead (see above) once the average fixation duration of 2.6/3.4s is taken into account. In experiment 3 search time for both owls decreased: $y(HBtime) = -0.02x + 3.04$ and $y(WHtime) = -0.01x + 4.28$ (**Fig. 4-8e**). However, there were no statistical outliers between the set sizes for each owl ($p = 0.07$, $p = 0.31$). The pooled function was $y(saccades) = -0.014x + 3.75$ (**Fig. 4-8f**). The search times for both experiments do not differ from each other.

In summary, the number of saccades increases slightly with set size for orientation feature search, but not for intensity feature search. The search time for both feature searches does not change with set size, indicating that barn owls do exhibit a pop-out effect.

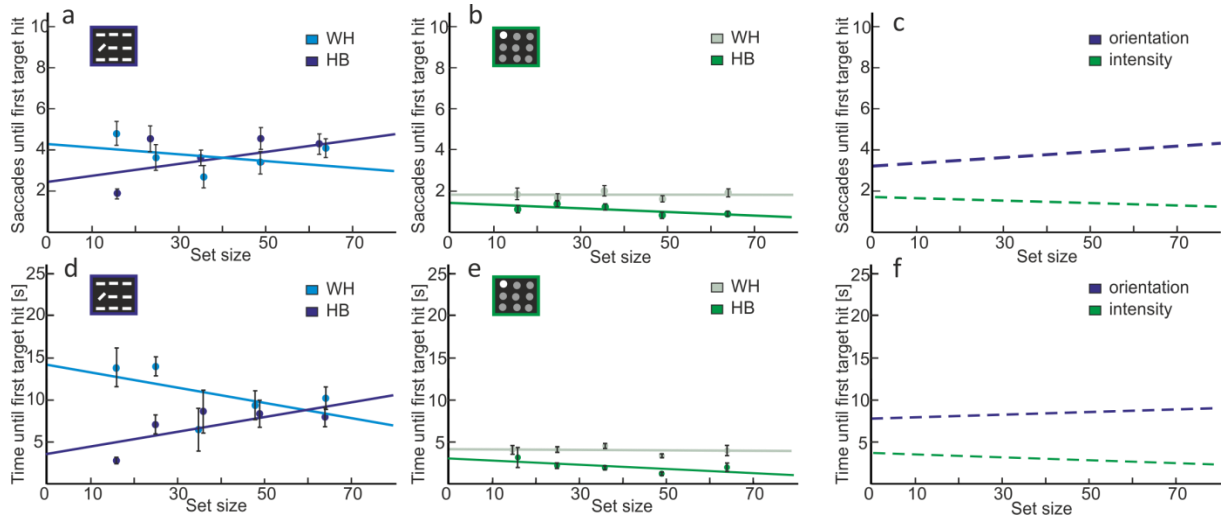


Figure 4-8: Influence of set size on number of saccades and time until first target hit for both feature searches. The upper row (a-c) shows the number of saccades until target detection, the lower row (d-e) shows the search time until detection. Orientation feature (a and d) search is color coded blue (owl HB)/light blue (owl WH), intensity feature search (b and e) is green / pale green. Error bars are standard error of the mean. The left row shows linear best fits to the combined data of both owls (orientation: blue, intensity: green). The linear best fit for saccades until first hit for orientation is: $y(saccades) = 0.013x + 3.24$, for intensity it is $y(saccades) = -0.003x + 1.72$ (c). The slope for orientation differs significantly from zero; the intensity slope does not (Anocova T-probability, $p = 0.05$ / $p > 0.05$). The slope and intercept for orientation is significantly larger than for intensity (Anocova T test with Tukey's least significant difference post hoc analysis). The linear best fit for time until first hit for orientation is: $y(search\ time) = 0.012x + 8.08$, for intensity it is $y(search\ time) = -0.014x + 3.75$ (f). Both slopes do not differ from zero slope (Anocova T probability, $p > 0.05$ / $p > 0.05$). The intercept for orientation is significantly larger than for intensity, but not the slope (Anocova T test with Tukey's least significant difference post hoc analysis).

5 Serial search in barn owls: Conjunction search and search asymmetries

Julius Orlowski designed the research, together with Yoram Gutfreund, and Hermann Wagner. Wolf Harmening built the OwlCam. Julius Orlowski performed the research. The data was analyzed by Julius Orlowski.

5.1 Introduction

In the previous chapter I could show that barn owls have a pop-out effect for orientation and intensity, as humans do (Nothdurft 1991; Theeuwes 1994b). However, for barn owls there were differences between the two features; search for intensity was more efficient than search for orientation. That is unsurprising; similar feature differences have been found with human subjects, too (Treisman and Gormican 1988). So, searches vary in their efficiency for barn owls. In their natural environment barn owls seldom search for targets that are defined by a single feature only. A common prey item like a mouse is, visually, not only defined by its size, but also by its color, shape, and velocity. Searches for such multitudes of features in complex environments are usually more difficult than searches for single features alone. The general assumption based on Treisman's (1980) feature attention theory is that attention is a two staged process: a fast pre-attentive process and a slower process of focused serial attention. In feature searches, search can be conducted by measuring saliency alone – this is no longer possible in conjunction searches. Here the target is a unique combination of 2 or more features, in which the target has no obvious saliency effect (Baluch and Itti 2011). Then, a serial step by step inspection of the search array is necessary to find the target. Without focused attention, features forming a conjunction cannot be bound together (Treisman and Gelade 1980). However, conjunction searches may be facilitated by top down guidance (Wolfe 1994; Wolfe 2007). That is, during a search for dark and horizontal oriented items search can be guided to both dark and horizontal items. The intersection of both sets is then the most salient location in the array.

An interesting phenomenon are search asymmetries. These appear in situations in which search for a target “Q” among distracters “O” is efficient, but the search for “O” among “Q” is not – or at least not as efficient. Usually, feature search asymmetries occur in one of two

cases: The first is if the target is differentiated from the distracters by the presence or absence of a feature, like the added line in the “Q” compared to the “O”. Here, the presence of a feature in the target facilitates search. The other option is if target and distracter differ in the amount of a feature present. For instance, a white circle among grey distracters is easier detectable on a dark background than a grey among white circles (Wolfe 2001). Search asymmetries can also occur in conjunction searches; in that case, one target configuration is detected easier than another due to different serial scanning speed (Treisman and Souther 1985).

