Do you see the point?

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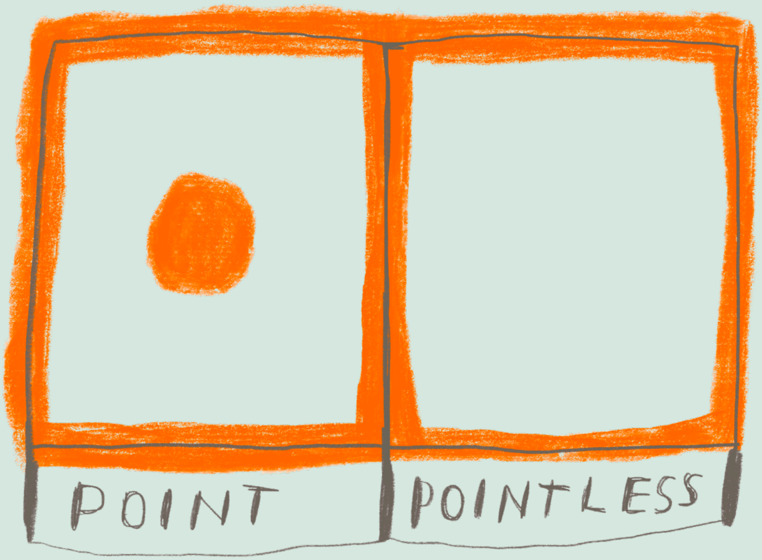

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Sandra Chaib

DOCTORAL THESIS

Doctoral thesis for the degree of Doctor of Philosophy (PhD) at the Faculty of Science at Lund University to be publicly defended on the 3:rd of October at 09.00 in the Blue Hall, Department of Biology, Sölvegatan 37, Lund

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Abstract:

The vision of birds has been extensively studied, and alot is known about what they are able to see contrast sensitivity and acuity, in different light intensities, is known Still, visual perception depends on a combination of many stimulus parameters, which can make it difficult to predict the visibility of ecologically relevant stimuli.

In this doctoral thesis I have investigate visual thresholds of budgerigars (*Melopittacus undulatus*) using stimuli designed to better match visual tasks which birds encounter naturally. Starting from questions regarding the visual thresholds of birds in ecologically relevant tasks, I have used a psychophysical approach in an attempt to reveal their limits of vision.

A number of different species, including umans, are able to detect visual targets below the resolving limit of the retinal mosaik, given they provide enough contrast to the background. In Paper I we tested the detection threshold for circular single dark targets against a brighter background, the single target acuity, of budgerigars. We found that, in contrast to humans, the single target acuity of budgerigars is not higher than their grating acuity. Detection threshold varied with luminance contrast, in a similar way as for gratings, but also with the target luminance profile (0.065° for sinusoidal wave and 0.098° for square-wave shaped target). We concluded that the low contrast sensitivity of budgerigars likely limits their single target acuity.

The single target acuity of budgerigars was further investigated in Paper II were we added a semi-random movement (1.69 degrees s^{-1}) to a “square-wave” single target. Motion can increase the saliency of visual targets through attentional capture, but has also been shown to increase the luminance contrast sensitivity of budgerigars for gratings. Despite this, the single target acuity for moving targets (0.107°) did not differ from the single target acuity for static targets measured in Paper I.

In Paper III we explored the luminance vision of budgerigars immediately after experiencing a decrease in light intensity. Our goal was to simulate the light intensity dynamics experienced by cavity-nesting birds upon nest-entry. We tested the luminance detection, and discrimination, threshold for circular grey targets (9.6 degrees) on a black background as the birds went from a bright environment into a darker facility. The experiments included thresholds measured at illumination drops of ranging between 0.5 and 3.5 log units. Despite having no time limits, the birds made a response within about 1 second after stimulus onset (which was at the same time as the light decrease), and did not wait to adapt to the lower light intensities. The luminance detection threshold was in the same range when the decrease in illumination was 1.7-3.5 log units, while it was considerably higher when the illumination only dropped by 0.5 log units. The birds were able to discriminate between two grey targets with Weber fractions between 0.41 and 0.54 for all light levels. Although the visual performance is inferior to previously measured contrast- or brightness discrimination in fully adapted budgerigars, it is consistent with Weber’ law. Thus, our result indicates that budgerigars partially adapt to light drops of at least -3.5 log units within ~1 second.

Key words: Bird vision, Visual ecology, Spatial acuity, Contrast sensitivity, Budgerigar, Cavity nesting. Target detection, Psittaciformes

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II. **Chaib, S.**, Mussoi, J. G., Lind, O., & Kelber, A. (2021). Visual acuity of budgerigars for moving targets. *Biology Open*, 10(9), Article bio058796.

III. **Chaib, S.**, Lind, O., & Kelber, A. (2023) Fast visual adaptation to dim light in a cavity-nesting bird. *Proceedings of the Royal Society B*. 290(1998), Article 20230596.

Authors' contributions

I. S.C.: conceptualization, data curation, formal analysis, investigation, methodology, software, validation, visualization, writing – original draft and editing; M.L.: methodology, software, validation; O.L.: conceptualization, methodology, supervision, writing – review and editing; A.K.: conceptualization, funding acquisition, methodology, project administration, resources, supervision, writing – review and editing.

II. S.C.: conceptualization, methodology, software, validation, investigation, formal analysis, visualization, writing – original draft and editing; J.G.M.: methodology, investigation, writing – review & editing; O.L.: conceptualization, methodology, software, supervision, writing – review & editing; A.K.: conceptualization, methodology, funding acquisition, project administration, resources, supervision, writing – review & editing.

III. S.C.: conceptualization, data curation, formal analysis, investigation, methodology, software, validation, visualization, writing – original draft, writing – review and editing; O.L.: conceptualization, methodology, supervision, writing – review and editing; A.K.: conceptualization, funding acquisition, methodology, project administration, resources, supervision, writing – review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Papers not included in this thesis

Lind, O., **Karlsson, S.**, & Kelber, A. (2013). Brightness discrimination in budgerigars (*Melopsittacus undulatus*). *Plos One*, *8*(1), Article e54650.

Mitkus, M., **Chaib, S.**, Lind, O., & Kelber, A. (2014). Retinal ganglion cell topography and spatial resolution of two parrot species: budgerigar (*Melopsittacus undulatus*) and Bourke's parrot (*Neopsephotus bourkii*). *Journal of Comparative Physiology A*, 200(5), 371-384.

Chaib, S., Dacke, M., Wcislo, W., & Warrant, E. (2021). Dorsal landmark navigation in a Neotropical nocturnal bee. *Current Biology*, 31(16), 3601-3605.

“I have no idea where this will lead us. But I have a definite feeling it will be a place both wonderful and strange”

Dale Cooper

Populärvetenskaplig sammanfattning

Fåglar uppfattar världen i högre upplösning, både vad gäller tid och rum, jämfört med andra ryggradsdjur. Detta gör det möjligt för dem att manövrera snabbt i flykt, men även att upptäcka fara eller föda från långa avstånd. Fåglar har dessutom ett mer avancerat färgseende och kan därför uppfatta färgnyanser som är osynliga för till exempel oss människor. Jag har i min forskning använt mig av beteendeexperiment för att ta reda på hur bra fåglar är på att urskilja enskilda föremål under olika förutsättningar. Även om mina frågeställningar har varit relativt allmänna för fåglar, har jag använt mig av undulaten (*Melopsittacus undulatus*) som min modellorganism. Undulater är en liten fröätande papegoja (Psittaciformes) med naturlig hemvist i Australiens inland. Eftersom de är lättränade och vanliga att ha som husdjur har de emellertid använts flitigt inom forskning.

När forskare mäter synförmågan hos fåglar (och många andra djur) genom beteendeexperiment är det vanligt att de använder sig av standardmässiga synstimuli (bilder) med mönster av lika breda ljusa och mörka ränder. Genom att presentera bilder med olika kontrast och bredd på ränderna kan man uppskatta fågelns kontrastkänslighet – det vill säga förmågan att se skillnader på olika nyanser av grå – och synskärpa. Resultaten av sådana tester är användbara då de visar hur kontrastkänsligheten varierar med detaljstorlek (representerat av bredden på ränderna), vilket ger en helhetsbild av vad en fågel kan se. Ett ögas upplösningsförmåga begränsas av ögats storlek samt tätheten av nervceller i näthinnan, där varje nervcell (förenklat) utgör en ”pixel” i synfältet. Detta anatomiska mått på synskärpa stämmer i regel överens med måttet på det allra finaste randiga mönster som en fågel kan urskilja. Synsinnet är dock komplext och gränsen för vad en individ kan uppfatta i en given situation påverkas även av faktorer som färg, form, rörelse och ljusintensitet.

Även om vi vet en del om hur olika parametrar påverkar fåglars synförmåga så finns det fortfarande mycket som är okänt. Människor kan uppfatta en enskild linje, mot en i övrigt slät bakgrund, som är smalare än någon av linjerna i det finaste svart och vit-randiga mönstret vi kan se. Samma sak gäller för enskilda punkter, vilket innebär att vi kan uppfatta individuella stjärnor på natthimlen trots att de befinner sig tusentals ljusår bort. Givet att ett föremål har tillräckligt hög konstrast gentemot bakgrunden kan vi människor alltså uppfatta det på ett längre avstånd än vad upplösningsförmågan hos vårt synsystem egentligen tillåter. Den här förmågan är inte unik för människan utan har påvisats hos flera andra djurarter, till exempel ödlor, trollsländor och bin.

Fåglars skarpa syn tillskrivs ofta deras behov av att kunna upptäcka farliga rovdjur eller bytesdjur på långt håll. I den första artikeln undersöker vi därför undulaters synskärpa när det gäller att uppfatta mörka punkter mot en ljus bakgrund. Vi tränade fåglar till att skilja mellan två bilder – en med en punkt och en utan en punkt – för att få en matbelöning. Vi använde oss av olika typer av punkter för att undersöka hur synskärpan förändras med egenskaper som till exempel kontrast. Undulaters förmåga att urskilja enskilda punkter överstiger inte de mått på synskärpa som tidigare gjorts med randiga mönster. Snarare kan synskärpan för enskilda punkter betecknas som något sämre, beroende på om punkten har skarpa eller suddiga kanter. Undulaters relativt låga synskärpa för enskilda mörka punkter tror vi främst beror på deras låga kontrastkänslighet, en egenskap som de delar med andra fågelarter.

I den andra artikeln visar vi att rörelse inte påverkar undulaters förmåga att uppfatta enskilda punkter. Då ett annalkande rovdjur ofta rör sig så förväntade vi oss att rörelse skulle underlätta upptäckten av enskilda punkter. Tidigare forskning har visat att undulater har högre kontrastkänslighet för randiga mönster som rör sig horisontellt jämfört med om de är stilla, men detta verkar inte påverka synskärpan för enskilda punkter.

Fokus i den tredje artikeln är på undulaters synförmåga under plötsliga minskningar i ljusintensitet. Många fåglar häckar i trädhålor, liksom undulater som i sin naturliga miljö bygger bon i ihåliga gamla eukalyptusträd. Ljusskillnaden mellan den mörka bohålan och den soliga utsidan är troligtvis hög, vilket påverkar deras synförmåga. Liksom för människor så tar det tid för fåglar att helt anpassa sina ögon till mörker – upp till 45 minuter. Ändå spenderar hålhäckande fåglar oftast bara några sekunder åt gången i boet när de matar sina ungar. Vi ville veta hur bra hålhäckande fåglar kan se när de precis kommit in i sitt bo efter att ha vistats i dagsljus. För att ta reda på detta behövde vi testa synförmågan hos fåglar under ljusförhållanden som efterliknar dem som de naturligt möter i denna situation. Vi tränade undulater till att, från en ljus bur, flyga in i en mörkare låda. Väl inne i lådan fick de välja mellan två olika bilder (större punkter med olika grå nyanser på en svart bakgrund) i utbyte mot en matbelöning. Våra resultat visar att undulater delvis anpassar sin synförmåga till den mörkare miljön i lådan redan inom en sekund. Undulater är lika bra på att se skillnad på större punkter med olika grå nyanser oavsett om ljusintensiteten i lådan är mycket eller bara lite lägre jämfört med utanför. Även om synförmågan försämras vid en hastig minskning av ljuset, så sker en viss anpassning nästan med en gång. Detta innebär att fåglar troligtvis kan se sina ägg och ungar även i en mörk bohåla.

Sammantaget visar mina studier att synförmågan hos fåglar är ett område som kräver fortsatt forskning, inte minst om hur den påverkas av dynamiska ljus-förhållanden. Studier inom beteendeekologi, fysiologi och anatomi är nödvändiga för att förstå synens funktionella betydelse samt hur detta avspeglar sig i både fysiska och beteendemässiga anpassningar. Att mäta fåglars synförmåga genom kontrollerade beteendeexperiment ger dock direkt vetskap om vad de kan uppfatta, något som ofta behövs för korrekta tolkningar av synrelaterade beteenden och anpassningar.

Introduction

For the majority of bird species, vision is the primary sense (Martin, 2017a). It allows instant gathering of information about remote objects and events, making it especially useful when moving in mid-air. Indeed, birds depend more on vision than any other vertebrate class (Hodos, 1993; Walls, 1942). The visual system of birds allows them to experience their surroundings both fast (Boström et al., 2016) and in great spatial detail, the latter reflected in some species of raptors having the highest spatial resolving power measured in an animal (Potier, Mitkus, et al., 2020). In addition, birds have highly advanced colour vision (Kelber, 2019). However, even though birds are visual champions the interspecific variation is great and some visual aspects, such as contrast sensitivity, are comparatively poor in all birds (Ghim & Hodos, 2006; Potier et al., 2018).

Visual thresholds in animals are commonly measured under controlled conditions using standard stimuli. Experiments performed in this way are needed to compare different species and make deductions based on previous knowledge. However, if one is interested in what an animal can perceive during specific tasks in its behavioural repertoire, the standard measurements do not always suffice. Visual thresholds are often influenced by context, and different dimensions of visual perception might affect each other (e.g., Haller et al., 2014; Lind, 2016; van den Berg et al., 2020).

The aim of this thesis is to investigate visual thresholds of birds using stimuli designed to better match visual tasks which birds encounter naturally. Starting from questions regarding the visual thresholds of birds in ecologically relevant tasks, I have used a psychophysical approach to investigate their limits of vision.

Even though my questions apply to many species, I have used the budgerigar (*Melopsittacus undulatus*) as a model throughout the papers included in this thesis. The budgerigar is commonly known as a sociable, affectionate, and easily trained pet bird. Indeed, it is probably the most common pet bird in the world. Many of the same qualities which make it appreciated as a pet also make it the perfect bird for behavioural experiments. The budgerigar has been studied quite extensively regarding vision (e.g., Bhagavatula et al., 2009; Goldsmith & Butler, 2003; Haller et al., 2014; Lind et al., 2014; Lind et al., 2013; Lind et al., 2012; Mitkus et al., 2014), but also behaviour (Brockway, 1964a, 1964b; Stamps et al., 1985, 1989; Stamps et al., 1987), providing me with a stable ground of knowledge for asking further questions.

Besides being a popular pet and a model animal in science, the budgerigar is native to the inland of Australia. The budgerigar belongs to the psittacines (parrots), and wild birds are small (20-40 g), mostly bright green with a yellow face and black and yellow wings (Menkhorst et al., 2017). Preferentially they inhabit arid and semi-arid open grasslands with few trees where they move around in large flocks feeding on grass-seeds (Menkhorst et al., 2017; Wyndham, 1980a, 1980b). While hawks (Accipitridae) and falcons (Falconidae) belong to the natural threats of budgerigars (Cowie, 2014; Wyndham, 1980a), their open foraging habitat enables detection of predators at a long distance. But at what distance would a budgerigar be able to detect a potential aerial threat? In Papers I and II, we explored the visual acuity and contrast sensitivity of budgerigars for single targets in an attempt to answer such questions.

In Paper III we asked what birds nesting in dark cavities are able to see when they enter the nest to feed their chicks. Having growing offspring, cavity nesting birds are obliged to move repeatedly in and out of the nest to provide the young with food. Visits to the nest are often quick, and the light intensity difference between the inside and outside can be substantial (Maziarz & Wesolowski, 2014; Reynolds et al., 2009; Wesolowski & Maziarz, 2012). To be able to use vision during these circumstances the visual system would need to adapt rapidly. While feeding in cavity nesting birds likely involves more than one sensory modality, many studies show that visual cues play a role (e.g., Dugas, 2015; Heeb et al., 2003; Podkowa et al., 2019; Podkowa & Surmacki, 2017). Budgerigars typically nest in old hollowed out eucalyptus trees (Higgins, 1999; Wyndham, 1981). The nest entrance hole is small (3-6 cm) and the eggs may be laid up to several metres below (Higgins, 1999; Schrader, 1975), likely out of reach of much illumination. In paper III we explored whether it would be possible for budgerigars to use visual cues when feeding their nestlings.

The outcome of our studies will be further discussed in the last chapter, “Spatial vision in birds”, where I also summarize current knowledge on bird spatial vision and visual ecology. The papers can be found in full length at the end of this thesis. In the chapter following this introduction, ”The vertebrate eye”, I present the main structure and building blocks of the vertebrate eye. Next, in “Spatial vision” I briefly discuss some of the basic principles of luminance mediated vision with an emphasis on vertebrates in general. The following chapter, “Measuring spatial vision”, introduces methods for the quantification of stimuli parameters and spatial visual abilities.

The vertebrate eye

The general structure of the eye

Vertebrates have *camera-type* eyes, in which all entering light is refracted through a single optical unit (the *lens* and the *cornea*) and focused on the light sensitive inner surface of the eye (Cronin et al., 2014) (fig. 1a). While the lens accounts for all refraction in aquatic vertebrates, most of the refraction in terrestrial vertebrates is caused by the cornea, which is the curved outer surface at the front of the eye (Land & Nilsson, 2012). In front of the lens is the *iris*, a pigment-containing thin structure, with an aperture, the *pupil*, which regulates the amount of incoming light (Douglas, 2018). The space between the cornea and the lens is filled with a clear liquid (*aqueous humour*).

The back of the eye, the "eye cup", has a roughly hemispherical or tubular (in owls and some fish) shape. Its inside, the *vitreous body*, is filled with a transparent gel-like substance (*vitreous humour*). The eye cup itself consists of several layers of tissue including sturdy connective tissue (the *sclera*), thin blood vessels (the *choroid*), and a layer of dark melanin containing cells (the *retinal pigment epithelium*). At the innermost lining of the eye cup is the *retina*, a sheet of specialized neurons, whose purpose is to turn light into a visual signal and transport it via the optic nerve to the brain. In mammals, thin blood-vessels running across retina provide it with necessary nutrients. Birds lack these vessels but instead have a pleated pigmented vascular structure, called the *pecten oculi*, which protrudes into the vitreous body where it emits nutrients into the vitreous humour (Pettigrew et al., 1990).

The organization of retinal neurons

The vertebrate retina contains five main types of neurons whose cell bodies and intricate synaptic network are arranged in distinct layers. The eye-cup of vertebrate eyes has evolved from evaginations of the frontal parts of the brain and the organization of the retinal layers is therefore "inverted" (Lamb et al., 2007). As a consequence, the *photoreceptors* initiating the visual pathway are situated in the outermost retinal neuronal layer, and the visual signal while downstream retinal neurons are positioned further in (fig. 1b).

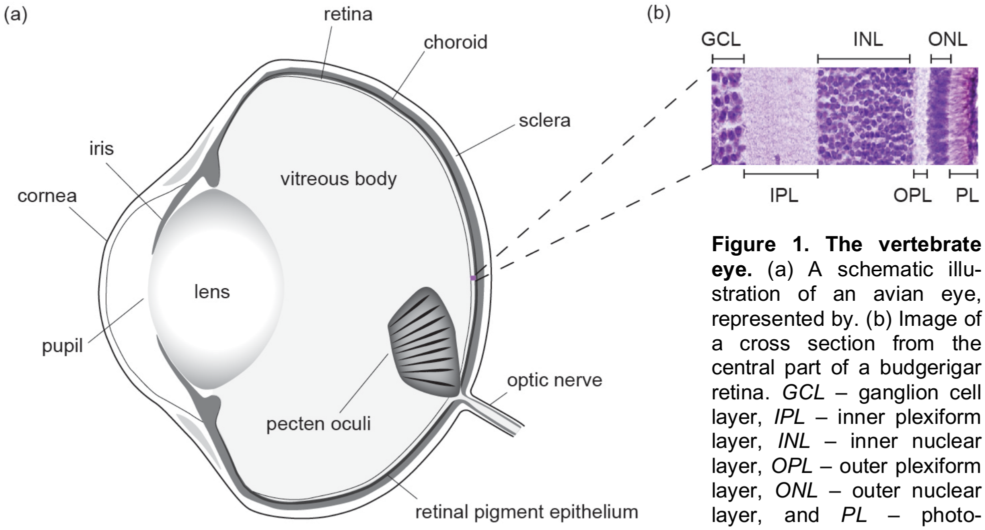

Figure 1. The vertebrate eye. (a) A schematic illustration of an avian eye, represented by. (b) Image of a cross section from the central part of a budgerigar retina. *GCL* – ganglion cell layer, *IPL* – inner plexiform layer, *INL* – inner nuclear layer, *OPL* – outer plexiform layer, *ONL* – outer nuclear layer, and *PL* – photoreceptor layer. Adapted from Mitkus et al. (2014).

Vision starts when incoming photons are absorbed by photosensitive pigments in the photoreceptors, initiating an electric response in a process called photo-transduction. The photoreceptors forward the signal to the *outer plexiform layer* (OPL), which is the first synaptic layer, where they contact *horizontal cells* (HCs) and *bipolar cells* (BC). BCs connect the OPL to the *inner plexiform layer* (IPL), the second synaptic layer, where they make connections with *amacrine cells* (ACs) and *retinal ganglion cells* (RGCs) (Baden et al., 2020). In between the OPL and the IPL is the *inner nuclear layer*, housing the cell bodies of BCs, HCs and ACs. The innermost layer of the retina contains the cell bodies of RGCs and is referred to as the *ganglion cell layer*. The axons of the RGCs carry the integrated visual signal, via the optic nerve, to the visual centres in the brain.

In the OPL, each photoreceptor commonly synapses with several BCs. Different BCs have distinct response characteristics, thereby creating several parallel information channels from the output of the same photoreceptors (Masland, 2012). Classically, BCs are divided into "ON" BCs cells, responding to light onset (bright stimuli), and "OFF" BCs, which respond to light off-set (dark stimuli). The temporal characteristic of their response further divides them into "transient" or "sustained" BCs (Masland, 2012).

HCs connect laterally to photoreceptors and BCs, where they provide both feedback, as well as feedforward information. The lateral connections of horizontal cells typically organise the bipolar cells in *centre-surround* structures, where the surrounding BCs typically respond in an antagonistic manner to the centre BC. This type of lateral organization of neurons is also referred to as *surround suppression* and is present at several levels in the visual pathway. A classic example of surround suppression is the ON-OFF centre-surround organization, where a light stimulus will make the bipolar cell in the centre respond maximally, while the surround will suppress this response (Barlow, 1953; Kuffler, 1953).

Bipolar cells of different types carry their information to specific levels of the IPL where they synapse with ganglion cells and amacrine cells (Masland, 2001; Masland, 2012). Amacrine cells work laterally in a similar way as horizontal cells do in the outer OPL although their function is more multifaceted, and they build more complex networks (Masland, 2012). They modify the output of bipolar cells to ganglion cells, but they also connect directly to ganglion cells as well as other amacrine cells. The function of amacrine cells are often refined to code intricate visual features. Some amacrine cells have large axonal arbores enabling wide-field computations of visual input; others are sensitive to motion in specific directions (Berson, 2020; Masland, 2012).

Input from several bipolar and amacrine cells are typically combined to create the receptive fields of ganglion cells. Like the neurons in the OPL, the receptive fields of retinal ganglion cells almost always have a centre-surround organization, although their feature selectivity is typically more complex. Different types of retinal ganglion cells often selective to specific spatio-temporal features and send their output along parallel pathways to different brain regions (Ibbotson & Meffin, 2020; Schwartz & Swygart, 2020). Example of feature selectivity of ganglion cells are movement direction, orientation, and object motion (Schwartz & Swygart, 2020).

Spatial vision

Vision, a bit simplified, is the sampling of light reflected or emitted from structures in the environment. Light reaching an eye has a number of different properties which can be used to extract information: its spatial origin, intensity (luminance), spectral composition, polarization, and temporal properties. The most basic form of true vision involves the simultaneous sampling of luminance from different directions (Land & Nilsson, 2012), information which can be used to create a spatial representation of the surroundings and guide behaviour. This is what is commonly referred to as spatial vision. However, spatial information is not only extracted from the variation of light intensity across space, but also from its change over time. The retinal image is almost never completely still and even when fixating targets, most vertebrates make small involuntary eye movements (Martinez-Conde & Macknik, 2008). Image motion is integrated with spatial perception already at the level of retinal processing and has an impact, for example, on object saliency, depth vision, spatial resolution, and contrast sensitivity. Although luminance, spatial resolution, and motion are greatly entangled and inter-dependent, this chapter is divided into separate sections which are primarily dedicated to each of these properties separately.

Luminance and contrast

Objects and structures are visible to the eye because they emit or reflect light. Perceiving spatial differences in the intensity of this light is a fundamental visual ability, which can be used to extract information about, for example, texture, form, and depth. The amount of light reflected from a surface (the luminance) is proportional to the intensity of the incident light (the illuminance) (Shapley & Enroth-Cugell, 1984). Since the ambient illumination changes by more than 9 log units over a 24-hour period (Rieke & Rudd, 2009) spatial luminance differences in absolute values are most often not reliable visual cues. Thus, the visual system strives to keep its response invariant to the ambient light conditions to be able to extract useful information from its surroundings (Shapley & Enroth-Cugell, 1984). This is achieved by scaling the response to the overall luminance in the scene, thereby measuring proportional rather than absolute differences. As a result, visual stimuli will convey information about the characteristics of the reflecting surfaces, rather than of the ambient light level.

Proportional processing is present in many different sensory modalities and can be described by *Weber's law* (Akre & Johnsen, 2014). Weber's law states that the minimum perceptible change in a stimulus is proportional to the stimulus magnitude. Applied to spatial luminance vision, Weber's law predicts that the minimum luminance difference ΔI needed for an object to be visible against its background, is proportional to the absolute luminance of the background I:

$$\Delta I \sim I \tag{0.1}$$

In other words, the smallest detectable luminance difference on a light background is larger than on a dark background (fig. 2). However, the ratio of the smallest detectable luminance difference to the background luminance is the same, and is commonly referred to as the *Weber fraction* (ω):

$$\frac{\Delta I}{I} = \omega \tag{0.2}$$

Weber's law holds well for large, long duration stimuli and over a wide range of intensities (Perlman & Normann, 1998). At very high light levels Weber's law fails due to photoreceptor response saturation, while quantal fluctuations – also called photon shot noise – limit visual sensitivity at low light levels (Shapley & Enroth-Cugell, 1984). The absorption of photons is stochastic and follows Poisson statistics, which means that the photon shot noise (the "uncertainty") in a signal of N photons is $\sqrt{N}$. The reliability of the signal, expressed as the signal to noise ratio $N/\sqrt{N}$, thus decreases with light intensity (Cronin et al., 2014; Land & Nilsson, 2012). The *DeVries-Rose law* (or the square root law) tells us that the minimum detectable luminance difference, ΔI, at low light levels is proportional to the square root of the background intensity I:

$$\Delta I \sim \sqrt{I} \tag{0.3}$$

At even lower light intensities an additional source of noise, *dark light*, is noticeable (fig. 2). Dark light originates from spontaneous thermal activation in the photoreceptors and is what ultimately sets the limit to vision (Barlow, 1957; Warrant, 1999).

Luminance contrast is the physical measure of relative luminance variation in a visual stimulus. Although luminance contrast can be calculated in a few different ways, depending on stimulus type, it always describes the magnitude of luminance variation in relation to the average luminance (see "Measuring spatial vision").

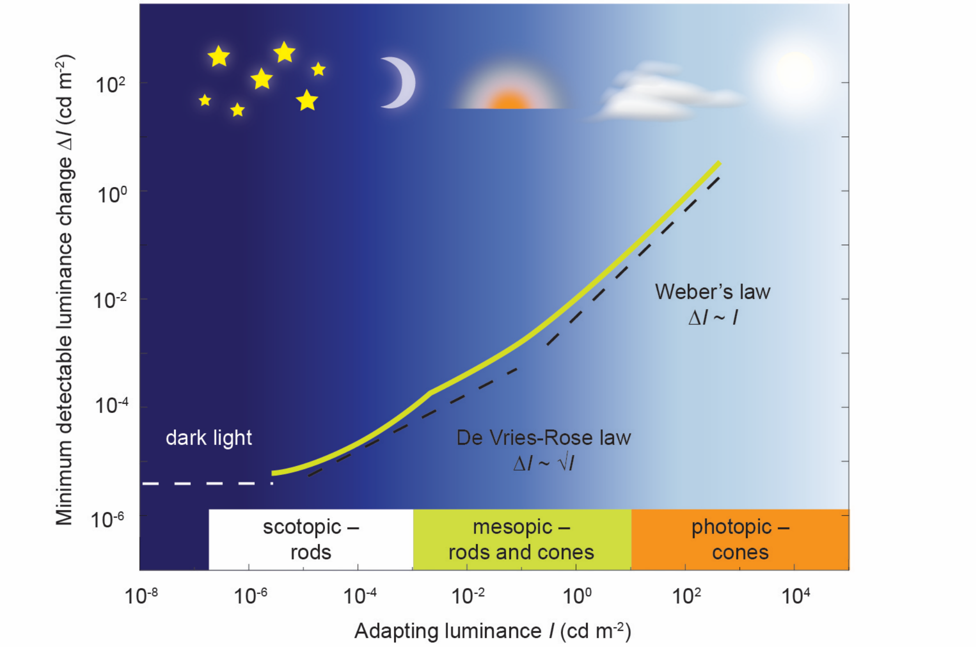

Figure 2. Visual sensitivity of humans at different light intensities. The yellow line shows the minimum detectable luminance change (Δ*I*) for different adapting luminances (*I*). The dashed lines illustrates the effect of noise and adaptation on Δ*I* in different regions. Adapted from (Cronin et al., 2014). The sensitivity ranges of rods and cones in are noted in the bottom of the figure.

Luminance adaptation

The visual system responds to relative luminance differences by adapting to the prevailing luminance. Luminance adaptation includes numerous mechanisms which are active at different light intensity ranges, and which work at different retinal processing levels (Rieke & Rudd, 2009). The timeframes for the different adaptation processes are also diverse, suiting the array of different instances in which light intensity might vary throughout the active hours of an animal (Schwartz & Levine, 2021). Some mechanisms are slow and suite the larger cyclic changes in light availability between day and night. Others are fast and operate in the millisecond range and therefore work well for the rapid luminance changes that occur when moving the gaze (Dunn et al., 2007; Rieke & Rudd, 2009) or moving rapidly between different light environments.

The pupillary light response

The most distal luminance adapting mechanism is the pupillary light response, which controls the amount of light reaching the retina by contraction or dilation of the iris muscles. In most animals, pupil movement only has a marginal effect on luminance adaptation and is therefore believed to have primarily other functions (i.e., enhancing spatial acuity by preventing optical aberrations; Douglas, 2018; Lind et al., 2008).

Retinal duplicity

In contrast, the "duplex retina" of vertebrates contributes greatly to the adaptability of their luminance sensitivity. Most vertebrates, including humans and birds, have two major classes of photoreceptors, rods, which dominate vision at low light intensities, and cones, which are the primary photoreceptors at high light intensities. Based on the human visual system, the light intensities in which only rods are active are referred to as *scotopic*, whereas the ones in which only cones are active are called *photopic* (fig. 2). The working ranges of rods and cones overlap in the *mesopic* light intensity range (Barbur & Stockman, 2010).

Pigment bleaching

In addition to the shift between different types of photoreceptors, luminance adaptational mechanisms also operate at the level of the individual receptors. For example, the sensitivity of both rods and cones is partly regulated by the concentration of the light sensitive visual pigments. Visual pigment molecules consist of an opsin molecule which is bound to a chromophore. The absorption of a photon by a pigment changes the shape of the chromophore, transforming the pigment from an inactive form to an active form, an event which is the start of the visual process (Cronin, 2020). The active form of the visual pigment is said to be "bleached" and must be regenerated into its inactive form before it can absorb another photon (Perlman & Normann, 1998). At higher light intensities a larger proportion of pigment in the receptor cell is bleached, which makes the photoreceptor less likely to absorb photons. Rods are more sensitive than cones and bleach at lower light intensities.

The recovery from full bleaching is commonly referred to as "dark adaptation". In cones this process is limited by pigment regeneration and usually takes around 5 minutes (Jiang & Mahroo, 2022). Dark adaptation in rods is slower, likely as a consequence of local photoproduct concentrations which hampers the regeneration process (Hecht et al., 1937; Lamb & Pugh, 2004). Full dark adaptation of rods takes between 15-40 minutes, depending on degree of bleaching (Hecht et al., 1937; Lamb & Pugh, 2004).

Spatial integration

At low light levels luminance sensitivity is increased by integration of visual signals across both space and time. Partly this is a consequence of the transition from cones to rods, since rods have a wider receptive field size and a longer integration time, but the cone and rod pathways are also individually adjusted. The reliability of visual signals is increased at low light levels by averaging the signals of adjacent retinal neurons. The ambient light level regulates the production of “gap-junctions” which mediate the electric coupling between neurons (Schwartz & Levine, 2021). Increased neuronal coupling may, for example, result in a weakening of the surround suppression mechanism (see “The organization of retinal neurons”), whereupon the receptive field of retinal ganglion cells becomes dominated by its centre (Barlow, 1953; Kuffler, 1953; but se: Warwick et al., 2023). The functional consequence of this adjustment is an increased sensitivity at the expense of spatial resolution (Barlow, 1958; Barlow et al., 1957).