Apart from verifying that barn owls also use serial search mechanisms, the objective of this part is twofold: First to determine whether search asymmetries also occur in barn owls. To do that, I inversed the more efficient search, experiment 3, so that the search target is darker than the distracters. Experiment 3 yielded a search slope of -0.014 seconds / item, if a search asymmetry is present in experiment 4, there should be a distinct search slope after contrast inversion. Secondly, I will show the results of two conjunction search experiments. The question here was first, whether the owls are able to learn this more complex search task and if so, whether the learn time would be longer than for a new feature search experiment. The two conjunction searches were conducted using the same two basic features. In the first, experiment 5, the target was white 45° oriented bar, in the second, experiment 6, the target was a grey horizontal bar.

5.2 Methods

Three new experiments were conducted, experiment 4: intensity(-), experiment 5: conjunction, and experiment 6: conjunction2. Experimental procedures and basic setup followed those described in chapter 4. Briefly, owls wearing the OwlCam were confronted with arrays of items that were organized in a rectangular array on the floor of the experimental chamber. All arrays contained one target item among 15 - 63 distracter items. In the intensity search the items were round discs 5 cm in radius with a grey target and white distractors (**Fig 2-1d**). In the first conjunction experiment the target was a white 45° oriented bar – similar to experiment 1 and 2. The distracters were a random distribution of either horizontal white bars, horizontal grey bars, or oriented grey bars (**Fig 2-1e**). In the second

conjunction experiment – experiment 5 - the target was a horizontal grey bar and the distracters random distributions of the other combinations (**Fig 2-1f**). Experiment 5 was partly conducted in the same room as experiment 2 and 3 and partly in the newer setup used for experiments 4 and 6. The size of the new experimental chamber was 576 x 325 x 275 cm; its walls were coated with pyramidal foam to provide sound attenuation. The owl's perch was placed at the same height, 200 cm above the floor close to the smaller wall. The main difference between the setups was the use of a projector (Epson EB-410W) to present the stimuli. It was installed in the room's ceiling and projected the stimuli on the ground. The item-size, inter-item distance, and thus the array size was similar to the previous experiments (15 cm inter item distance, angular array size $30^{\circ} \times 15^{\circ}$ in set size 16 to $55^{\circ} \times 30^{\circ}$ in set size 64). The stimuli were created with Matlab, using the Psychophysics Toolbox extensions (Brainard 1997; Pelli 1997; Kleiner et al. 2007). Due to the use of a projector the experimental procedure was simplified. The curtain was no longer necessary to prevent the owl from seeing the array. Prior to each trial the owl was placed on the perch, then the experimenter left the room and initiated the trial. Individual trials lasted up to 1 minute or until the owl flew from its perch. Overall, the experimentation period for the three experiments lasted 129 days for 850 trials, not counting training (approximately 1 - 2 months for each experiment) and reinforcement trials.

Unless otherwise noted I used the same analysis as for experiment 2 and 3: Data groups were analyzed using a Kruskal-Wallis test to test for significant differences, in the case of significant differences I used "Tukey's least significant difference procedure" as post hoc analysis to determine which data points differed from the group. To compare slopes and to check whether they deviated from a zero slope I used the Matlab toolbox 'aocool' for an ANOCOVA covariance analysis.

The results in this section are shown first for intensity(-) search (experiment 4), second for conjunction (experiment 5), and third for conjunction2 (experiment 6). They are reported by the individual subject (using a HB / WH notation) and later pooled over subjects when applicable. In all cases I report mean performance and the standard error of the mean. Before each class of experiment the owls were trained extensively: experiment 4: 24 / 24 days, experiment 5: 10 / 16 days, and experiment 6: 14 / 48 days. During the training period for

experiment 4 the owls were also getting acquainted with a new experimental setup. After training both owls conducted more than 40 trials for each of the five set sizes (16, 25, 36, 49, and 64) in experiment 5 and more than 20 trials each for each set size in experiments 4 and 6. On a single day, they could perform up to 15 trials. However several of these trials were reinforcement trials with food items placed on the target. In a typical trial, the owl would wait on its perch in darkness until the stimuli were projected on the ground. No cue was provided prior to the stimulus onset and the owls were not trained to fixate a specific location. The owls would then inspect the array, usually making several saccadic deployments while searching for the target. These fixations were usually on other items or the area between items – or on the target, similar to what is shown in figure 3-2 for experiment 1. Usually, the owls would start flying towards a location after some time. If this was the target location, they were rewarded, otherwise not.

5.3 Results

In experiment 4 254 videos were recorded, 136 for owl WH and 118 for owl HB. In 77% of these the owls fixated the target, in owl WH this percentage decreased from 85% at set size 16 to 50% at set size 64. A decrease of 35% might indicate that target detection was more difficult for large set sizes, either because the owl was not able to find the target in the 1 minute time window of analysis or because it aborted the search. However, for owl HB this ratio decreased only marginally from 84% to 83.3%.

To measure the target's saliency to the owls it is helpful to look at the proportion of target fixations out of all fixations as set size increases. This ratio decreased in both owls from .27 / .35 to .16 / .13 (**Fig 5-1**). Even though these ratios are much lower at set size 64, they are still far above chance level, that is above .06 (set size 16) or .02 (set size 64). In experiment 5 the owls performed in 438 (221 / 217) trials; in 78.5% of these the target was fixated. The probability of target fixations per video decreased with set size from 100% / 88.1% (set size 16) to 70.4% / 68% (set size 64). The ratio of target fixations out of all array fixations decreased, too (.29 / .25 at set size 16 to .12 / .13 at set size 64). In experiment 6 258 (141 / 107) trials were performed. Due to time limitations owl WH only conducted experiments for set sizes 16, 36, and 64. The target was fixated in 56.6% of all videos, again decreasing for

both owls when set size was increased: from 81.5% / 67.5% to 60% / 54.5%. The ratio of target fixations out of all array fixations decreased, too (.27 / .10 at set size 16 to .10 / .05 at set size 64).

So, the target detection was always high (above 80%) at small set sizes for owl HB. This is similar for owl WH with the exception of experiment 6. With larger set sizes this ratio decreased by more than 10% with an exception of owl HB in experiment 4. The proportion of target fixations out of all array fixations were decreasing by about factor 2 from set size 16 to 64, but they were always above chance level.