Background adaptation

The luminance range encountered by an eye in just a single visual scene is wide and often changes abruptly by a shift of gaze (Frazor & Geisler, 2006). To keep up with rapid light fluctuations, the retina uses adaptation mechanisms that work in less than a second (Fain et al., 2001). These mechanisms are often referred to as *background adaptation* and they modify both the gain (response magnitude for a fixed signal input) and the speed of signal integration, and operate at several retinal levels (Dunn et al., 2007; Rider et al., 2019). Furthermore, different adaptational mechanisms work at different light levels. As a general rule, mechanisms working early in the visual pathway (e.g. in the phototransduction cascade) are active at higher light levels, while those working at later stages, where the signal convergence rate is high (e.g. at the synapses between bipolar cells and ganglion cells), are active at lower light levels (Dunn et al., 2007; Schwartz & Levine, 2021).

Contrast adaptation

The visual system does not only adapt to the average luminance but also to the average amount of luminance contrast. Like luminance adaptation, *contrast adaptation* involves several mechanisms which act at both different stages in the visual pathway and different timeframes (Baccus & Meister, 2002; Kaplan, 2020).

Other factors affecting contrast sensitivity

As previously mentioned, Weber’s law works best for luminance differences in stimuli with large spatial extent and long temporal duration. Both the receptive field size and integration time of the retinal pathways are affected by luminance adaptation, which in turn may affect the processing of fine or fast-moving stimuli.

Retinal processing mechanisms which are independent on the general light level may also affect the perception of spatial luminance differences. Lateral inhibition between retinal neurons (see previous chapter) can enhance luminance differences at sharp transitions while they are reduced at gradual changes (Enroth-Cugell & Robson, 1966; Kuffler, 1953). Other factors that may affect perceived luminance difference are stimulus area (Campbell & Robson, 1968; Robson & Graham, 1981), spatio-temporal characteristics (Burr, 1981; Haller et al., 2014; Robson, 1966) and luminance polarity (Adrian, 1989; Lu & Sperling, 2012; van den Berg et al., 2020).

Spatial acuity

Spatial acuity is the maximum fineness with which the visual system can resolve an image. It can vary a lot between different species, but specific behaviours or contexts also require more or less detailed visual information. Many visually controlled behaviours, such as movement control or obstacle avoidance, need only a rough representation of the environment; other behaviours, such as prey identification, or communication, require detailed visual information (Land & Nilsson, 2012). The limit to the spatial acuity of an eye depends primarily on the optical quality and the sampling frequency of the retina.

Optical factors affecting spatial acuity

The optical unit of the eye strives to focus the incoming light onto the retina to create a sharp image. However, imperfections of the optical unit and the physical properties of light cause the image to lose some of its sharpness in this process. Typically, smaller details (higher spatial frequencies) are blurred more than larger details (lower spatial frequencies). The loss of image quality caused by the passage through an optical device is usually described by the modulation transfer function, which is an expression of the decrease in contrast as a function of spatial frequency.

Diffraction

When passing an edge or an opening a flat wavefront will “curve”, causing the part of the wave closest to the obstacle to be out of phase with the rest of the wavefront (fig. 3a). The same thing happens to light when passing the pupil, which cause a delay to some parts of the wave fronts. When reaching the retina, those parts of the wavefront that are in phase will reinforce while those that are out of phase will cancel out, giving rise to a diffraction pattern. The diffraction pattern leads to a “blurring” of the image, which is more prominent for finer spatial details and for smaller pupil sizes (Cronin et al., 2014; Land & Nilsson, 2012). The finest details of an image passing the pupil will be completely filtered out.

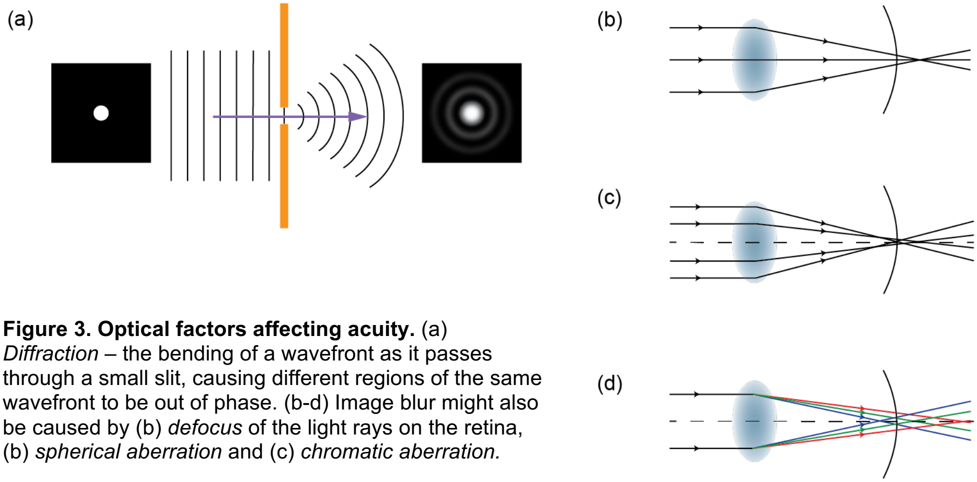

Figure 3. Optical factors affecting acuity. (a) *Diffraction* – the bending of a wavefront as it passes through a small slit, causing different regions of the same wavefront to be out of phase. (b-d) Image blur might also be caused by (b) *defocus* of the light rays on the retina, (b) *spherical aberration* and (c) *chromatic aberration.*

Defocus

Although diffraction sets the ultimate limit to image resolution, other optical phenomena can also contribute to decreased image sharpness. One obvious cause of image blur is defocus – that is, when the image is focused in front or behind the retinal plane (fig. 3b). Nearby objects are brought to focus further away from the lens than more distant objects, creating difficulties in maintaining a sharp image in a three-dimensional world. Among vertebrates there are different solutions to this problem. Fishes move their lens back and forth, which changes the distance between the lens and retina, allowing them to keep the desired object in focus. Mammals, birds, and reptiles change the curvature of their optic unit, they accommodate, which alters its focal length (Land & Nilsson, 2012; Ott, 2006). Some cartilaginous fishes (i.e. bluntnose stingray [*Hypanus say*], Atlantic stingray [*H. sabinus*] and smooth butterfly ray [*Gymnura micrura*]) have so-called “ramp retina”, where the dorsal and ventral parts of the retina have different distances to the lens. Thus, the viewing distance at which an object is in focus differs for different areas of their field of view (Ott, 2006; Sivak, 1976; Walls, 1942). In a similar fashion, some animals that forage on the ground (a few species of bird included) instead have a variable state of refraction across the lens (Vietnamese leaf turtle [*Geoemyda spengleri*]: Henze et al., 2004; Hodos & Erichsen, 1990; rock pigeon [*Columba livia*] and domestic chicken [*Gallus domesticus*]: Millodot & Blough, 1971; Rounsley & McFadden, 2005; northern leopard frog [*Rana pipiens*] and Common frog [*R. temporaria*]: Schaeffel et al., 1994). The lower and frontal visual field of these species are myopic, making it possible to keep the nearby ground in focus while at the same time looking out for more distant objects in the rest of the visual field (Hodos & Erichsen, 1990; Millodot & Blough, 1971).

Aberration

Spherical aberration is an additional phenomenon which may cause image blur. Light which enters the eye at the periphery of the lens comes to focus closer to the lens than light entering through the center or the lens. The focus plane of parallel light rays will thus differ depending on where they pass the lens, and the result is a decreases sharpness of the image (fig. 3c). Many animals, such as fishes and humans, compensate for spherical aberration by having a lower refractive index at the edges of the lens (Cronin et al., 2014; Land & Nilsson, 2012).

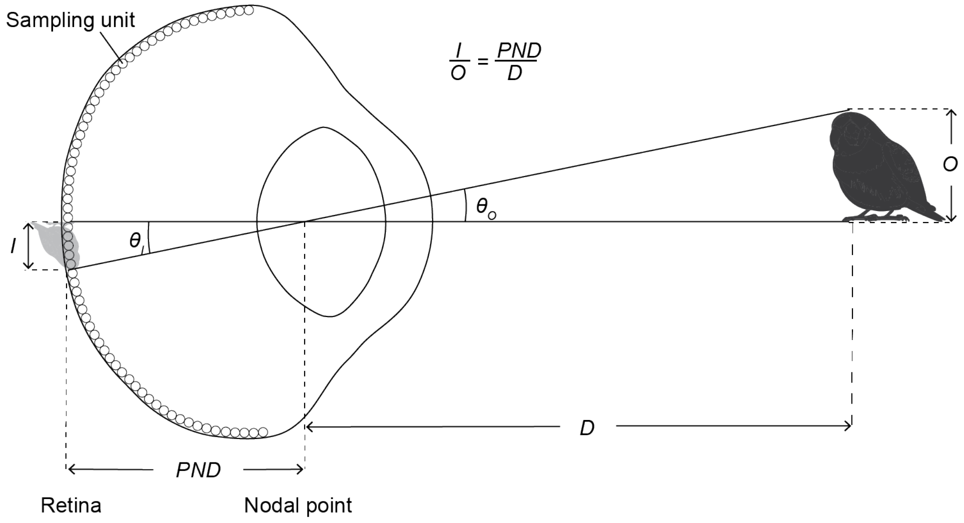

Figure 4. Retinal sampling frequency. The resolution in which an image is seen depends on how many retinal units that samples it. Light passing through the nodal point is refracted minimally, and the angular subtense of an object (θO) in the visual field thus corresponds to the angular subtense of the retinal image (θI). The size of the retinal image (I) depends further on the posterial nodal distance (PND) of the eye.

Chromatic aberration is caused by the different refractive index of light of different wavelengths. Short wavelength light ("blue light") refracts stronger than long wavelength light ("red light"), in the same medium, and will consequently come to focus closer to the lens (fig. 3d; Land & Nilsson, 2012). To work around chromatic aberration some vertebrates have developed "multi-focal lenses" which have concentric zones with different refractive indices, allowing a part of the light from all visible wavelengths to be focused on the retinal plane (Kröger et al., 1999).

Retinal factors affecting spatial acuity

There is little use to pass high-quality images through the optics of an eye unless the retina can sample it. The resolution in which the retina can sample an image, the *retinal sampling frequency*, depends on two main factors: the size of the image projected onto the retina, and the density of retinal units which sample the image (Land & Nilsson, 2012).

The size of the image reaching the retina is decided by the *retinal magnification factor* (RMF), which is a measure of the retinal distance covered by 1° of the visual field (Pettigrew et al., 1988). The RMF depends on the *posterior nodal distance* (PND), which is the distance between the nodal point (center of curvature of the lens) and the back of the eye (fig. 4). A large eye (with a large PND) generally has a high RMF, which can create large retinal images.

The resolving power of the eye further depends on the density of retinal sampling units. One sampling unit may correspond to one single photoreceptor, but more often several, if their signals converge onto the same ganglion cell. (See "The organization of retinal neurons").

Other factors affecting spatial acuity

Not all images are perceived with the highest spatial acuity, but the resolving power of the visual system varies with several parameters. One example is the luminance contrast of the image. Since the contrast of small details is attenuated by passing the optics (but also other tissue), only high contrast images can be perceived at the highest resolution (De Valois & De Valois, 1991). Luminance intensity also has a profound effect on spatial acuity because of the increased spatial pooling with adaptation to lower light levels (Barlow et al., 1957; Lind et al., 2012).

Center-surround mechanisms are known to increase the luminance contrast of small spatial details and thus improve their sharpness. However, the receptive fields of these units are too large to have an effect at the spatial acuity limit (Westheimer, 2009b).

Feature detection below the theoretical resolution limit

Predicted acuity limits based on optical quality and retinal sampling frequency generally agrees well with the behavioral ability to visually resolve gratings and conventional optotypes (e.g. tumbling E or Landholt C; Crossland, 2010; Rossi & Roorda 2010; Williams and Coletta 1987). For some visual tasks, however, the ability to perceive spatial detail may exceed the resolution limit. For example, some vertebrates, including humans, are better at detecting small single objects or targets against a uniform background, compared to resolving fine details in a pattern

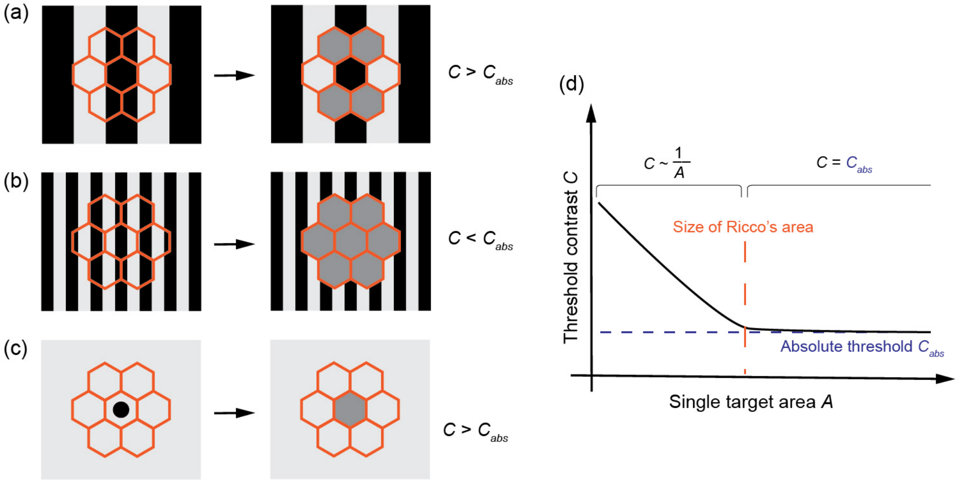

Figure 1 **Figure 5. Ricco's law of complete spatial summation.** (a-c) The red hexagons represent *Ricco detectors*, which are hypothetical receptive field units the size of Ricco's area. The figures in the left column illustrate the image before spatial summation and the figures in the right column after spatial summation. (a) A grating is visible if the contrast between adjacent Ricco detectors (*C*) exceeds the threshold contrast (C_{abs}). (b) Single stripes in a grating cannot be perceived below the retinal sampling limit, (c) unlike single targets provided the contrast is high enough. (d) Below the size of Ricco's area, the threshold contrast is inversely proportional to the target area, while above it is constant.

(Ehrenhardt, 1937; Hecht et al., 1947; Sandow & Hanke, 2024). A uniform target which is too small to be fully resolved by the retinal mosaic, can still be detected if it has enough contrast to the background (O'Carroll & Wiederman, 2014; Thibos et al., 2019). For such small targets, the detection threshold contrast is inversely proportional to the target area (fig. 5b). This relation is known as *Ricco's law of complete spatial summation*[1]. Ricco's law is valid for uniform targets below a critical angular size, "Ricco's area", within which visual signals are spatially summed (Crumey, 2014; Thibos et al., 2019). For targets exceeding the size of Ricco's area, the detection threshold approaches an asymptote of the absolute contrast threshold (Blackwell, 1946; Crumey, 2014). The size of Ricco's area depends on factors like retinal locus and the adaptational state of the eye. In humans, the Ricco's area is smallest in the center of the eye while it increases in size towards the periphery. The size of Ricco's area also expands as the eye adapts to lower light levels (Barlow et al., 1957). The exact anatomical and physiological basis for Ricco's law is debated but it is commonly assumed that the size of Ricco's area corresponds to the receptive

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[1] Ricco's law of complete spatial summation: $C=A*k$, where C is the threshold contrast, A is target area and k is a constant. Annibale Riccó (1844-1919), Italian astronomer.

field center of retinal ganglion cells, or is related to ganglion cell density (Glezer, 1965; Lie, 1980; Thibos et al., 2019; Volbrecht et al., 2000).

Another example where visual perception can exceed the limits of retinal sampling frequency is the detection of small displacements of borders and lines, a phenomenon known as *hyperacuity* (Westheimer, 1975). Humans have been shown to be able to see misalignments that are 5 to 10 times finer than what the retinal sampling rate would predict (Westheimer & McKee, 1977; Westheimer, 2009a).

Motion vision

As mentioned in the first paragraph of this chapter, motion vision is often an integral part of spatial visual perception. The retinal image is in constant change due to movement of external objects or to movement by the eyes of the animal itself. Many times the retinal motion per se carries important information, like the sudden movement of a prey animal, while at other times, the motion is rather a “side-effect” of a behaviour, like the motion of the background during visual tracking of a prey.

Retinal image motion is broadly divided into two classes: 1) *self-induced motion*, and 2) *object motion* (Frost, 2010). How the motion signal is interpreted and what type of action (if any) it will invoke, usually depends on which of these two categories it belongs to. The division between self-induced and object motion signals is thus often made already at the retinal level, and the information is processed along separate visual pathways (Wurtz, 1998; Wylie, 2013).