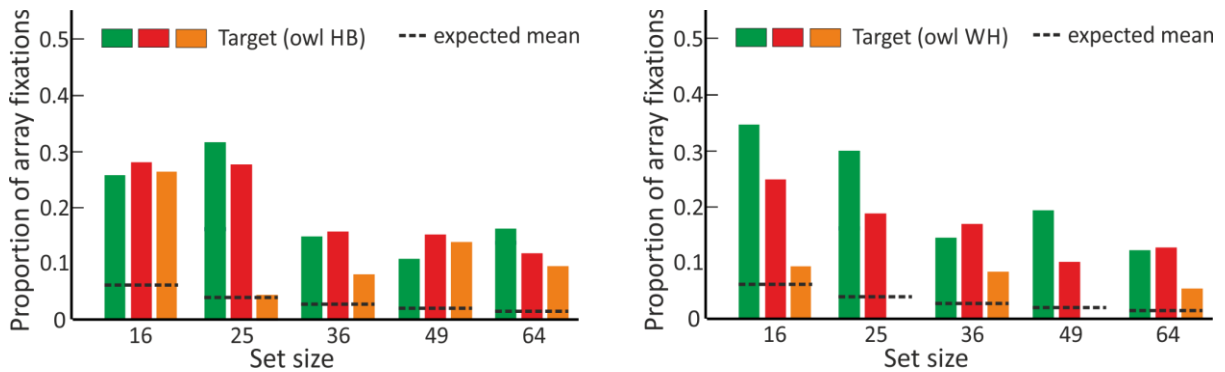


Figure 5-1: Ratio of target fixations with outside fixations discounted. The black dashed line shows the expected proportion of fixations on a random item for each array size. Data from owl HB is based on 1634 / 3487 / 1737 (intensity(-) / conjunction / conjunction2) fixations in 118 / 221 / 141 videos, data from owl WH is from 994 / 2015 / 2261 fixations in 136 / 217 / 180 videos.

In experiment 4 both owls show the same trend when comparing the different set sizes to the search time and saccades. On average across all set sizes, the two owls fixated the 'target' after 3.38 ± 0.38 saccades for owl HB and 2.57 ± 0.24 saccades for owl WH. The average duration of a fixation increased for owl HB and decreased for owl WH at larger set sizes: 2.1 / 3.7 seconds per saccade at 16 items towards 2.57 / 3.22 seconds at 64 items. Even though owl WH was faster on average in detecting the target, both owls show a significant increase for number of saccades and search time when set size is increased (all $p < 0.01$, **Fig 5-1**). In experiment 5 the overall trends are similar to experiment 4, number of saccades and search time increase with set size ($p < 0.01$). Across all set sizes the target was fixated after 4.22 ± 0.39 / 4.15 ± 0.30 saccades. Here, average fixation durations were similar across set sizes: 1.55 / 1.94 at set size 16 and 1.98 / 1.93 at set size 64. In experiment 6 the target was fixated after an average of 5.02 ± 0.63 / 5.93 ± 0.54 saccades. Again, an increase in set size did not

change the fixation duration: 1.68 / 2.92 at set size 16 and 2.03 / 2.81 at set size 64. The number of saccades and search time did increase with set size in experiment 6, too (both $p \leq 0.00$). Overall, the number of saccades was quite similar for all experiments at low set sizes, ranging from 1.90 / 1.35 to 2.23 / 3.92. This was different for high set sizes, where the number of saccades was lowest in the feature search (4.75 / 2.73, experiment 4) and highest in the second conjunction search (9.88 / 8.90, experiment 6). Across all set sizes the reaction times at each individual set size were similar for both owls, with the only exception in set size 16 of experiment 6, where owl WH was significantly slower than owl HB in fixating the target. However, the search slopes for both owls did not differ significantly in any experiment (**Fig 5-2**). To summarize, both owls show only slight individual differences in the three experiments. Set size has little to no impact on the duration of a fixation. Therefore, search time and number of saccades are proportional to each other; they always show the same effect.