Self-induced motion

The most common cause of retinal image motion is movement of the eyes of the viewer itself (Cronin et al., 2014; Frost, 2010). Self-induced motion, also referred to as “global motion”, typically covers the entire, or a large part of the visual field. The pattern of retinal motion created by a viewer moving relative a static environment is called an *optic flow field*. The optic flow field varies in a predictable way with the viewer’s direction, speed, and type of movement, but also with the distance to objects in the environment (Gibson, 2015). Optic flow can thus be used to derive information both about one’s own movement and the spatial construction of the environment.

Translational optic flow is caused by a spatial displacement of the viewer relative to its surroundings, for example forward locomotion. Perpendicular to the direction of heading, the optic flow field moves in a single direction, the opposite direction of the translation of the viewer (fig. 6a). The strength of the optic flow depends on the speed of the viewer, but also on the distance to the objects and structures which are imaged on the retina, where objects close by move faster than objects far away (Lee & Kalmus, 1980). The use of optic flow for distance assessment is also called motion parallax and is thought to be utilized by several animal species which during visual fixation move their heads repeatedly from side to side (Kral, 2003).

In the direction of heading, the optic flow field moves radially outward or expands (fig. 6b). In the focus of expansion, which indicates the direct heading, the retinal image is completely still, while the strength of the optic flow increase with increasing distance to this point. This information can thus provide useful information on the heading of translation (Warren Jr et al., 1988). The expanding flow field can also be used to assess the ”time to contact” with external objects; the rate of expansion of the image of an object at the focus of expansion increases when one approaches it (Lee & Kalmus, 1980).

Rotational optic flow is experienced by an animal as it rotates around its own axis. In contrast to translational optic flow, rotational optic flow does not contain information about the distance to external objects since the entire surroundings will move

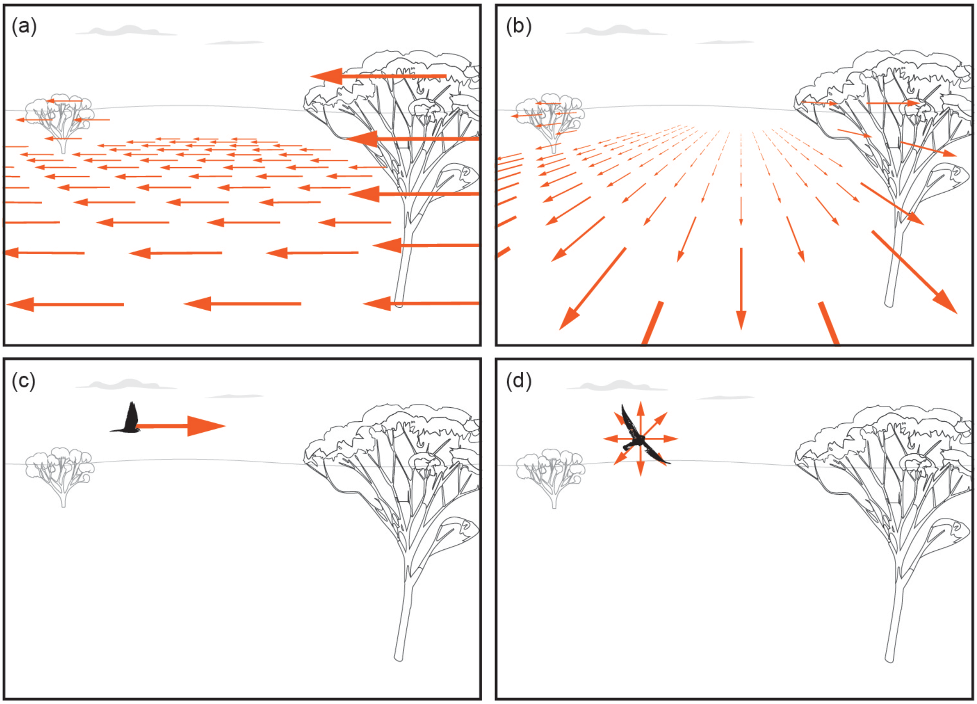

Figure 6. Retinal image motion. The direction and speed of image motion is indicated by the direction and size of the arrows. (a,b) Illustrations of self-induced translational image motion. (a) The left lateral field of view of someone moving “to the right” relative the image, and (b) the field of view in the direction of travel when moving “into” the image. Inspired by illustrations in Gibson (2015) (c,d) Illustrations of objects motion. (c) A raptor passing by the viewer, and (d) a raptor approaching the viewer (“looming motion”).

at the same angular speed. Usually, animals strive to separate the translational components of the optical flow field from the rotational components. This can partly be achieved by making compensatory movements eye- or head movements (e.g. the optokinetic- and optomotor reflexes) when experiencing rotation (Land, 1999). These movements typically consist of a slow stabilizing phase in which the animal fixates its gaze at a point in the moving surrounding followed by a fast saccade directing the eyes a new fixating point (Land, 2014). During the slow phase, the rotational optic flow is minimized, whereas other visual information becomes more conspicuous.

Most vertebrate species do saccadic eye and head movements also during other types of visual behaviour, such as visual search and target tracking. The fast gaze shift in between fixations is thought to minimize image smear (Land, 2014). During the fixation phase of the saccades, the eyes of many vertebrates are counterintuitively not still, but make small fixational eye movements (e.g. microsaccades, ocular drift; Martinez-Conde & Macknik, 2008). Fixational eye movements have been found to prevent image fading (Riggs et al., 1953) but have also been suggested to have a function in perception of spatial information through dynamic visual sampling (Ahissar & Arieli, 2001; Ehud & Amos, 2012; Rucci et al., 2018).

Object motion

Object motion, or "local motion", is retinal image motion that is restricted to a smaller area of the visual field (fig. 6c-d). It is important to most species since it often involves the presence of other animals (Frost, 2010). The detection of a predator, prey, or conspecifics, may cause for immediate action (Franconeri & Simons, 2003) and needs to be discriminated from other motion input at an early stage. Thus, object motion, in particular if it has a sudden onset or expands, is effective at catching the viewer attention (Abrams & Christ, 2003; Christ & Abrams, 2008; Pratt et al., 2010). Indeed, locally moving objects will "pop out" even against a background of optic flow (Rushton et al., 2007).

Effect of motion on contrast sensitivity and spatial acuity

Motion can have a considerable effect on some aspects of the visual image. Image motion may increase the sensitivity for luminance contrast, in particular for larger spatial structures (low spatial frequencies), while it typically decreases for finer structures (high spatial frequencies; Burr, 1981; Burr & Ross, 1982; Robson, 1966). At high velocities the finite integration time of photoreceptors can cause motion blur, which most strongly impacts small spatial details, while large structures become more conspicuous due to impaired lateral inhibition (Burr, 1981; Land & Nilsson, 2012; Lewis et al., 2011).

"I am not crazy; my reality is just different from yours"

Cheshire cat

Measuring spatial vision

The world surrounding an animal is often highly complex and can contain an endless amount of information. Even excluding parameters like wavelength composition and polarization of light, the visual information brought by spatial and temporal intensity changes is substantial within just a single field of view (Frazor & Geisler, 2006). The photoreceptors of any species samples only a fraction of the available light, which provide information that is further filtered and processed along the visual pathway before providing the animal with relevant information (Douglas & Cronin, 2016). Although a lot of image processing takes place already in the retina, the brain continues the analysis through many parallel pathways, integrating information from different locations in the visual field, but also from other sensory modalities and previous knowledge (Isa et al., 2021).

A species' natural environment and behaviour can provide insight into how it uses vision in different contexts and which stimulus parameters are most relevant to them. Furthermore, morphological traits, for example the size and placement of their eyes (e.g. if at the side of their head or at the front), often offer cues on sensory adaptation (Martin, 2017a). However, to find out the limits to what an animal can or cannot see, behavioural experiments are usually needed. Linking a visual stimulus to a behavioural (or sometimes physiological) response provides a robust indication that the animal can perceive the stimulus.

Quantification of visual stimuli

When measuring visual capacity, quantification of the physical components that make up the visual stimulus is required. For these parameters to accurately reflect the visual ability being tested, it is important that they are measured from the subject's point of view. For example, spatial distance is better measured by the angular subtense from the subject's field of view, rather than by absolute distance, since this is the information that reaches its eyes. Furthermore, quantification with objective units enables comparisons between species, but also with the physical characteristics of the habitat of the study species. In the next section I will introduce some of the more common ways of quantifying visual stimuli in animal visual research.

Light intensity

Depending on the purpose, light intensity is commonly measured in two functionally different ways. For example, if one aims to measure the ambient light intensity in a specific habitat, *illuminance* is a suitable measure. Illuminance is the luminous flux (amount of light per time unit) received by a surface, per unit of area (BIPM, 2019). The SI (Système international d'unités) unit for illuminance is *lux* (or candela·sr·m^{-2})[2].

If one is interested in the light intensity of a visual stimulus, *luminance* is a suitable measure. Luminance signifies the amount of light, which is reflected from, or emitted by, surface and that reaches an observer from a specific viewing angle. The SI unit for luminance is *candela·m*$^{-2}$, and it is defined as the amount of luminous flux per unit area which falls within a given solid angle (BIPM, 2019).

Illuminance and luminance are based on the *candela* (luminous intensity), which historically refers to the amount of light produced by a pure spermaceti[3] candle (Johnsen, 2012). The candela, and units derived from it, are *photometric* units which are weighted for the spectral sensitivity of the human visual system. Other photometric units used in vision research include lamberts (Adler & Dalland, 1959; Blough, 1956), footcandles (Hersloff et al., 1974; Wells et al., 1975), and footlamberts (Blackwell, 1946), which can all easily be converted into candela m^{-2} or lux.

An alternative to measuring light in photometric units, is to use *radiometric* units. Radiometric units are either based on the number of photons or the energy content of light and is in contrast to photometric units independent on the spectral sensitivity of the human eye (Johnsen, 2012; Land & Nilsson, 2012). In radiometric units irradiance (photons s^{-1} m^{-2} or watts m^{-2}) is analogous to illuminance and radiance (photons·s^{-1}·sr^{-1}·m^{-2} or watts sr^{-1} m^{-2}) to luminance.

Since the spectral sensitivity differs between various animal species, a unit based on the spectral sensitivity of humans is not ideal. In the experiments included in this thesis we anyway chose to do measurements in photometric units. The main reason for this approach was to simplify comparison with the plethora of literature involving bird vision where light intensities are given in photometric units (e.g. Blough, 1956; Donner, 1951; Heeb et al., 2003; Hodos et al., 1976; Lind et al., 2012; Martin, 1977; Wesolowski & Maziarz, 2012). Furthermore, all stimuli in our experiments vary only in intensity and have the same overall broad spectral composition.

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[2] Sr, steradian, is the unit of a solid angle subtended at the centre of a sphere, with the radius *r*, to a circular surface area r^2.

[3] Spermaceti is a waxlike substance found in the head of toothed whales (Odontoceti), especially the sperm whale (*Physeter macrocephalus*).

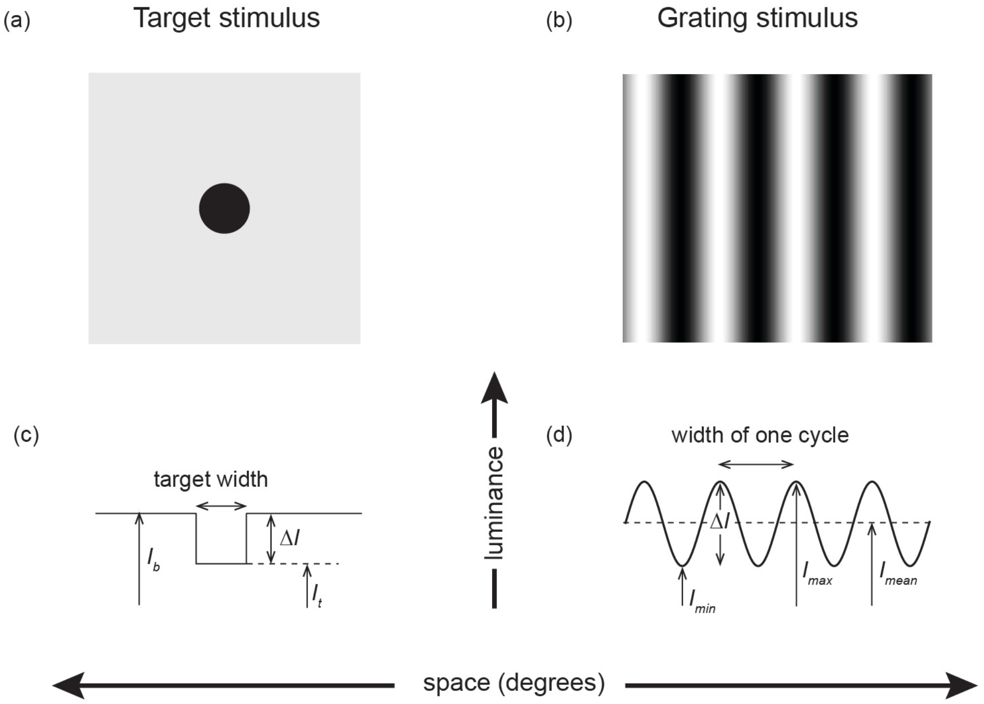

Figure 7. Luminance distribution of visual stimuli. Example of (a) a target (aperiodic) stimulus and (b) a sinusoidal grating (periodic) stimulus. The luminance profile of (c) the target stimulus and (d) the grating stimulus, illustrating how their luminance contrast and spatial extent is quantified.

Luminance contrast

The visual system is tuned to detect relative, rather than absolute, differences in light intensity (see "Luminance and contrast"). The luminance difference of visual stimuli is quantified in a similar way. Depending on the spatial distribution of light intensities in the stimulus, contrast can be defined as either *Weber contrast* or *Michelson contrast*. They both describe the magnitude of luminance variation relative to the overall luminance (Shapley & Enroth-Cugell, 1984). Weber contrast C_W, which is typically applied to the contrast between a smaller target and a uniform background (fig. 7a,c), is defined as:

$$C_W = \frac{I_t - I_b}{I_b} = \frac{\Delta I}{I_b} \tag{4.1}$$

where I_t is the luminance of the target and I_b is the luminance of the background. The definition of Weber contrast is based on Weber's law (eq. 2.2), where $|C_W|$ is equivalent to ω (Weber fraction). Weber contrast is applicable to stimuli where the background luminance have the main influence of the adaptive state of the eye.

If the dark and light areas occupy equal parts of the stimulus, they are assumed to affect the adaptive state of the eye to the same extent. The contrast of such stimuli are best represented by the Michelson contrast C_M:

$$C_M = \frac{I_{\max} - I_{\min}}{I_{\max} + I_{\min}} = \frac{\Delta I}{2I_{mean}} \tag{4.2}$$

where $I_{\max}$ and $I_{\min}$ are the maximum and minimum luminance values (fig. 7d).

Spatial structure of visual stimuli

The size of the retinal image of an object does not reflect its absolute size but rather the angle of visual space that it subtends. Spatial measures of visual stimuli, such as distance and resolution, is thus best described in angular subtense from the point of view of the test subject.

Periodic visual stimuli – grating stimuli

One of the most commonly used stimulus types when measuring the resolving power of the visual system is a grating stimulus (fig. 7b). The luminance of such stimuli varies periodically (i.e. according to a sinusoid or a square-wave) between a maximum and a minimum value, forming the light and dark bars in a grating. The use of grating stimuli facilitates the analysis of vision as a linear system (De Valois & De Valois, 1991). Through Fourier transformation, any visual stimulus can be decomposed into a combination of different sinusoidal wave functions with different amplitude (luminance difference), frequency (size) and phase (position in space). In the realm of linear systems analysis, the response to any visual stimulus is equal to the sum of the responses to each of its wave components. Similarly, it is possible to predict the response to any visual stimulus, if the response to each of its components is known. Since the basic components of Fourier transformation are sinusoidal waves, the simplest visual stimulus is a grating composed of a single frequency.

The resolution of a grating stimulus is quantified in *spatial frequencies*, which have the unit cycles degree^{-1}, where one cycle corresponds to one period of the fundamental wave function (one dark and one light bar in a grating; fig. 7b,d). It is assumed that a grating stimulus can be resolved as long as adjacent dark and bright stripes are sampled by the receptive field centres of separate retinal ganglion cells.

Grating stimuli are also used to measure the *contrast sensitivity function* (CSF), which describes the contrast sensitivity of the visual system as a function of spatial frequency (De Valois & De Valois, 1991). The CSF typically has a band-pass shape, which means that contrast sensitivty is highest for intermediate spatial frequencies (fig. 8). Contrast sensitivity falls slowly for low frequencies, while the drop is comparably sharp for high frequencies. The function reaches the baseline at the cut-off frequency, which corresponds to the acuity limit. The general shape of the CSF for all animals tested is similar, although the position on the frequency axis, contrast sensitivity peak and cutoff frequency may vary (De Valois & De Valois, 1991; Souza et al., 2011).