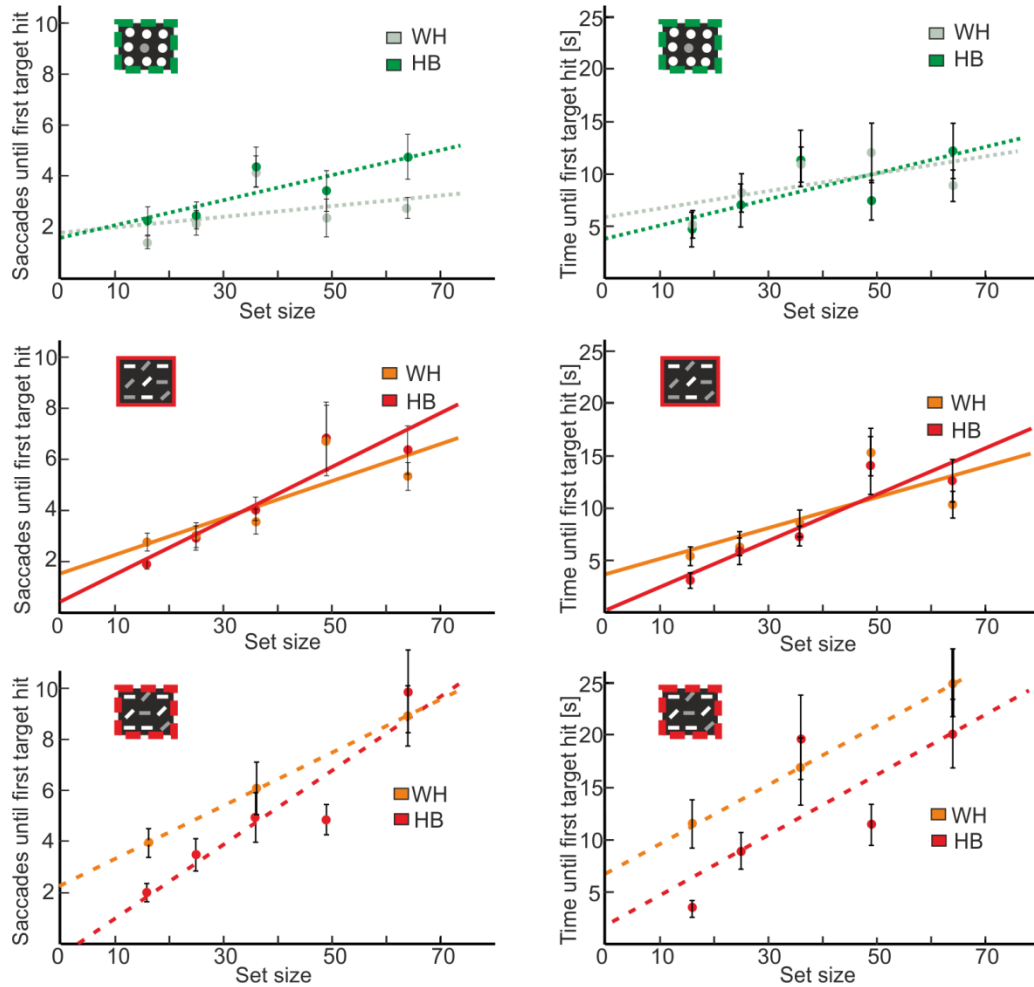


Figure 5-2: Influence of set size on number of saccades and time until first target hit for experiments 4-6. The left column shows the number of saccades until target detection, the right row the search time until detection, both plotted against set size. The inset in each graph shows a schematic of each stimulus type with the target in the center. The upper row shows results from intensity(-) feature search (experiment 4, dashed green lines, data from 254 videos), the second row shows conjunction (experiment 5, red lines, 438 videos) and the bottom row conjunction2 (experiment 6, red dashed lines, 258 videos). The dots are the average of all trials for each set size, error bars are standard error of the mean, and lines are the linear best fits to the data for each owl.

Once the data for both owls is combined it provides an easy method to measure search difficulty by comparing the linear fits to the function of search time (or saccades) and set sizes. For saccades these are in experiment 4: $y(\text{saccades}) = 0.037x + 1.61$, in experiment 5: $y(\text{saccades}) = 0.088x + 0.96$, and in experiment 6: $y(\text{saccades}) = 0.12x + 0.86$; for search times they are: experiment 4: $y(\text{search time}) = 0.111x + 4.59$, experiment 5: $y(\text{search time}) = 0.185x$

+ 1.67, and experiment 6: $y(\text{search time}) = 0.27x + 3.69$ (Fig3-2). It is obvious that the range of the y-intercept is not as informative as in experiment 2 and 3 (chapter 4), as its position is strongly influenced by the slope of the linear fit function. A more informative method to rank the experiments is to compare the number of saccades until the target has been detected averaged across all set sizes. In the following the data from experiments 2 and 3 is used to compare the results to known simple searches. So, these are for experiments 2-6: experiment 2: 3.73 ± 0.18 saccades; experiment 3: 1.47 ± 0.06 ; experiment 4: 2.99 ± 0.23 ; experiment 5: 4.19 ± 0.25 ; experiment 6: 5.53 ± 0.42 . Therefore, according to this measurement, both intensity feature searches are easier than the orientation feature search; the conjunction searches are more difficult. It is notable, that in experiment 3 the target is detected more than one saccade earlier than in the next difficult search, while this takes more than 1 saccade longer in experiment 6 compared to the other searches.

The standard measure of search efficiency is the slope of the search time vs. set size function; it gives an estimate of the search throughput per time, or per saccade the case of the saccades per set size slope. Looking at saccades, search slopes range from -0.003 to saccades / item to 0.12 saccades / item. With increasing search slopes the experiments are ranked as following: Experiment $3 < 2 < 4 < 5 < 6$. Even though the slopes of experiment 2 (0.013) and 3 (-0.003) differ, both have no significant search slopes, that is they do not differ from zero slope ($p > 0.05$, Anocova T probability). The other experiments have significant slopes (experiment 4: 0.037, experiment 5: 0.088, experiment 6: 0.12). The slopes of the search time vs set size function are similar in ranking and significance: exp2: 0.012, exp3: -0.014, exp4: 0.111, exp5: 0.185, experiment6: 0.27.