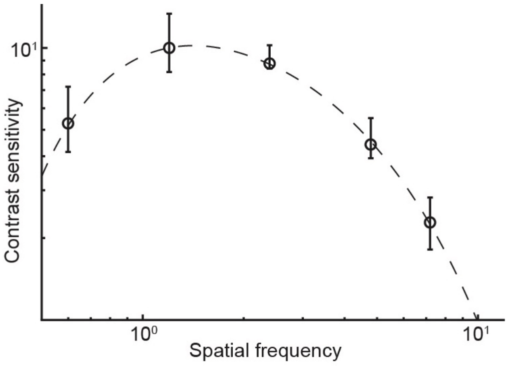

Figure 8. The contrast sensitivity function (CSF). The contrast sensitivity (in Michalson contrast^{-1}) of budgerigars as a function of the spatial frequency (cycles degree^{-1}) of a square-wave grating (cycles degree^{-1}) of a grating. Adapted from Lind and Kelber (2011).

Aperiodic visual stimuli – target stimuli

Aperiodic visual stimuli, or *target stimuli*, does not have a repeating pattern but instead one or several targets, for example dots, lines, or circles. The spatial properties of target stimuli are often quantified by their angular subtense (in degrees), because they constitute a discrete event. Spatial frequencies (cycles degree^{-1}) can also be an appropriate measure, for example when using targets that have been constructed from a discrete piece of a wavefunction.

Many classical studies on the interaction between area, luminance contrast, exposure time, and adaptational state on visual thresholds were conducted with target stimuli (Barlow, 1957, 1958; Blackwell, 1946; Blough, 1956; Hecht et al., 1947). The detection threshold for small uniform targets of high contrast, *single target acuity*[4], can be utilised for making estimates of detection distances of ecologically relevant targets (Adrian, 1989; Champ et al., 2014; Hecht et al., 1947; Sandow & Hanke, 2024; Spratte et al., 2021), but also for studying the receptive field properties (i.e. spatial summation) of retinal neurons (e.g. Donner, 1987; Tuten et al., 2018; Volbrecht et al., 2000).

Although the detection threshold for uniform single targets is limited by contrast sensitivity (see: “Feature detection below the theoretical resolution limit”), it is possible to sidestep luminance cues by using isoluminant targets, which have the same overall luminance as the background. For such targets to be visible, the dark and

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[4] This measure is also known as single object threshold (Land, 1997), single object resolution, single target detection (Spaethe and Chittka, 2003) and minimum visible (e.g., Lythgoe, 1932; Donner 1951).

light regions need to be differentially sampled (i.e. sampled by both ON- and OFF receptive fields of retinal neurons). Examples of isoluminant targets are wavelet bar stimuli, composed of a single period of a wave function (difference of Gaussians: Kirwan, Bok, et al., 2018; Haar and piecewise sine: Kirwan, Graf, et al., 2018; Kirwan & Nilsson, 2019; Sumner-Rooney et al., 2020), and vanishing optotypes, which are constructed by providing a contrasting core to classic ophthalmological targets like tumbling E or Landholt C (Demirel et al., 2012).

Temporal structure of visual stimuli

Motion is spatial displacement in time, which means that moving visual stimuli have both spatial and temporal components. The temporal resolving power depends on the *critical duration time*, which is the time-frame over which incoming photons can be summed to create a visual signal (Donner, 2021).Temporal resolution is usually estimated using a light source with a periodically modulated intensity (Barten, 1999). Below the temporal frequency threshold, the visual system perceives the light as flickering, while above, the light is perceived as continuous (Donner, 2021). The frequency at which the light goes from flickering to continuous is referred to as the *critical flicker-fusion frequency* (CFF) and is measured in hertz or cycles second^{-1}.

The CFF is often used as a proxy for motion vision (Donner, 2021). Still, motion vision is not simply a sum of temporal and spatial vision but involves intricate retinal computations where these properties are entangled (Murphy-Baum et al., 2021; Schwartz & Swygart, 2021). Thus, stimuli for motion vision experiments most often have both spatial and temporal characteristics. A common stimulus type used for assessing motion vision involves drifting gratings or targets. The temporal aspect of target stimuli is typically quantified by angular velocity (degrees s^{-1}) while grating stimuli in addition can be quantified by temporal frequency (cycles s^{-1}).

Methods for measuring visual capacity

Visual capacity is commonly measured by the minimum perceptible stimulus intensity, the *absolute threshold*, or the minimum perceptible difference in stimulus intensity, the *difference threshold*. Visual thresholds can be assessed with behavioural experiments (*psychophysics*), or with electrophysiological measurements. Luminance contrast sensitivity and spatial acuity are also possible to estimate through modelling or calculations if specific physiological and anatomical parameters are known. Below, I summarise some of the most frequently used approaches to study luminance vision in vertebrates.

Modelling the perception of luminance contrast with the receptor noise limited model

Luminance contrast thresholds can be estimated based on photoreceptor noise and spectral sensitivity. The *receptor noise limited model* (RNL model) was originally developed for estimating colour vision thresholds (Vorobyev et al., 2001; Vorobyev & Osorio, 1998) but has since been adapted to work also for luminance vision (Siddiqi et al., 2004; Olsson et al., 2018).

In the RNL model, the discriminability between a target on a background is described by the *perceptual distance* ΔS defined as:

$$\Delta S = \left|\frac{\Delta f}{e}\right| \tag{4.3}$$

Δf is the *receptor contrast*, which is derived from the relative *quantum catch* (the number of photons absorbed by each photoreceptor) between the target and the background, and e is the receptor noise of the luminance channel. ΔS is described in terms of *just noticeable differences* JNDs, and ΔS =1 JND at the visual threshold.

Estimating spatial acuity from the retinal mosaic

The resolving power of an eye depends largely on the retinal sampling density and the posterior nodal distance (PND; see “Retinal factors affecting spatial acuity”). Thus, these measures can be used to make an estimate of the spatial acuity of an eye.

Generally, retinal ganglion cell (RGC) density is used as a proxy for retinal sampling density. The signal from several photoreceptors often converges on the same ganglion cell, whose axon forms the only connection between the retina and the brain (Pettigrew et al., 1988). In cases where RGCs outnumber photoreceptors, or there is a 1:1 relationship, photoreceptor density may be used instead. An additional exception is for species with a *fovea* (retinal invagination: see “Retinal topography”), where RGCs are “displaced” making it difficult to estimate their local density (Coimbra et al., 2015).

RGC and photoreceptor densities are estimated from cell counts in selected retinal areas. Cell counts are done either on retinal wholemounts, or on a combination of wholemounts and cross-sections, for regions in which RGCs are organized in many layers (Mitkus et al., 2014). Typically the spatial resolving power is calculated from the region(s) with the highest density of sampling units.

The retinal magnification factor (*RMF*) is defined as the retinal distance corresponding to 1° of the visual field, and is calculated as

$$RMF = \frac{2\pi PND}{360} \tag{4.5}$$

The maximum resolving power (*F*) of the eye can then be estimated by:

$$F = \frac{RMF}{2} \times \sqrt{\frac{2D}{\sqrt{3}}} \tag{4.6}$$

where D is the peak density of sampling units (cells mm^{-2}), and F is expressed in cycles $degree^{-1}$ (Snyder & Miller, 1977; Williams & Coletta, 1987).

Electroretinogram

Electrophysiological measurement of visual thresholds can be made at different processing levels along the visual pathway. However, responses to basic physical stimulus parameters, like acuity and contrast, are usually measured at the retinal level using a method called the *electroretinogram* (ERG). Using this method, a small electrode, in contact with the cornea, measures the electric activity generated by the retinal neurons as the subject is presented with a visual stimulus. The ERG amplitude is plotted as a function of stimulus intensity, and the threshold is obtained by extrapolating the function down to the "noise level" (= electric potential recorded in the absence of stimuli; Hodos, 2012).

Flash ERG is generated from the presentation of a spatially homogenous test field that produces flashes of light. This method is often used to measure the absolute sensitivity to light (Hodos, 2012), a periodically modulated flash can also be used to measure the CFF (e.g. Lisney, Ekesten, et al., 2012).

The stimuli used in *pattern ERG* varies in both space and time, many times a counter-phase modulated grating. Pattern ERG can be used for testing spatio-temporal contrast sensitivity.

Psychophysics

Psychophysics is defined as the science of relating physical stimuli to a sensation (Gescheider, 1997). Since a sensation by itself cannot be objectively measured, it needs to be approximated with something which is. If the perception of a sensory stimulus is linked, either via an innate mechanism or associative learning, to a specific behavioural (or sometimes physiological) response, this response can be used as a proxy for sensation.

Behavioural experiments usually provide the most robust measure of visual perception. The methods described above estimate or measure an upper limit of vision at the retinal level, without considering the processing that occurs further up the visual pathway. Behavioural experiments, in contrast, demonstrates the existence of a link all the way from retinal detection of a visual signal to a behavioural output. Behavioural responses employed in animal visual psychophysics may range from simple innate reflexes, like the visual fixation of new objects, to more elaborate experimentally learned behavioural repertoires.

Innate responses to visual stimuli

Most animal species have innate behavioural responses that can be induced by visual stimulation (e.g. reflexes, taxes, fixed action patterns). Some responses have a long evolutionary history and are present in entire phyla (Land, 2019), while others have developed to suit the specific needs of single species (Tinbergen & Perdeck, 1950; Williams, 2022).

Phototaxis, a directional movement in response to a light stimulus, might be the oldest innate behavioural response to light and is found in unicellular organisms as well as in vertebrates (Jékely, 2009; Land & Nilsson, 2012). The phototactic response has been utilized to measure visual thresholds in a range of species for example the common diving petrel (*Pelecanoides urinatrix*: Brooke, 1989) and frogs (*R. temporara* and *R. pipiens*: Aho, Donner, & Reuter, 1993).

Moving or looming visual targets tend to capture attention. In species hunted by aerial predators, a target moving or looming can induce an innate defence response (e.g. escape- and freeze response; Carlile et al., 2006; De Franceschi et al., 2016; Hébert et al., 2019; Marquez-Legorreta et al., 2020). For a predatory species, in contrast, a moving target can induce prey-catching response (Bianco et al., 2011; Ewert et al., 2001). Although defence and prey-catching responses often are highly context dependent, they can be used in vision experiments. The spatial acuity of mice have been assessed by their innate defence response to looming target stimuli (Storchi et al., 2019), while the luminance sensitivity of toads (*Bufo bufo*) was measured using their prey-catching response triggered by moving targets (Aho, Donner, Helenius et al., 1993).

In vision research, the most widely used innate response is likely what is referred to as the *optokinetic*, *optocollic*, or *optomotor response* (depending on whether the subject moves its eyes, head, or body; Land, 2019; Wagner et al., 2022). This reflexive response has the function to stabilize vision and can be found in almost all vertebrates. The optokinetic-, optocollic-, or optomotor response and can be induced by rotational optic flow (see "Self-induced motion"). Typically, the subject (if sufficiently small) is placed inside a devise called an "optomotor cylinder", which has a vertically oriented grating at the inside wall. Rotation of the cylinder around the subject elicits a reflex if the grating can be seen, but not if the cylinder is still or if the stimulus is below the visual threshold.

Other behavioural responses related to self-induced motion can be studied by letting the subject itself move in a stationary experimental arena. Behaviours that rely on cues from retinal image motion is then studied under controlled changes in stimulus parameters such as contrast or spatial resolution. The influence of translational optic flow on locomotion has been investigated in several vertebrate species trained to move through a tunnel with grating stimuli on the walls (Bhagavatula et al., 2011; Dakin et al., 2016; Kugler et al., 2019; Scholtyssek et al., 2014).

Methods using innate responses to visual stimuli allow for comparatively fast collection of data and seldom require training of the subject. However, only a narrow range of visual stimuli elicit innate behaviours, and the threshold for eliciting a behavioural response is not necessarily the same as the sensory threshold. In fact, visual thresholds can be context dependent and differ between different behavioural realms (Yovanovich et al., 2017). Assessment of thresholds for specific parameters might be further complicated if the response depends on a combination of several stimulus parameters, and the change in one parameter might result in a lack of response or even in a different response (Bianco et al., 2011; Carlile et al., 2006; De Franceschi et al., 2016; Ewert et al., 2001; Hébert et al., 2019; Procacci et al., 2020; Solomon et al., 2023). Innate responses might thus not necessarily reveal the absolute sensory threshold of a subject, although they will likely better reflect the sensory constraints met in a specific behavioural context.

Classical and instrumental conditioning of visual stimuli

When testing the threshold for visual stimuli that do not elicit any innate response in the subject, *conditioning* can be an alternative method. *Classical conditioning* (also Pavlovian conditioning, after I.P. Pavlov [1849–1936]) means that a subject is trained to associate one stimulus (the *conditioned stimulus*) with another stimulus (the *unconditioned stimulus*) which naturally triggers an innate reflex (the *conditioned response*). By conditioning the visual stimulus of choice, the presence or absence of the conditioned response can be used to evaluate visual capacity (Blake, 1998). Examples of unconditioned stimuli (and associated conditioned responses) are, brief electric shocks (increased heartrate), air-puffs to the eyes (blinking), or delivery of food item (increased salivation) (Blake, 1998; Haug & Florsheim, 2010).

Although classical conditioning is applied to animal psychophysics, *operant conditioning* (or instrumental conditioning) is a more common approach. In operant conditioning the subject is trained to elicit a specific behaviour (the *response*) when presented with a specific stimulus. A *reinforcer*, which can be a reward (*positive reinforcer*, e.g. food), or absence of aversive stimulation (*negative reinforcer*, e.g. an electric shock), following the response, will increase the prevalence of the response to the stimulus (Skinner, 1957). This sequence, stimulus → response → reinforcement, was referred to as a "three-term contingency" by behaviourist B.F. Skinner (1903-1993). In contrast to reinforcement, *punishment* will decrease the prevalence of a behaviour. In psychophysical experiments the behaviour and motivation of the subject can be shaped by reinforcing the response to one stimulus, while punishing the response to another stimulus. Common punishments are prolonged waiting time between trials (positive punishment) or simply the absence of a reward (negative punishment; Haug & Florsheim, 2010; Mora et al., 2009).

The test subject can be trained to perform either a *single response* or not, or to make a *choice* between two (or more) responses, when presented with a stimulus. The *go/no-go* method is an example of a single response method. The subject is presented with one stimulus at a time and trained to elicit a response (e.g. pressing a key or make an oriented movement) if it identifies it as the "correct stimulus" (S+) and to withhold the response if it identifies it as the "incorrect stimulus" (S-; Blough & Blough 2022).

In the *yes/no* method, which is a choice method, the subject is also presented with a single stimulus at a time. However, unlike in the go/no-go method, the subject in the yes/no method is expected to elicit one response (e.g. press the green key) in the presence of S+ and different response (e.g. press the red key) in the presence of S- (Blough, 1956; Hodos et al., 2002).

When applying the *forced-choice* method, several stimuli are presented simultaneously, and the subject is trained to identify which one of them is the S+ and make a response that indicate its choice (Gescheider, 1997). The *two-alternative forced choice* (2AFC) procedure, in which two stimuli (one S+ and one S-) are displayed simultaneously in each trial, is extensively used in animal vision psychophysics (Blough & Blough 2022), including the experiments in this thesis. The S+ and S- is usually displayed side by side, with their relative position varied pseudo randomly between each trial to avoid unwanted cueing. The response indicates the position of the S+ (e.g. pressing the right/left key or make an oriented movement).

Stimulus presentation

In psychophysical vision experiments, the subject is presented with a series of stimuli of varying intensities ranging from well below to well above its visual threshold. The threshold is not considered as a fixed intensity above which all stimuli are correctly identified. Rather, it is the intensity at which the subject can correctly identify a stimulus with a predefined likelihood (usually somewhere between "chance level" and correct identification nearly all the time; Gescheider, 1997). The likelihood of making a correct stimulus identification (for a specific intensity) is estimated from the proportions of correct stimulus identifications made during the experiment.

The stimulus intensity ("the level of difficultness") can be alternated from trial to trial according to various sequential methods. Those most commonly applied in animal vision research are based on a few classic methods developed by *G.T. Fechner* (1801-1887) (Gescheider, 1997; Malone, 2017). One of these are the *method of constant stimuli*, where a fixed set of stimulus intensities are repeatedly presented to the subject. The set commonly includes between five and nine stimulus intensities, ranging from just below the sensory threshold to well above it, which are presented in a random or semi-random sequence (Gescheider, 1997). Every intensity is tested many times throughout an experiment to obtain a ratio of correct stimulus identification at each intensity level. A *psychometric function* which expresses the likelihood of correct stimulus identification as a function of stimulus intensity, is then fitted to the data. The shape of the psychometric curve is sigmoid, with the lower asymptote at the ratio correct identifications below threshold by chance, and the higher asymptote at the ratio correct identifications well above threshold. The threshold intensity is usually found at the point of the psychometric curve that is halfway between the two asymptotes (e.g. 0.75 in a 2AFC; Gescheider, 1997).

The *method of limits* starts off with an intensity which is either well above (the "descending series") or below the sensory threshold ("ascending series"). In the descending series, the stimulus in each successive trial is slightly lower than the previous one until the subject fails to identify the S+, at which point the test is terminated. In the ascending series instead, the stimulus intensity increases with each trial, until the subject can identify the S+ stimulus (Gescheider, 1997). The threshold is usually defined by averaging the stimulus intensity of the last two trials (correct identification ↔ incorrect identification) of a series.