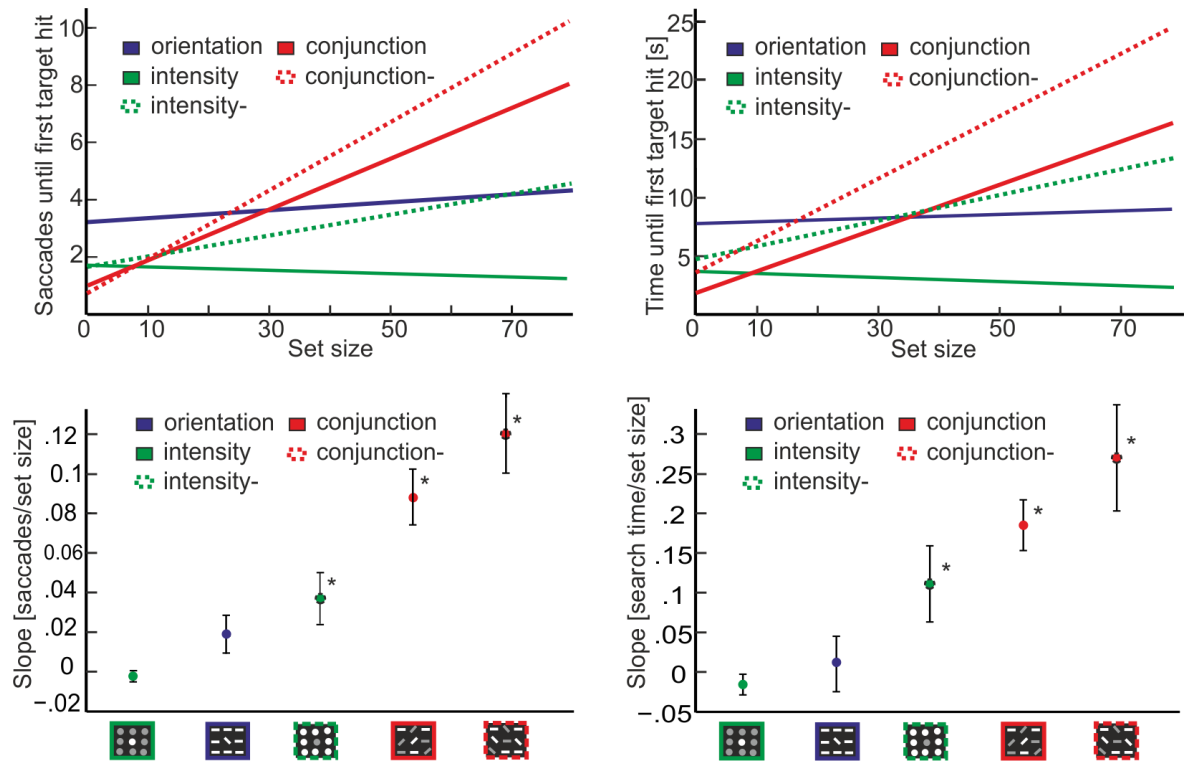


Figure 5-3: Combined linear fits and slopes of experiment 1-6. Top row: Influence of set size on number of saccades and time until first target hit for experiments 2-6, combined for both owls. Data from experiments 2 and 3 is taken from figure 3-8. The left graphs show the number of saccades until target detection, the right graphs the search time until target detection, both plotted as a function of set size. Lines are the linear best fit to the combined data of both owls. Experiments are color-coded: experiment 2: blue, experiment 3 green, experiment 4: green and dashed, experiment 5: red, experiment 6: red and dashed. Left graph (saccades): exp2: $y = 0.013x + 3.24$, exp3: $y = -0.003x + 1.72$, exp4: $y = 0.037x + 1.61$, exp5: $y = 0.088x + 0.96$, exp6: $y = 0.12x + 0.86$. Right graph (search time): exp2: $y = 0.012x + 8.08$, exp3: $y = -0.014x + 3.75$, exp4: $y = 0.111x + 4.59$, exp5: $y = 0.185x + 1.67$, exp6: $y = 0.27x + 3.69$. Bottom row: Search slopes for experiment 2-6. Dots are the slopes, error bars are standard deviations. Slopes are taken from the Matlab function aocool, which uses an ANOCOVA model to fit lines to data groups. Figure is color-coded as is fig 3-2. Shown on the left are saccade slopes, on the right the search-time slopes. In both graphs the search slopes are ranked similarly, intensity search (exp3) has the lowest slope, and conjunction- the highest slope. Asterisks denote significant difference from zero-slope using the T probability from aocool.

6 Discussion

Six experiments investigating overt visual search processes in barn owls with the head mounted OwlCam used for gaze tracking are described here. Experiment 1 showed that barn owls share basic overt attentional processes with primates, that is, they are attracted to salient stimuli. Experiments 2-6 investigated active visual search behavior in these birds. Experiments 2 and 3 described a pop-out effect for orientation and intensity feature search. Experiment 4 showed that barn owls have search asymmetries by exchanging the target and distracters of experiment 3. Finally, experiment 5 and 6 were conjunction-search tasks. The owls could learn to do these tasks, and indeed it took them longer on average to find the targets in the conjunction searches than in the simple feature searches. In the following I will discuss these findings. Since the results from each chapter led to the next, I will discuss these first individually in relation to what is known about visual search in humans. Then I speculate about the neural implications for pop-out and visual search of these results. Finally, I will give an overview of visual search in other animals and an outlook to further experiments.

6.1 Overt Attention

Experiment 1 demonstrates that the free-viewing animals looked longer, more often, and faster (after trial onset) at differently oriented targets than at a control item, in a manner resembling human overt attention (Yarbus 1967). 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, driving forces in evolution, 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 (Willigen et al. 2010; Orłowski et al. 2012), needs to catch approximately 2 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 (Mebs and Scherzinger 2000). 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 (Ilany and Eilam 2007), and thus the exploitation 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 to discriminate the resulting figure from bars with a different orientation (Cook et al. 1996). Pigeons also can detect odd objects in a scene and even discriminate letters and faces (Blough 1977; Dittrich et al. 2010). Thus, birds seem to have the neural machinery necessary for complex scene analysis.

My research is similar to a recent study on archer fish, which have been shown to exhibit orientation-based saliency similar to humans (Mokeichev et al. 2010). Unlike the latter authors, however, who explored orientation-based saliency using a rapid forced choice procedure, my 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 present in humans. Unveiling the neural mechanisms that facilitate these processes in animals like the barn owl may provide important insight into saliency processing in general. In humans, classical visual search experiments are also used to discriminate between pre-attentive, pop-out, parallel processes and serial attentive processes by measuring how target detection time varies with the number of distracters (Treisman and Gelade 1980; Wolfe and Horowitz 2004). However, in experiment 1 the barn owls did not have a specified search task; they were observing the target or distracters at their own volition – and could choose to actively avoid them. But, comparing the results for differently oriented targets and food items reveals that both were looked at after approximately the same number of head saccades. This comparable performance to the “most desirable” target indicates a strong saliency effect for the differently oriented target against the distracter array. It draws the animal's attention equally effectively as the food items do.

Experiment 1 could show that species as distant as humans and barn owls exhibit striking similarities in a fundamental visual behavior like orientation-based saliency effects suggesting that orientation saliency has computational optimality in a wide variety of contexts and provides a universal building block for efficient visual information processing. These findings are the starting point in investigating whether theories hypothesized for human visual search (Treisman and Gelade 1980; Wolfe 1994; Hochstein and Ahissar 2002) can model visual processes in barn owls as well, or whether nature has found a different solution. Given the similarity in saliency effects, the next question is whether barn owls do have a pop-out effect. This is investigated in experiments 2 and 3.

6.2 Pop-out in barn owls

In chapter 4 I presented data from two experiments that tested visual pop-out in barn owls. In experiment 2, a target different in orientation was shown to pop-out, while in experiment 3 the target was different by its intensity from the distractors. Pop-out was demonstrated by search time and the number of saccades until the target was fixated, two measures that remain largely independent of the number of distractors in both experiments. In the following I discuss these findings in relation to what is known about visual pop-out in humans.

In human visual search, a pop-out effect is well established and usually occurs in very easy feature search tasks (Wolfe and Horowitz 2004). It is characterized by a rapid detection and fixation of a salient object. This occurs independently of the number of distractors and may be explained with the involvement of parallel processes across the visual field (Treisman and Gelade 1980). I chose two features (orientation and intensity) for my studies in barn owls that are known to exhibit pop-out in humans (Sagi and Julesz 1985; Nothdurft 1991; Nothdurft 1992; Theeuwes 1994a). In such studies it is common to measure reaction time from stimulus onset until the detection of the salient target. In barn owls this type of measurement is more problematic, because I had little control over the actual time when the owls start the trial. In particular, it typically took some time from stimulus onset until the animal even directed its gaze at the stimulus. To remain as close as possible to the criteria used in humans, I set the beginning of the trial as the time when the stimulus first appeared into view in the OwlCam video and then measured both search time and the number of saccades until the target was

fixated. Indeed, both parameters remained largely independent of the number of distractors in both experiments, suggesting pop-out type of behavior at the phenomenological level. Although both experiments indicated similar behavior, I *did* find differences in the corresponding results. First, the target was fixated relatively more often per trial in the intensity search compared to the orientation search. In addition, the target was detected approximately twice as fast and in half as many saccades in the intensity task. Thus, while both feature searches indicated a type of parallel search mechanism, the barn owl's visual system appears to solve the intensity task more efficiently than the orientation task. The reason might be intrinsic and described by the more efficient processing of luminance compared to orientation, but in this case it could also have resulted from the fact that my owls were trained for and tested on orientation feature searches *before* the training for and testing on the intensity feature search. A reduction in task difficulty and therefore in response time is a common training effect in visual search (Schneider and Shiffrin 1977; Wolfe et al. 2000), and thus the improved performance in the intensity visual search experiment may be attributed to the animals' longer familiarity and better expertise in coping with visual search tasks in general. This possibility in itself would be a remarkable and interesting finding, because although I know that barn owls are capable of information transfer from motion parallax to stereo (van der Willigen et al. 2002), the transfer of acquired knowledge between domains is considered a cognitive achievement (Zentall and Hogan 1976; Blaisdell and Cook 2005). At the same time, the explanation may be confounded by the mere fact that the training phase was lengthy, lasting several months long before each experiment. It is, therefore, likely that the familiarization curve have hit ceiling already before the first experiment started. Thus, it is possible but unlikely that the observed differences are due to training effects.

Now, we know that barn owls use the same search mechanics as humans do in simple searches. Next I will discuss the findings for more complex tasks.

6.3 Search asymmetries and conjunction search

In chapter 5 I presented data from 3 different experiments and compared these to experiment 2 and 3 (**Fig. 5-2**). Experiment 4, was the same as experiment 3, but the luminance of the

target and the distractors was inverted to test for search asymmetry. In contrast to experiment 3, search time and number of saccades in experiment 4 increased with set size. Thus, in experiment 4, the search process undoubtedly was serial and not parallel as in experiment 3. This is consistent with findings on search asymmetries in humans (Wolfe 2001; Vincent 2011). In their seminal paper on search asymmetries Treisman and Gormican (1988) showed that many feature searches become search asymmetries, if target and distractor identity are exchanged. They could show that search was facilitated in searches with an added feature in the target (for instance the line in a Q versus O search), or in searches in which the target had “more” of a feature than the distractors, i.e. it was longer, faster, or brighter. They also tested a configuration similar to the one used in my experiment, using darker or brighter bars as target. As in barn owls, a brighter target facilitated search in humans. This result, in a way, is surprising. When search asymmetries were tested for in another bird species – pigeons - no change in search time was evident when target or distracter identity was exchanged (Allan and Blough 1989). It is unexpected, that search asymmetries in one bird species are found but not in the other, especially considering that both show parallel and serial search mechanisms (Blough 1979; Blough and Blough 1997). However, all asymmetry experiments in the pigeon study were based on the presence or absence of a feature, and not on the “more” of a feature as in my experiment 4. Also, when measuring discrimination accuracy in a similar task asymmetries were found in pigeons (Pearce and George 2003). So, it is still possible that barn owls and pigeons show the same search asymmetry effects.

Experiment 5 was a conjunction-search experiment, in which the target was the combination of both pop-out targets (45° oriented and bright) used in experiment 2 and 3. So, this experiment should be a rather easy conjunction search, since both features themselves are highly salient to the owl. Indeed owls were able to learn this task. Moreover, search time and number of saccades increased linearly with set size, similar to experiments in humans or macaques (Treisman 1982; Treisman and Sato 1990; Bichot and Schall 1999). In the pop-out experiments 2 and 3, the search slope of the search time vs set-size curves was between -.01 and .01 seconds. That is, an increase in set size by one item increased the search time in the case of the slower orientation experiments by about 0.01 s – only a small fraction of the overall response delay (i.e. the y-intercept in **Fig 4-3**). The increase in slope was 15 times higher in the conjunction experiment, indicating an increase in search difficulty compared to

experiment 2 and 3. The target in experiment 6 was a combination of the distractor features of experiment 2 and 3. Experiment 4 had already shown that search for a dark target is more difficult than searching for a white target. Therefore, it was unsurprising that experiment 6 yielded the steepest slopes for both search time and number of saccades. Each additional item increased search time by approximately .27 seconds in experiment 6. Thus, using only this average search rate, search time in the smallest set size was 4.3 seconds and 17.3 seconds on the largest. This increase in search difficulty between the two conjunction searches may be attributed to an asymmetry effect, too. The search for one target configuration is more difficult than searching for another. A similar effect – if not in quantity, but in quality – was also observed in human subjects (Treisman and Souther 1985).

However, a few issues need further consideration when interpreting the data of experiments 4 and 6. In these experiments, the owl had to unlearn the identity of a target and learn to search for a new target that previously was a distracter. This is difficult for animals (Carter and Werner 1978). To achieve this, a rather long training period was necessary: 24/24 days for experiment 4 and 14/48 days for experiment 6 compared to 10/16 days for experiment 5. Especially the 48 days of training for owl WH showed the difficulty of retraining barn owls. So, it might be possible that the longer search times in these experiments might in part be due to learning issues – and not only be attributed to the task difficulty itself.

6.4 Saccades in visual search

It is known from human visual search that reaction time and the number of saccades/fixations are closely related. Quantitatively, the ratio between number of fixations and the response time is mostly unaffected by set size, especially in easy searches (Williams et al. 1997; Zelinsky and Sheinberg 1997). I find this effect in my barn owl experiments, too. The slopes for saccades and search time were quite similar in all experiments. Also the average number of saccades per second did not differ much across experiments and set sizes. Overall, the average number of saccades ranged only from 2.0 ± 0.07 seconds in experiment 5 to 3.07 ± 0.28 seconds in experiment 4. The other experiments yielded data in between.

When comparing my results to human visual search one difference is nevertheless striking: barn owls needed a rather long time to detect (i.e., fixate) the pop-out target – approximately 8 seconds in Experiment 2 (orientation) and approximately 3 seconds in Experiment 3 (intensity). In the other experiments these times were 8.5 seconds in experiment 4, 8.5 seconds in experiment 5, and 14.7s in experiment 6. Human *reaction times* in similar experiments are at least one and sometimes up to two orders of magnitude faster, especially in easy search tasks (Williams et al. 1997; Young and Hulleman 2013). On the other hand, the *number of saccades* until target fixation were not noticeably different in my second experiment from what is commonly observed in human feature-search experiments (Williams et al. 1997; Young and Hulleman 2013), and the speed of saccades is comparable also: 800°/s peak speed in barn owl head saccades compared to 900°/s peak speed in human eye saccade (du Lac and Knudsen 1990). Human fixations during search experiments, while somewhat dependent on task difficulty, last approximately 0.25s, with 3-4 new fixation points selected every second (Vlaskamp et al. 2005; Young and Hulleman 2013). This number is approximately 10 times shorter than the owl's. Therefore, the differences in reaction times, and more generally in visual search behavior, between owls and humans can be attributed to a large extent to the duration of the fixation *between* the saccades. This last conclusion, thus, indicates that the differences between the two species are in this particular stage of the behavioral sequence (i.e., the fixations).