The *staircase method* is a modification of the method of limits (Gescheider, 1997; Levitt, 1971). This method begins as a descending series, only the test is not terminated when the subject fails to identify the S+. Instead, the direction of change in intensity is reversed. In other words, the intensity of the subsequent stimulus will have increased. A correct stimulus identification will again make the series descend, and so it continues throughout the experiment. A change in direction (descending ↔ ascending) is called a reversal, and usually a pre-defined minimum number of reversals must occur before a test sequence is terminated (Levitt, 1971).

The experiments described in the articles that are part of this thesis were performed using the *1-up/2-down staircase method*. This is a variant of the staircase method where the stimulus intensity decreases after *two* consecutive correct responses but increases after only *one* incorrect response (fig. 9; Levitt, 1971). The stimulus intensity will eventually oscillate around the threshold level, where the probability of a descending step (two consecutive correct responses) is the same as that of an ascending step (one incorrect response). The threshold intensity is calculated from the mean value of the intensity at the reversals, which corresponds to the intensity that the subject can identify with 70.7% probability. (Levitt, 1971).

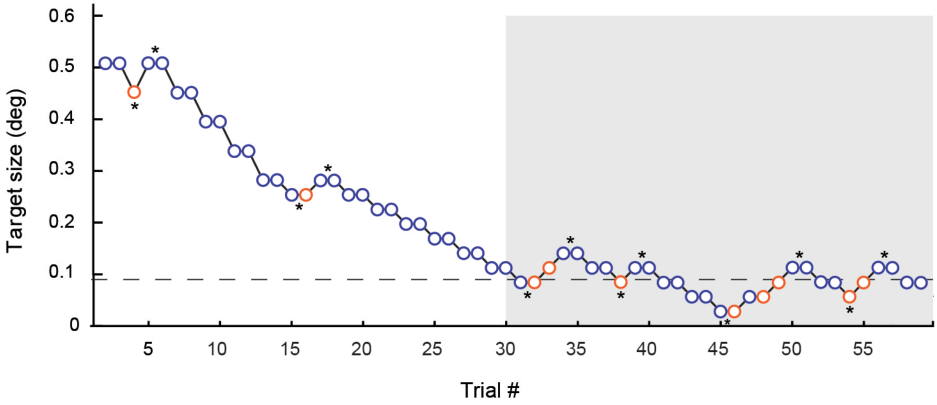

Figure 9. The 1-up/2-down staircase method. The stimulus intensity (in this example, target size) of the initial trials in a staircase session are well above the threshold. After two consequtive correct responses (blue circle) on the same intensity level, the stimulus intensity level decrease, while one incorrect response (red circle) is followed by an increase of stimulus intensity. Reversals (increase → decrease or decrease → increase) are indicated by asterisks. The threshold level (dashed line) is in this example calculated from the 8 last reversals (indicated by the grey background).

In the *method of adjustment*, which is one of Fechner's original methods, the test subject itself controls the increment or decrement of the stimulus intensity. The subject starts at a random intensity level and adjusts it gradually until the threshold is reached (Gescheider, 1997).

The *threshold tracking method* developed for testing hearing in humans (Békésy, 1947) resembles both the method of adjustment and the staircase method. It was later adapted by Blough (1955) to track visual sensitivity of pigeons. The pigeon was trained to peck at one key when a bright patch was present (S+) and to peck at another key when the bright patch was absent (S-), in a yes/no procedure. A peck on the first key would lower the luminance of the patch, while a peck on the second key would raise the intensity of the patch, causing it to fluctuate around the threshold intensity throughout the experiment. This adapted method has been used to track visual threshold curves during dark-adaptation in several species (Adler & Dalland, 1959; Blough, 1956; Hersloff et al., 1974; LaMotte & Brown, 1970; Wells et al., 1975).

Training animals to perform in psychophysical experiments is often time-consuming. Furthermore, sometimes the experimental subject continues to improve its visual performance even after a task has been learned (Blough & Blough, 2022; Blough, 1971; Chaib et al., 2019; Chaib et al., 2021; Ghim, 2003; Sandow & Hanke, 2024). This phenomenon is commonly referred to as the *learning effect* and may persist for a few trials or sometimes several months (Ghim, 2003; Gilbert, 1994). The learning effect is in some instances a consequence of actual improvement of sensory perception (i.e. *perceptual learning*; Tsushima & Watanabe, 2009).

We experienced a learning effect in all experiments included in this thesis. Despite successful training of the bird subjects for specific experimental tasks, we would notice a gradual improvement of the performance once we started running the staircase test sessions. The birds would reduce their threshold over several consecutive test session (in the experiments in paper I up to 9 tests sessions) before reaching a stable plateau of performance. We do not know if the birds increased their performance because of perceptual learning, or if they improved their ability to focus on the experimental tasks. A similar learning effect was noticed in single target acuity experiments with both the common sunfish (*Lepomis gibbosus*; Spratte et al., 2021) and harbour seal (*Phoca vitulina*; Sandow & Hanke, 2024).

Spatial vision in birds

The avian eye

For most species of birds, vision is the primary sense, and as a group they rely more on visual information than any other vertebrate class (Martin, 2017a). The high importance of vision is reflected in the anatomy of the avian visual system in several ways. For example, birds typically have large eyes that occupy a considerable portion of the cranial volume (Shimizu & Watanabe, 2012), and the part of their brain devoted to processing of visual information is greater than in other animals (Martin, 2017a). In addition, the avian retina is among the most complex of all and it expresses a large variation between species (Hart, 2001a; Meyer, 1977; Walls, 1942).

Photoreceptors

In common with most other vertebrates, the retina of birds has two major classes of photoreceptors, *cones* and *rods*. Both rods and cones are elongated cells which can be divided into an inner segment, containing the nucleus, organelles and as synaptic terminal, and an outer segment, which houses the visual pigments. Cones mediate vision at daylight, while they lose their function at night. Rods, on the other hand, are about 25-100 times more sensitive than cones (Martin, 2017a). This means that they work at significantly lower light intensities but also that they are saturated in daylight.

Most birds have four spectrally distinctive types of single cones which enable them to have tetrachromatic colour vision (Kelber, 2019). The various single cones are mainly characterized by their different pigments which makes them sensitive to light at different wavelengths; the V-cone have a λ_{max} (peak absorbance) at 355-424 nm, the S-cone at 427-463 nm, the M-cone at 497-514 nm, and the L-cone at 505-630 nm (Hart & Hunt, 2007). The spectral sensitivity of bird cones is further affected by the oil droplet, a spherical organelle located at the distal end of the inner segment, through which incoming light is filtered before reaching the outer segment (Toomey & Corbo, 2017). V-cones have transparent oil droplets that are thought to increase the light catch of the outer segment (Wilby & Roberts, 2017). The other three types of single cones (S, M, and L) have carotenoid-containing oil droplets that act as optical long-pass filters, improving colour contrast at the expense of overall sensitivity (Toomey & Corbo, 2017; Wilby & Roberts, 2017).

In addition to the four types of single cones birds also have one type of *double cone*. Double cones are present in most vertebrate groups where they show a great diversity in their pigment content and morphology (Bowmaker, 2012). In birds, double cones consist of one larger principal member and one smaller accessory member, which are thought to be optically and electrically coupled (Hart & Hunt, 2007). Both members express the same pigment as the L single cone (LWS opsin). However, while the pigmented oil droplet of the L single cone shifts its λ_{max} to longer wavelengths, the principal member of the double cone has a clear, or almost clear, oil-droplet which likely transmits a larger fraction of the incoming light (Wilby & Roberts, 2017. The accessory member most often lacks an oil droplet completely (Hart, 2001b).

Although the double cone is the most abundant photoreceptor in the retina of diurnal birds their function is not fully understood. Likely, they serve a function in luminance-mediated vision but not in spectral discrimination (Kelber, 2019; Goldsmith & Butler, 2005). Behavioural experiments indicate an involvement in the perception of luminance contrast and fine texture (Jones & Osorio, 2004; Lind & Kelber, 2011), although high-resolution vision likely also involve input from single cones (Lind & Kelber, 2011; Mitkus et al., 2017; Seifert et al., 2023). Motion perception, which is likely driven by luminance cues, is another suggested function of double cones (Bhagavatula et al., 2009; Campenhausen & Kirschfeld, 1998; Seifert et al., 2023; but see: Sun & Frost, 1997).

One of the difficulties with studying the function of double cones is that their λ_{max} lies between that of M and L single cones. This makes it difficult to distinguish double cone stimulation from a weighted sum of M and L single cone stimulation (Osorio et al., 1999). In any case, double cones form multiple retinal networks, both with rods and single cones, indicating that they play a role in multiple visual channels (Günther et al., 2021; Seifert et al., 2020).

Retinal topography

In common with most vertebrates, the retinas of birds are not functionally homogenous. Ganglion cell density, photoreceptor composition, and retinal wiring vary with spatial location (Hart, 2001a). Different parts of the retina sample light coming from different directions in the visual field. As the light from these directions usually differs in terms of for example spectral composition, contrast, mean luminance (Nilsson et al., 2022), as well as temporal aspects (Martin, 2017b), different parts of the retina need to fulfil different requirements.

Retinal ganglion cell topography

Retinal ganglion cell (RGC) density, which is associated with spatial acuity (see "Retinal factors affecting spatial acuity"), often varies substantially across different retinal locations (Martin, 2017a; Meyer, 1977). Although the topographic variation of RGC density follows a general pattern, it also differs between species and has been shown to correlate with factors such as habitat structure, foraging technique and vulnerability to predators.

Birds typically have one or two retinal regions with elevated ganglion cell density, referred to as *areae* (Meyer, 1977). The *area centralis*, which as the name suggests is located in the central retina, is the most prevalent. Since the eyes of most birds are located on the side of the head, the *areae centralis* of the two eyes are oriented laterally (with a horizontal angle slightly less than 90° to the midline of the beak) and thus view separate parts of the world.

Many species have an additional *area*, the position of which can vary but which is usually directed to the frontal visual field. This type of *area* typically has a temporal or dorso-temporal placement in the retina (*area temporalis* or *area dorso-temporalis*), and is associated with hunting of live prey, or a need for fine-tuned bill control (Coimbra et al., 2014; Coimbra et al., 2009; Lisney, Iwaniuk, Bandet, et al., 2012; Lisney et al., 2015; Potier, Mitkus, et al., 2020; Tyrrell & Fernandez-Juricic, 2017).

Increased RGC density is also often seen as an elongated horizontal *area* across the retina and is then referred to as a *visual streak*. According to the "terrain theory", proposed by Hughes (1977), the visual streak is an adaptation in animals that occupy open habitats and provides them with a panoramic view of the free horizon. Studies of the retinas of birds have, on the other hand, provided inconclusive support for the terrain hypothesis (Lisney, Iwaniuk, Kolominsky, et al., 2012).

Budgerigars forage on the ground in a predominantly open habitat and should therefore, according to the terrain hypothesis, possess visual streaks. Topographical mapping of their RGC density nevertheless revealed only a weak visual streak in one of five retinas (Mitkus et al., 2014). The same study also found no visual streak in the retina of the closely related Bourke's parakeet (*Neopsephotus bourkii*) which occupies the same habitat type. Both species possessed an *area* centralis while the budgerigars also had an *area nasalis* that projected slightly backwards in the visual field (fig. 10). Since budgerigars use their beak when climbing the *area* nasalis is suggested to be used in visual scanning for predators as the head mobility is constrained during this activity (Mitkus et al., 2014). Although budgerigars often forage on grass seeds that have fallen to the ground, they frequently climb up directly on sturdier grass plants (Higgins, 1999).

Cockatoos are, like budgerigars, seed eating psittacines that live in Australia. However, unlike budgerigars, cockatoos have been found to possess visual streaks

(Coimbra et al., 2014). Five of six species that have been studied also had a dorso-temporal *areae*, assumed to project into the frontal visual field. As these same species are known to use their feet to grasp and manipulate food items during foraging, the enhanced acuity in the frontal visual field is thought to serve a purpose in such activities (Coimbra et al., 2014). Only the cockatiel (*Nymphicus hollandicus*), which like budgerigars and Bourke's parrots, only use their beak in food manipulation, were found to lack a dorso-temporal *area*.

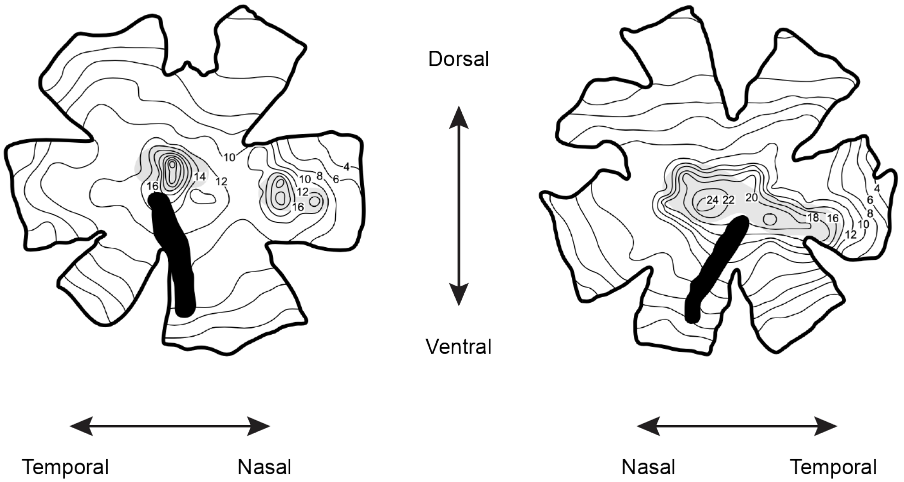

Figure 10. Retinal ganglion cell (RGC) topography in the budgerigar. Numbers represent x1000 cells mm^{-2}, grey shading indicates regions with RGCs stacked in layers, and black bars the position of the pecten oculi. Adapted from Mitkus et al. (2014).

The rock pigeon is another seed-eating species that, like cockatoos, has a retinal *area* that is directed into the frontal visual field (Querubin et al., 2009). Although rock pigeons are ground foragers, temporal or dorso-temporal *areae* are generally absent in species with this foraging practice (i.e. European starling [*Sturnus vulgaris*], brown-headed cowbird [*Molothrus ater*], house sparrow [*Passer domesticus*], house finch [*Carpodacus mexicanus*] and mourning dove [*Zenaida macroura*]: Dolan & Fernández-Juricic, 2010; tree sparrow [*Passer montanus*]: Rahman et al., 2006; seven phasianid species: Lisney, Iwaniuk, Kolominsky, et al., 2012); peafowl [*Pavo cristatus*]: Hart, 2002; red-winged blackbird [*Agelaius phoeniceus*]: Fernández-Juricic et al., 2019).

The RGC density distribution in the budgerigar, as well as Bourke's parrot, expresses a high inter-individual variation (Mitkus et al., 2014). Possibly, this is a consequence of domestication and human-controlled breeding, as the individuals examined in the cited study were not wild-caught. Phenotypic traits that exert a high selection pressure on a species in its natural habitat (e.g. traits associated with predator avoidance or foraging) have been observed to exhibit a substantial variability in domesticated individuals (Mignon-Grasteau et al., 2005). Furthermore, Lisney et al. (2011) found evidence that domestication might have affected the temporal visual resolution of the chicken negatively. On the other hand, the chicken has not only been domesticated for a much longer time (~3500 years ago) than the budgie (less than 200 years ago) but has also been subjected to a higher artificial selection pressure, as it is used as livestock. Although the visual capacity of wild and domestic budgerigars has never been compared, their acoustic sense has been shown to be unaffected by domestication (Farabaugh et al., 1998).

Photoreceptors

As with RGCs, the distribution of photoreceptors also shows a high variation between bird species as well as across the same retina. The overall density of photoreceptors roughly follows the topographical pattern of RGC, although the photoreceptor to RGC convergence ratio is comparatively low in high density regions (Querubin et al., 2009).

The photoreceptor population of nocturnal owls consists mainly of rods (Fite, 1973; Lisney, Iwaniuk, Bandet, et al., 2012), while diurnal birds typically have a cone-dominated retina (Hart, 2001b). The *area* and *fovea* of many diurnal species have even been shown to lack rods entirely, presumably to accommodate a greater number of the smaller cones (Coimbra et al., 2015; Querubin et al., 2009).

The most prevalent cone type in diurnal birds is the double cone, which may constitute over half of the cone population in some species (Hart, 2001b). Many ground-foraging species (including the budgerigar) have the highest proportion of double cones in the ventral region of the retina, while arboreal species have the most double cones in the dorsal region (Hart, 2001a). This difference has been suggested to be an adaptation for detecting predators: while ground-foraging birds are vulnerable to airborne threats, arboreal birds often face attacks from below (Hart, 2001a). Despite their prevalence, double cones are absent in the central the *fovea* of some raptor species (Mitkus et al., 2017).

Foveae

In many species, the *area* or visual streak is accompanied by a *fovea*, which is an invagination in the inner layers of the retina (Bringmann, 2019; Meyer, 1977; Walls, 1942). As *foveae* overlies densely packed photoreceptors, with low RGC convergence ratio, they are commonly assumed to be involved in mediating high acuity vision. However, the complete function of the *fovea* is debated, some suggestions being the reduction of light scattering, image magnification, movement detection, and “focus indication” (reviewed in: Bringmann, 2019; Moore et al., 2017). *Foveae* located in the centre of the retina are widely distributed taxonomically and have been documented in species belonging to most lineages, such as raptors, psittacines, passerines, fulmars, and Columbiformes (Bringmann, 2019). Some birds, such as the sacred kingfisher (*Halcyon sancta*), the laughing kookaburra (*Dacelo novaeguineae*), the least tern (*Sternula antillarum*), as well as most actively foraging raptors (Accipitriformes and Falconiformes), have both a central and a temporal *fovea* (Bringmann, 2019; Mitkus et al., 2017; Moroney & Pettigrew, 1987; Potier et al., 2016; Potier, Mitkus, et al., 2020). Having a temporal *fovea* without having a central *fovea* is comparatively rare but occurs in the common swift (*Apus apus*) and most species of owl (Strigiformes) (Bringmann, 2019; Fite, 1973; Lisney, Iwaniuk, Bandet, et al., 2012).

The visual field and eye movements in birds

Birds have their eyes positioned on the sides of their head. As a result, their visual field extends laterally around the head, typically leaving only a small "blind angle" at the back. Usually, the visual fields of the individual eyes have a small binocular overlap at the front, while most of the visual field is seen monocularly. The visual field variation seen in various species is suggested to be a product of primarily foraging method but also of the need for predator detection (Martin, 2017b).

When a bird spots a target of interest it will typically move it into either one of its central *areae*/*foveae* (*lateral fixation*) or the frontal visual field (*frontal fixation*). In general, lateral fixation is used for targets that are further away, while frontal fixation is used for targets nearby (Bloch & Martinoya, 1982; Kano et al., 2022; Martin & Katzir, 1999; Martinoya et al., 1983; Rounsley & McFadden, 2005). Many species have a refractive state that varies across the field of view: while the frontal visual field is myopic, the lateral visual field is emmetropic (Fitzke et al., 1985; Hodos & Erichsen, 1990). This means that they do not have to accommodate when switching between frontal fixation and lateral fixation, but also that they can forage on the ground while on the same time scan their surroundings for predators.

The frontal and lateral visual fields of birds differ not only in terms of optimal viewing distance but also in functionality. For example, moving targets are preferentially fixed by the lateral visual field, which is thought to be better adapted for predator detection (Evans et al., 1993; Maldonado et al., 1988). Indeed, information from frontal and lateral visual fields are associated with different processing pathways that are thought to handle separate aspects of visual information (Clark & Colombo, 2022; Güntürkün & Hahmann, 1999). Intraocular transfer is likely also restricted (Jimenez Ortega et al., 2008; Remy & Emmerton, 1991; Roberts et al., 1996), and birds often alternate between different parts of the visual field when inspecting unknown objects (Kano et al., 2022; Stamp Dawkins, 2002).

When a bird fixates a target in their frontal visual field, both eyes make a converging movement (Bloch et al., 1984; Martinoya et al., 1984). Frontal fixation is often made in association with pecking or lunging at a target, suggesting that the frontal visual field is used for visual control of the beak and feet (Kano et al., 2022; Martin & Katzir, 1999; Martinoya et al., 1983). A larger degree of binocular overlap has been observed in species with a need for precise control of the bill or feet, primarily in foraging, but also in provisioning of young, and in nest construction (Martin, 2017b). Passerines generally have the widest binocular overlap, and the tool-using New Caledonian crow (*Corvus moneduloides*) has a maximum overlap of a full 61° (Troscianko et al., 2012).

It has been proposed that the function of the binocular overlap in birds is to provide depth perception by stereopsis. Although stereopsis has been demonstrated in the barn owl (*Tyto alba*; van der Willigen, 2011; van der Willigen et al., 1998) it is likely not widespread among birds. The binocular overlap may also increase visual sensitivity, which is important in nocturnal species that often have frontally oriented eyes (Read, 2021). Still, the primary purpose of frontal fixation is not necessarily the binocular overlap per se. The visual field of symmetrically converging eyes enables an expanding optic flow field in the direction of travel, which for example can be used for guidance of the beak (Martin, 2009). The binocular overlap has also been proposed to be a secondary consequence of minimizing the anterior blind area; viewing items in, or close to, the beak indirectly requires a wide binocular overlap (Tyrrell & Fernández-Juricic, 2017).

Species that are not at the top of the food chain must balance the need for binocular vision with having a wide cyclopean visual field (binocular + monocular visual fields) for predator detection (Martin, 2017b). A wider cyclopean field is often found in species which primarily rely on tactile senses when foraging (e.g. filter-feeding, or dabbling ducks, and shorebirds) and thus do not need to have precision control of the bill (Cantlay et al., 2023; Martin, 2017b). The Eurasian woodcock (*Scolopax rusticola*) and the mallard (*Anas platyrhynchos*), for example, both have total panoramic visual fields, and comprehensive visual coverage of the hemisphere (Martin, 1986, 1994).

Psittacines are extractive foragers, and although they use vision to locate food (mostly seeds, nuts and fruits), the beak, tongue, and in some species the feet, are used to extract the embedded eatable parts. At the tip of the upper mandible of parrots there are touch receptors (the "bill-tip organ"), which are used in food handling and object exploration (Martin & Martin, 2022). The visual field has so far only been measured in one psittacine, the Senegal parrot (*Poicephalus senegalus*), but the configuration is likely similar in closely related species (Martin & Martin, 2022). The Senegal parrot has a comparatively a wide frontal binocular overlap, but also a near total panoramic view above the head (Demery et al., 2011). The beak is located at the edge of the frontal binocular field, meaning they cannot see things held in it. Likely, the bill-tip organ of parrots compensates for a more comprehensive visual field around the beak, which instead extend above the head. Nevertheless, the Senegal parrot has a rather broad binocular overlap above the beak which allows visual inspection of objects up close (Demery et al., 2011).

Contrast sensitivity

Although birds have remarkably good vision in many ways, their contrast sensitivity is relatively low. Measurements of the maximum contrast sensitivity in different species range between 4.6 and 31 Michelson contrast^{-1} (Blary et al., 2024; Ghim & Hodos, 2006; Haller et al., 2014; Harmening et al., 2009; Hirsch, 1982; Hodos et al., 2002; Jarvis et al., 2009; Lind et al., 2013; Lind et al., 2012; Potier et al., 2018; Reymond & Wolfe, 1981). In comparison, fishes have contrast sensitivities between 33 and 125 (Bilotta & Powers, 1991; Northmore & Dvorak, 1979; Northmore et al., 2007; Santon et al., 2019), primates between 90 and 200 (De Valois et al., 1974; Jacobs, 1977), and the domestic cat (*Felis silvestris*) 116 Michelson contrast^{-1} (Bisti & Maffei, 1974). Among birds, the highest contrast sensitivities are found in raptors, notably Falconiformes species, but also in the raven (*Corvus corax*) (Blary et al., 2024; Hirsch, 1982). Why birds have such a low contrast sensitivity in general is not known but has been suggested to be a trade-off for other visual capacities such as UV-sensitivity (Blary et al., 2024; Ghim & Hodos, 2006).

The contrast sensitivity function (CSF) in birds can show some variation depending on the method applied. CSFs obtained from pattern electroretinogram (PERG) show a lower (by $\sqrt{2}$) peak sensitivity compared to behavioural experiments with operant conditioning (Hodos et al. 2002). Furthermore, studies that have used the optocollic reflex generally describe CSFs that are tuned to lower spatial frequencies than those that have used operant conditioning (Blary et al. 2024).

The CSF of budgerigars for grating stimuli has been measured in two different studies, both using operant conditioning and a two-alternative forced choice (2AFC) procedure. The maximum contrast sensitivity was estimated to be 10.2 Michelson contrast^{-1} at 1.4 cycles degree^{-1} (Lind & Kelber, 2011), and 13.3 Michelson contrast^{-1} at 1.7 cycles degree^{-1} (Haller et al., 2014) respectively. A similar contrast sensitivity was found in a brightness discrimination experiment with spatially separated homogeneously grey stimuli (11 Michelson contrast^{-1}: Lind et al., 2013). The contrast sensitivity of budgerigars is thus in the same range as for other granivorous species (Blary et al., 2024; Ghim & Hodos, 2006; Hodos et al., 2002; Jarvis et al., 2009; Lind et al., 2012).

In Paper I we tested the budgerigar detection threshold for single (non-periodic) targets with different contrast to the background. The targets all had a negative contrast to the background varying between >-99 and -41 in Weber contrast (>99 and 25 in Michelson contrast) and had a luminance profile of a single period of a sine wave. We found a similar spatial frequency-dependent contrast sensitivity for single targets as had previously been measured for gratings (fig.11). However, since we only included a limited range of contrasts in our experiments, it is not possible to draw any conclusions on peak contrast sensitivity or contrast sensitivity for low spatial frequencies.

Spatial acuity

Some birds have the sharpest visual acuity of all animals. The wedge-tailed eagle (*Aquila audax*) has an acuity of 138 cycles degree^{-1} (Reymond, 1985) and the Egyptian vulture (*Neophron percnopterus*) and Indian vulture (*Gyps indicus*) of 135 cycles degree^{-1} (Fischer, 1969). In comparison, humans have a spatial acuity of around 60 cycles degree^{-1} (Campbell & Green, 1965). Human spatial acuity is still very impressive compared to most animal species; birds included. In fact, the exceptionally sharp vision of some raptors is not common in birds, whose visual acuity shows a great variation with 84% of all species having an acuity below 30 cycles degree^{-1} (Caves et al., 2018).

One of the main drivers of avian visual capacity, including spatial acuity, is thought to be foraging (Martin, 2017a). Species which need to detect single food-items at a distance, primarily those feeding on vertebrates or scavenged prey (e.g. diurnal raptors), generally have the highest spatial acuity (Caves et al., 2024). In contrast, ground foraging species which feed on seeds or invertebrates (e.g. many small passerines, parrots, and pigeons) tend to have low spatial acuity (Coimbra et al., 2014; Dolan & Fernández-Juricic, 2010; Donner, 1951; Moore et al., 2015).

Budgerigars, which feed primarily on grass seeds, have a similar comparatively low spatial acuity as other small ground foraging birds. Their spatial acuity has been assessed with both behavioural experiments of grating acuity and anatomical measurements based on RGC density, methods which have yielded similar results. In the behavioural experiments, spatial acuity was estimated by extrapolating the cut-off point from the behaviourally measures CSF. Studies by Lind and Kelber (2011) and by Haller et al. (2014) reported spatial acuities of 10 cycles degree^{-1} and 7.7 cycles degree^{-1}, respectively. Spatial acuity based on anatomical measurements was estimated to 7.9 cycles degree^{-1} by Mitkus et al. (2014).

Single target acuity in birds

In addition to foraging, predator detection is believed to have a major impact on shaping vision in birds (Martin, 2017b). Ground-foraging birds that live in open habitats are visually exposed to aerial predators. High spatial acuity is thought to benefit these species because it allows them to detect predators at greater distances (Caves et al., 2024; Tisdale & Fernández-Juricic, 2009). The distance from which a bird can detect a predator, is often assumed to be deductible from their grating acuity. However, as discussed in "Feature detection below the theoretical resolution limit", several non-avian animals have shown a higher acuity for single targets compared to gratings (sand lizard (*Lacerta agilis*), Ehrenhardt, 1937; human, Hecht et al., 1947; dragonflies (Odonata) and flies (Diptera), O'Carroll & Wiederman, 2014; harbour seal: Sandow & Hanke, 2024; carpenter bee (*Xylocopa tenuiscapa*), Somanathan et al., 2017; honey bee (*Apis mellifera*), Vallet & Coles, 1993). This made us wonder how well budgerigars, which inhabit mostly open landscapes, can detect single targets against a plain background.

In Paper I we assessed the target acuity of budgerigars using three different circular targets, two of which had a negative contrast to the background (lower luminance than the background), and one which was isoluminant with the background (see “Aperiodic visual stimuli – target stimuli”). The first target (which we tested at five different contrast levels, see “Spatial vision in birds - Contrast sensitivity”) had a radial luminance profile shaped like a single period of a sine wave function (Fig. 11a), which facilitated direct comparison with budgerigar acuity measured with sinusoidal gratings.

The target size was measured as the *full width at half maximum* (fig. 11a-c), which equals half a period of a sine wave in a grating with the same resolution. From our data we estimated that budgerigars can detect a “sinusoidal target” subtending 0.065 degrees of their visual field, a measure which corresponds to a sinusoidal grating of 7.7 cycles degree^{-1}. This is very similar to the previous estimates of grating acuity in budgies, both from behavioural and anatomical studies (Haller et al., 2014; Lind & Kelber, 2011; Lind et al., 2012; Mitkus et al., 2014), suggesting that budgerigars are as good at detecting gratings as they are at detecting single targets with a sinusoidal luminance profile (fig. 11d).

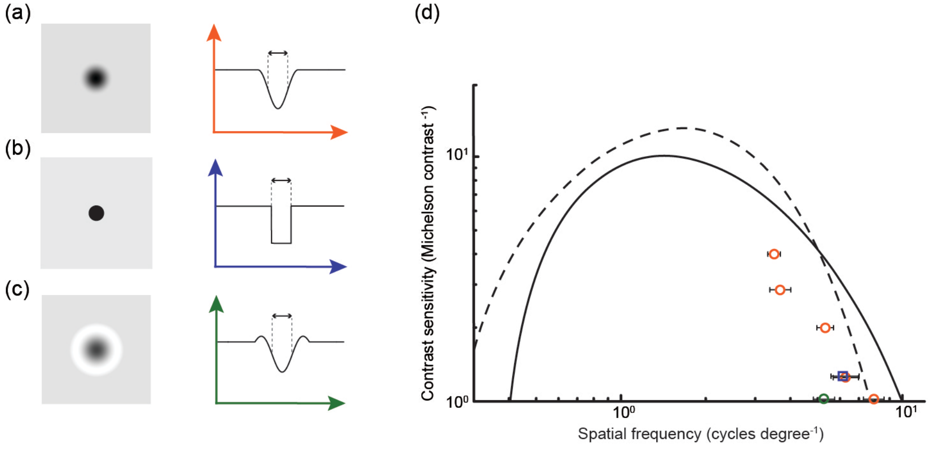

Figure 11. Single target acuity of budgerigars. (a-c) Single target designs and target luminance profiles from the experiments in Paper I: (a) sinusoidal target, (b) square-wave target and (c) isoluminant target. The small black arrows indicate the full width at half maximum. (d) The single target thresholds (color codes from luminance profiles a-c) plotted together with the contrast sensitivity function for budgerigars by Lind and Kelber (2011) and Haller et al. (2014), with a solid line and dashed line respectively.

The second target in our study had a radial luminance profile with the shape of a single period of a square wave (a "dot"; fig. 11b). Interestingly, this target had a significantly higher detection threshold (0.098 degrees, or 5.1 cycles degree^{-1}) than the sinusoidal target with the same contrast.

Previous research has established that the luminance profile of grating stimuli (sine or square wave) does not affect the CSF in in budgerigars (Lind et al., 2012). This does not apply to humans which have a contrast sensitivity that is 1.27 ($4/\pi$) times higher for square gratings than for sinusoidal gratings (Campbell & Robson, 1968). This can be explained by the Fourier transform: while a sinusoidal grating contains a single spatial frequency, a square wave grating contains additional higher frequency components. The higher sensitivity for the square wave grating is believed to reflect the summed response at all frequencies. However, the cut-off frequency for both gratings will be the same, as the highest spatial frequencies are filtered out by the optics. human spatial acuity is thus not affected by the luminance profile of the grating (Campbell & Robson, 1968).

We could rule out that the higher detection threshold for square wave targets, compared to sinewave targets, was a consequence of its higher harmonics as this would have produced the opposite result. A different result would also have been expected if the target sizes at threshold were below the size of Ricco's area (see "Feature detection below the theoretical resolution limit"); a summation of the luminance over the square wave target would have resulted in a higher contrast compared to the sinewave target (Supplementary material A, Paper I). Instead, we found that the two measures of target acuity agreed if we considered only the portion of the target that has at least 10% Michelson contrast (equivalent to the contrast detection threshold in budgies) against the background.

Although the sinewave target acuity in budgerigars correspond well with the previously measured grating acuity, their square wave target acuity is lower. Given that real targets typically have ”sharp edges”, rather than gradual transitions to the background, square wave target acuity is likely to provide more realistic estimates of detection distance to such.

The detection threshold for the third, isoluminant, target was very similar to the detection threshold for the sinewave target with the same contrast to the background. The two targets were basically the same, except the isoluminant target was extended with a light "annulus" that made it overall isoluminant with the background (fig. 11c). Thus, the target would appear ”invisible” at sizes below Ricco's area.