The last conclusion is representative of a more general issue. Scan paths and saccade programming are closely related to attentional deployment. While this is known in humans even in parallel visual search tasks (e.g. Zelinsky and Sheinberg 1997), my study suggests that barn owls have a similar type of exploration. Indeed, gaze tracking in any species during visual search is a powerful tool to analyze how the observer structures this fascinating visual behavior. In studying this structure, it can be argued that saccades and the content of fixations are more informative than response times only. While the latter indicate the conclusion of searches, the former provide information about the search procedure itself (Zelinsky and Sheinberg 1997). As one of the few animals whose scan paths can be easily tracked and analyzed without impeding their normal behavior, barn owls provide a unique non-primate model to study attentional deployments.

6.5 Broader impacts: from behavior to neural substrate of pop-out

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. There is a substantial amount of studies asking how the primate brain performs visual search tasks, often focusing on cortical structures (for instance Bichot et al. 2005, Chelazzi et al. 1993). While it was speculated for some time that only animals with large neocortex may have mechanisms of visual search, it seems now clear that a structure like a neocortex is not necessary for pop-out sensitivity. But what are then the minimal requirements? Clearly the responses within the classical receptive field of neurons are not enough. There must also be *interactions* between cells beyond the classical receptive field. While such interactions are abundant in the visual cortex (Hubel and Wiesel 1977), in lower animals without a cortex similar connections are found at several levels of the visual pathway, amongst them the midbrain optic tectum, a structure known to be involved in gaze control and attention (Mysore et al. 2010). For instance, cross-modal competition in barn owls was also found to occur in intermediate and deep layers of the optic tectum (Knudsen 1982; Zahar et al. 2009). And indeed, some pop-out like sensitivity has been observed in tectal cells of barn owls (Zahar et al. 2012). However, the data of Zahar et al. (2012) did not show pop-out sensitivity in orientation as was found in this thesis. Therefore, it seems that more interactions than those present in the optic tectum are necessary to create pop-out sensitivity for orientation. Such substrates may be found in the visual Wulst that resembles in many respect the mammalian visual cortex (Pettigrew and Konishi 1976; Wagner and Frost 1993; Nieder and Wagner 1999). In primates, orientation-based saliency is facilitated by certain neural circuitries, particularly those creating orientation selectivity (Kastner et al. 1997; Supér et al. 2001). Long-range lateral connections found in the primary visual cortex (Hubel and Wiesel 1977; Rockland and Lund 1982) have been shown to be important as well (Ben-Shahar and Zucker 2004). Orientation sensitivity in the barn owl's visual Wulst is very similar to that seen in the visual cortex (Pettigrew and Konishi 1976; Liu and Pettigrew 2003). The function of the horizontal long-range connections in mammals may be accomplished in birds through the interconnectivity of many telencephalic nuclei (see Jarvis et al. 2005 for a review). Moreover, within the visual Wulst, organizational complexity increases as with increasing

latency of neuronal responses, indicating a hierarchy of processing (Nieder and Wagner 2001b). While not much is known about lateral connections in the visual Wulst of barn owls, and the Wulst is not layered as the mammalian cortex, the experiments of Nieder and Wagner (1999) on cognitive contours demonstrate a high level of connectivity which may also underlie pop-out, while its rich connectivity to other areas may also facilitate the interaction of bottom-up and top-down mechanisms for visual attention in general (Connor et al. 2004). More experiments are clearly necessary to find out what is that substrate and, perhaps more interestingly, what may be the minimal circuitry that can support pop-out sensitivity.

6.6 Visual search in other non-primate animals

Apart from human studies, most research on visual search has been conducted in non-human primates. They are the obvious choice. First, many psychophysical experiments can be replicated in primates with little or no change necessary (Tomonaga 1995; Bichot and Schall 1999; Nothdurft et al. 2009). Also, due to their similar neuroanatomy, many physiological investigations have been conducted in macaques, for instance on the neural substrate of saliency (Bichot et al. 1996; Bichot et al. 2005; Smith et al. 2007). To my knowledge, there have been few studies that tested visual search behavior in non-primate animals. The following will give an overview of these studies.

In non-primate mammals studies have been conducted in cats and rats. Kastner et al. (1997) investigated neural correlates for pop-out in the striate cortex of anaesthetized cats. They used feature arrays, with the target defined either by motion or orientation contrast. They found neurons that responded more strongly to salient elements in both test conditions, indicating their involvement in saliency computation. Botly and de Rosa (2012) conducted behavioral experiments with rats. They trained rats to use touch screens to indicate the location of learned target. They used shape (square versus triangle) and luminance contrast in feature and conjunction searches. The rats could detect the feature target faster than the conjunction target; however, no set size effect was detected in both searches. This might be related to their low maximum set size of 8 items. Lately, several studies on visual search and saliency have been conducted with fish species (Mokeichev et al. 2010; Rischawy and Schuster 2013; Proulx et al. 2014; Ben-tov et al. 2015). Proulx et al (2014) trained zebrafish

in a two alternative forced choice task. The fish had to indicate the location (left/right) of a differently colored target by swimming towards it. The authors found no set size effect for up to 12 targets, and concluded that zebrafish use parallel search mechanisms to detect the target position the target. One obvious drawback of the research with rats and zebrafish is that only a low number of items (12 or less) could be used due to the low visual acuity in these species. Thus, it is unclear how these animals would respond to larger set sizes.

There have been three studies on archer fish directly relevant to my study. Archer fish shoot water jets at prey items. They can be trained to shoot at specific targets making this innate behavior useful to investigate visual search and saliency effects. When presented with oriented bars containing one odd target among three identical distracters, archer fish prefer to shoot at the odd target, even without training (Mokeichev et al. 2010). This orientation saliency effect is similar to the results I show in experiment one – orientation saliency is important in fish and birds as it is for humans. In another study, archer fish were confronted with search arrays of up to 100 items, containing a prey image among uniformly shaped (easy) or diversely shaped (difficult) distracters (Rischawy and Schuster 2013). While the fish took longer to shoot at the target in the difficult task both searches were serial. Ben Tov et al. (2015) found a pop-out effect in archer fish for moving targets. They trained the fish to shoot at a differently moving target (faster or in the opposite direction) among up to seven uniform distracters and found no set size effect. When they changed the task to a conjunction task search time increased with set size, thus showing that archer fish use both parallel and serial search mechanisms. These authors could also show the same effect when exploring neural correlates of this behavior in the fish's optic tectum - similar as Zahar et al (2012) did in barn owls for motion pop-out stimuli. However, Ben Tov et al. (2015) only used up to 8 items. It is not impossible that the parallel search switches to a serial search mode when set size is increased. Of course, the same could apply to my use of a maximum of 64 items in barn owls.

In birds, apart from barn owls, extensive experiments on attention have been conducted in blue jays and especially pigeons (Pietrewicz and Kamil 1979; Blough 1991). Most of these studies focused on cueing, priming, and food detection and not on direct search mechanisms (Cook et al. 1995; Bond and Kamil 1999; Goto et al. 2014). However, several visual search

experiments investigating serial and parallel search mechanisms have been conducted in pigeons (for instance: Blough 1977; Blough 1979; Blough 1984). It appears to be relatively easy to train pigeons to peck at specific targets on a touch screen, a method used in many pigeon experiments. Using this setup, several findings in human psychophysics related to search time and accuracy could be replicated with pigeons, often showing the same effects. Visual search has been investigated in bees as well (Spaethe et al. 2006). Free flying bees are able to find a target among differently colored objects, but as set size increases so does their search time.

It is difficult to compare the results of experiments conducting visual search in different species. For instance, the barn owls exhibited longer response times than rats or pigeons in feature search tasks. This might be attributed to various factors, like different experimental design, different levels of training, or different computational capabilities, but in itself this fact does not confound my finding that barn owls exhibit pop-out sensitivity for set sizes up to 64 items.

6.7 Methodological contribution

While the OwlCam that was employed in this study was already proposed in past work, here it was used in conjunction with a novel algorithmic system that could analyze OwlCam videos automatically, thus facilitating the collection and analysis of the large amount of data associated with studies that require many trials and defy manual analysis. Clearly, the methodological implication of this combined system is not limited to the study of pop-out or visual search, as many types of visual behavior could benefit from the construction of the panoramic visual field and the scan path by which the bird explores it. For instance, head mounted camera systems have been used in recent studies with peahens and falcons (Yorzinski et al. 2013; Kane and Zamani 2014). Needless to say that the same methodology is highly useful for studying visual behavior in other species also, and in particular, it is directly applicable for other species with eyes that are relatively immobile in their sockets (from mammals like tarsiers, quite a few bird species, and upon further future miniaturization, to animals with compound eyes as well).

6.8 Outlook and follow up

In this thesis I conducted several behavioral experiments with barn owls. I could show that a) orientated bars are salient to barn owls; b) barn owls have search in parallel for at least two features: orientation and intensity pops out to them; c) barn owls use serial search in conjunction search experiments and have a search asymmetry for intensity stimuli. While these are important findings, these are only descriptive; this should only be the beginning of research in barn owl visual search. While lately some data on visual search in non-primate animals has been gathered a model for non-primate visual search is still lacking. As pointed out, barn owls are well suited to fill that role. The OwlCam is a unique method for tracking a bird's gaze without impeding the animal in its natural behavior. As shown in this thesis and many other studies barn owls are able to learn quite complex visual tasks. From the behavioral side there are still several interesting questions to answer. Do barn owls share the same basic visual features as primates do, and if so which feature is the most efficient and thus the most important to the owls. Once this information is gathered it might be fascinating to investigate how they incorporate these in complex searches, like the search for prey in natural environment.

So far, I only looked at saccades in a quantitative way. However, individual head-saccades during searches differ regarding to their velocity, duration, and size. Are they similar to primate eye-saccades in visual search? Also, this might give further insight into the complexity of a task. Even more fascinating is to look at the physiology. Here, for only a few non mammalian species is as much information available as for barn owls; barn owls have a history of 40 years of neurophysiology. Lately, it has been shown that the optic tectum of the owls appears to be involved in saliency processing, and other areas might be, too. The search for the neural substrates of visual search and saliency is a hot topic in primate and human visual search. Thus, further investigations on that topic in the barn owl would be fascinating and could yield insights about neural correlates in corresponding primate brain areas as well. Here, the OwlCam offers a unique advantage, as well – since in theory it could be coupled with neural implants record the gaze of these animals while recording in a pre-identified brain area involved in search.

7 References

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9.1 Breakdown of contributions to the thesis

Several people contributed to this study. In the following I will break to down these contributions for each chapter:

- Chapter 1: No one else contributed to chapter 1
- Chapter 2: Part 2.2 is an edited version of the supplemental information section to the publication “Overt attention towards oriented objects in free-viewing barn owls” in PNAS 2011 originally written by Wolf Harmening (W.M.H.).
- Chapter 3: This is an edited version of the publication “Overt attention towards oriented objects in free-viewing barn owls” in PNAS 2011. The individual contributions are as follows: W.M.H., Julius Orłowski (J.O.), Ohad Ben-Shahar (O.B.-S.), and Hermann Wagner (H.W.) designed research; W.M.H. built the OwlCam; W.M.H. and J.O. performed research; W.M.H., J.O., O.B.-S., Petra Nikolay (P.N.) and H.W. analyzed data; and W.M.H., O.B.-S., and H.W. wrote the paper.
- Chapter 4: This is an edited version of a manuscript ready to be submitted to a referred journal. The individual contributions are as follows: J.O., O.B.-S., and H.W. designed research; Christian Beissel (C.B.), Friederike Rohn (F.R.) and J.O. performed research; C.B., F.R. and J.O. analyzed data; and J.O., O.B.-S., and H.W. wrote the manuscript.
- Chapter 5: J.O. and H.W. designed the research, J.O. performed the research, P.N. and J.O. analyzed the data, J.O. wrote the chapter.
- Chapter 6: J.O. wrote the chapter, 6.1 and 6.2 are edited versions of the discussions written for the manuscripts used for chapter 3 and 4.

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- | | |
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