Altogether our results indicate that the target acuity in budgerigars is limited by their retinal sampling frequency. Probably their low contrast sensitivity does not allow for detection of targets smaller than Ricco's area. A lower detection threshold for (square wave) single targets compared to gratings was also found in the lagoon triggerfish (*Rhinecanthus aculeatus*: Champ et al., 2014), which like the budgerigar has a relatively low luminance contrast sensitivity (van den Berg et al., 2020).

A single target usually has a much smaller spatial extent compared to a grating. The ”effective” stimulus size therefore differs, which can affect its visibility in several ways. In humans, the contrast sensitivity for gratings increase with the angular size of the stimulus, but also with the number grating cycles (Chen et al., 2019; King-Smith & Kulikowski, 1975; Robson & Graham, 1981). This effect is thought to depend on spatial summation of responses (King-Smith & Kulikowski, 1975), or probability summation (Meese & Summers, 2012; Robson & Graham, 1981). The existence of a similar mechanism in birds would likely affect the visibility of target and grating stimuli to different extents.

Furthermore, the sampling frequency is not homogenous throughout the avian retina, but the highest acuity is restricted to specific locations (i.e. *areae*). The detection of a single target, in particular if it approaches the threshold, thus relies on the image of the target being projected onto this particular retinal location. The same problem does not arise for a grating stimulus because of its greater spatial extent.

The targets in the experiments in Paper I were presented in the centre of a circular stimulus windows, in an attempt improve target localization by the birds. “Spatial cueing” has shown to increase the speed and accuracy of target localization in chickens (Sridharan et al., 2014). However, whether spatial cueing had any effect on target detection in our study is difficult to evaluate.

Motion vision in birds

Birds participate in numerous activities which require fast motion vision; a lot of them make rapid flight manoeuvres in dense vegetation, others catch evasive prey in mid-air or fly in large acrobatic murmurations. Birds in general have good motion vision and the highest critical flicker fusion frequency (CFF) of all vertebrates, surpassed only by insects across the animal kingdom (Inger et al., 2014; Lafitte et al., 2022). Both birds and insects are known for their ability to fly, and flight control is a behaviour that is believed to require fast visual perception (Lafitte et al., 2022).

Although the temporal acuity of bird vision is generally high, it also shows appreciable variation between species. The main driver of high temporal acuity is thought to be foraging strategy, and the highest CFFs have been measured in species hunting fast-flying prey (collared flycatcher [*Ficedula albicollis*]: 128.1 Hz, pied flycatcher [*F. hypoleuca*]: 138.2 Hz, bluetit [*Cyanistes caeruleus*]: 130.3 Hz, Boström et al., 2016; peregrine falcon [*Falco peregrinus*]: 124.5 Hz, Potier, Lieuvin, et al., 2020). In contrast, species that eat static food (e.g. seeds or nectar) have lower temporal acuity (budgerigar: 84.2 Hz, Boström et al., 2017; Anna’s hummingbird [*Calypte anna*]: 70-80 Hz, Goller et al., 2019; chicken: 87 Hz, Lisney et al., 2011).

Self-induced motion

Birds rely on self-induced retinal image motion, optic flow, to guide their behaviour in several different contexts. For example, translational optic flow provides flying birds with information about their own speed and distance to external objects. Budgerigars have been shown to balance the speed of the optic flow on both their eyes when they pass through narrow passages, a behaviour that enables a centred route between obstacles thus preventing collisions (Bhagavatula et al., 2011). Interestingly, not all species use the same strategy to maintain safe flight: Anna's hummingbird instead uses the retinal image expansion rate for flight control (Dakin et al., 2016).

Translational optic flow can also be used to monitor flight speed (Schiffner & Srinivasan, 2015, 2016). Flying through corridors with dense foliage requires a lot of motion control and the ability to quickly fine-tune the course, something which is difficult at high speeds. Budgerigars achieve a safe flight by altering their speed in response to the magnitude of translational optic flow: they will fly slow if they experience a strong optic flow, fly fast if they experience weak optic flow (Schiffner & Srinivasan, 2015). This relationship between optic flow and flight speed is not linear, but budgerigars switch between two distinct flight speeds that likely correspond to local flight speed optima (Altshuler & Srinivasan, 2018; Hedenström & Alerstam, 1995; Schiffner & Srinivasan, 2016).

Birds are thought to use the expanding optic flow field in front of them to estimate the *time-to-contact*[5] with approaching objects (Lee & Kalmus, 1980). A similar strategy might also be utilized to time foot extension before landing, and to "streamline" before plummeting in gannets (Davies & Green, 1990; Lee et al., 1993; Lee & Kalmus, 1980; Lee & Reddish, 1981). Information derived from the expanding optic flow field is also likely used for controlling the bill, for example when eating or feeding chicks.

While translational and expanding optic flow provides knowledge about the position or distance to external objects, rotational optic flow only informs the bird about its own rotation. To separate the optic flow generated by rotation from that of translation, birds have been demonstrated to make stabilizing eye and head movements when they change the direction of flight (Eckmeier et al., 2008; Kress et al., 2015; Ros & Biewener, 2017). While the body change direction gradually during a turn, the head makes several fast saccadic movements interspersed with short periods of constant gaze orientation (Eckmeier et al., 2008; Kress et al., 2015; Ros & Biewener, 2017). During manoeuvring flights and obstacle avoidance, birds may also fixate salient edges in their frontal visual field to stabilize their gaze and facilitate

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[5] The *time-to-contact* is derived from the optical parameter τ. τ is defined as the angular distance between a point r and the focus of expansion (the radius, for circular objects), divided by the expansion velocity v at a given time t ($\tau(t) = r(t) / v(t)$)

extraction of information from the optic flow field (Eckmeier et al., 2008; Kress et al., 2015; Miñano et al., 2023; Raudies et al., 2012).

Object motion

Object motion is needed for the detection of predators, prey, or conspecifics, and is thus of great importance to most birds. Moving targets have been found to catch attention and induce lateral visual fixation in birds (Evans et al., 1993; Maldonado et al., 1988). For example, naïve chickens are predisposed to be attracted to moving objects, especially if exhibiting sudden changes in speed or direction (Rosa-Salva et al., 2016), a motion pattern that is believed to signal animacy (Abrams & Christ, 2003; Pratt et al., 2010; Tremoulet & Feldman, 2000).

Object motion that is induced by the presence of a predator is thought to be of particular importance to many birds, and they express strong innate reactions to targets mimicking the movement of a predator (e.g. Dessborn et al., 2012). Chickens react defensively also to simple visual targets moving in the dorsal visual field, presumably of the same reason (Evans et al., 1993; Hébert et al., 2019). The defence response of adult chickens is stronger if the moving target is large or fast, although a variety of moving targets induce visual fixation (Evans et al., 1993).

In birds, object motion is thought to be analysed by the *optic tectum*. The optic tectum is responsible for processing information about the location and relevance of visual targets and is also involved in attentional orientation behaviour (Knudsen & Schwarz, 2017). Tectal neurons in birds are highly responsive to targets that loom or drift in a contrasting direction relative its surrounding, which indicates that these stimuli induce attentional "pop-out" (Huang et al., 2022; Niu et al., 2020; Zahar et al., 2012).

Birds are capable of extracting valuable information simply from the motion of simple targets. They can categorize moving targets based on their speed or direction, suggesting that dynamic properties might contribute to the recognition of other animals or objects in their environment (Herbranson et al., 2002). This could allow birds to identify other individuals as predators or kin by their specific motion pattern at distances too great to resolve relevant spatial details.

The effect of motion on contrast sensitivity

Motion does not only catch the attention of birds but can also affect their visual threshold. Haller et al. (2014) demonstrated that the contrast sensitivity in budgerigars for "small-field" (6.7°) gratings stimuli increase with horizontal drift. Contrast sensitivity increased for all spatial frequencies included in the study, although the greatest changes were observed for very high (6.5 cycles deg^{-2}) and very low (0.48 cycles deg^{-2}) frequencies. The contrast sensitivity maximum occurred at the same spatial frequency whether the grating was moving or not but increased from 14 (Michelson contrast^{-1}) for the static stimulus to 17.4 for the grating moving at the highest velocity (6 degrees s^{-1}). In comparison, motion does not affect the maximum contrast sensitivity in humans but shifts its position to lower spatial frequencies. In chickens, it was found that the contrast sensitivity of the optokinetic reflex increases with grating drift velocity (Shi & Stell, 2013). However, only low spatial frequencies (0.1-0.5 cycles deg^{-2}) were tested in this study.

Other studies of the effect of movement on contrast sensitivity in birds have produced somewhat inconsistent results. Hodos et al. (2003) found that counter-phase sinusoidal modulation (1-32 Hz) of gratings, reduces the contrast sensitivity in pigeons (operant conditioning). In contrast, the contrast sensitivity of an American kestrel, increased with counter-phase modulation (abrupt changes at 0.25 Hz; Hirsch, 1982).

Detection of moving single targets

In Paper II we aimed to find out the effect of motion on single target acuity in budgerigars. We knew from Paper I that their spatial acuity assessed from sharp-edged (square wave) targets is higher than their grating acuity. Because motion has the potential to both increase the attentional capture of a visual stimulus and increase its perceived contrast, we wanted to find out whether adding motion would increase the visibility of a single target stimulus.

The training of the budgerigars for the experiments in Paper I was tedious, and the static targets were surprisingly difficult to condition. Martinoya et al. (1983) suggest that motion might facilitate the conditioning of visual stimuli when they are viewed through the lateral visual field. The reason for using moving target stimuli was thus twofold: 1) find out the effect of motion on the detection threshold for single targets, and 2) more time efficient training of the test subjects.

The experiment in Paper II included a single circular black target that moved semi-randomly within an “invisible” square. The target had a speed of 1.69 degrees s^{-1}, which was similar to the drift velocity that produced the greatest contrast sensitivity for high frequency gratings (1.4 degrees s^{-1}) in Haller et al. (2014). The detection threshold we found for the moving target stimulus was, however, very similar to the threshold for the static square wave target in Paper I. Although motion did not improve target acuity in our study, it is difficult to say whether we would get the same results with a different type of motion, such as lateral drifting. Furthermore, Haller et al. (2014) found the highest contrast sensitivity for the fastest driving gratings in their study. It is thus possible that a higher speed would also have improved the target acuity of the budgerigars in our experiment.

Random target movements did (to our knowledge) not capture the attention or facilitate the training process of the budgerigars. We had previously attempted to condition both budgerigars and zebra finches (*Taeniopygia guttata*) to a moving target presented on a horizontally placed monitor (method based on Lind, 2016) but were unsuccessful. An attempt by Simon Potier (personal communication) to condition Harris's hawks to the moving target from Paper II did not succeed either.

The initial disinterest in the moving target on the part of the budgerigars is consistent with observations reported from studies using head-restrained birds. Small simple moving targets presented in the lateral visual field do not capture the attention of either pigeons (small light-emitting diode: Bloch et al., 1984) or starlings (4° black dot: Tyrrell et al., 2014). Instead, fast and unexpected movements by larger objects are much more effective for pigeons, while starlings rather fixate images of real moving mealworms or raptors.

Visual exposure to close range small targets in freely moving pigeons and chickens, on the other hand, tend to elicit pecking (e.g. Bird, Goodwin & Hess, 1969; Blough, 1977; Goodale, 1983; Osorio et al., 1999; Wilkie & Saksida, 1994). Pecking behaviour is associated with foraging and exploration, among other things, and is controlled by vision in the frontal visual field (Goodale, 1983). Given the functional difference, it is possible that fixation in the frontal and lateral visual field is induced by different types of stimuli.

The experimental arena described in Paper II forced the budgerigars to view the stimuli from a distance of 0.73 m. Overhead video recordings confirmed that the birds used their lateral visual field when viewing the stimuli during the experiment. Future studies of single target acuity in birds should therefore preferably be done with more ecologically relevant target shapes, for example a predator silhouette, to improve the visual attention. Presenting the stimuli overhead could also improve target relevance for the birds.

Vision in different light intensities

Luminance sensitivity

Dark adaptation of the visual system of birds behaves in a similar way to that of humans. The adaptation curve (lowest detectable luminance threshold as a function of elapsed time) for birds usually shows two distinct segments that reflect the different timescales with which cones and rods recover their light sensitivity. The *cone segment* of the curve begins with a comparatively rapid drop, followed by a progressively slower decline. After up to 30 minutes, the threshold begins to drop more quickly again, at the so-called ”rod-cone brake”, when the recovered sensitivity of the rods becomes noticeable. The *rod segment* continues with a gradually slower threshold decrease. Full adaptation can take up to about 60 minutes to reach, for long or intense pre-exposure to light. The dark adaptation curve of pigeons reveal that their cone segment contribute to a proportionally larger part of the total threshold drop compared to for humans (Blough, 1956). This difference likely reflects that the avian retina is numerically dominated by cones, whereas the human retina is dominated by rods. Except for the pigeon, dark adaptation curves have been measured in only a few bird species, including the European starling (Adler & Dalland, 1959), the ring-billed gull (*Larus delawarensis*), the gray gull (*L. modestus*: Emond et al., 2006) the black-bellied tree duck (*Dendrocygna autumnalis*: Hersloff et al., 1974) and the mallard (Wells et al., 1975).

In addition to light intensity, the switch between cone- and rod-dominated vision is also likely controlled by the time of day. The rod activity of the chicken and the Japanese quail appears to be blocked during the day, while it is active during the night, regardless of the light level (Manglapus et al., 1998; Schaeffel et al., 1991). Spectral sensitivity measurements of the photoreceptors in budgerigars suggest a possible presence of a similar mechanism, as no rod activity could be observed at light intensities as low as 0.02 cd m^{-2} (Lind et al., 2014).

Effect of light intensity on spatial and temporal acuity

The spatial acuity in birds typically increases with the light intensity of the stimulus up to a maximum, whereby it plains out or decreases slightly (Donner, 1951; Fite, 1973; Gover et al., 2009; Hodos & Leibowitz, 1977; Hodos et al., 1976; Lind et al., 2012; Martin & Gordon, 1974; Reymond, 1985; Reymond, 1987). Spatial acuity peaks at different light levels in different species, which has been suggested to relate to the natural light range within which a species is active (Donner, 1951).

The temporal acuity of bird vision is affected by luminance in a similar way as spatial acuity. The integration time of visual signals is shortened, resulting in the flicker-fusion frequency (FFF) increasing logarithmically with light intensity, due to a shortened integration time of the visual signal (Boström et al., 2017; Boström et al., 2016; Lisney et al., 2011; Potier, Lieuvin, et al., 2020).

Best visual acuity is obtained when a bird is fully adapted to the luminance of the stimulus, even for higher light intensities. The spatial acuity of pigeons measured with a 1 cd m^{-2} grating is significantly lower when a bird has been preadapted to scotopic light intensity compared to photopic light intensity (Hodos and Leibowitz, 1977).

Fast luminance adaptation in birds

There is not much knowledge about how birds cope with fast changes in light intensity. Yet flying birds are likely to be subject to even more rapid light changes than most terrestrial vertebrates, as they move quickly between sky and protective vegetation. Adaptation mechanisms involving functional reconfigurations of retinal circuits take time and are therefore not particularly useful at such fast luminance transitions (Schwartz & Levine, 2021).

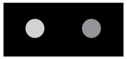
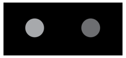
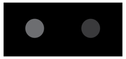
The pupillary light response is thought to smooth out fast changes in luminance by rapidly constricting the pupils in response to increasing light levels and dilating them as light levels drop (Douglas, 2018). The irises of birds are partly innervated by striated muscles (instead of only smooth muscle fibres as in mammals, fish, and amphibia), which enables comparatively fast (100-150 msec) constriction of the pupil (Douglas, 2018). The pupillary light response is likely to have only a limited effect on luminance adaptation in most birds, as the pupil can typically only change its area by a factor of 3-4 (less than 2, in budgerigars; Douglas, 2018; Lind & Kelber, 2009). An exception is the king penguin (*Aptenodytes patagonicus*) which has been suggested to use pupillary constriction to prevent scotopic light adaptation before foraging at deep waters (Martin, 1999). The pupils of king penguins have a rather extreme dynamic range and are capable of a 300-fold change in area.

Although the pupil of birds partly controls the light flux to the retina, this is likely not its only function. Pupillary constriction is thought to prevent blurring of the image in bright light by limiting the effect of spherical and chromatic aberration as light passes through the lens (Douglas, 2018; Kröger et al., 1999; Lind et al., 2008). Furthermore, rapid constrictions and dilations of the pupil, so-called ”eye-pinning”, occur in psittacines in contexts related to arousal or ambivalence (Brockway, 1964b; Gregory & Hopkins, 1974). Although seemingly well known among bird breeders and pet bird keepers, research on eye-pinning is, to my knowledge, scarce.

Visual sensitivity following a fast luminance drop

A situation that exposes birds to both rapid and large shifts in light intensity is the feeding of nestlings in tree cavities. Although cavity nests offer a safe place, the shielded design blocks out light, limiting vision (Wesołowski, 2007). Only a few percent of the incoming light reaches down to the tree cavity nests of passerines, where the median illuminance is 0.1-0.2 lux or lower (Maziarz & Wesolowski, 2014; Wesolowski & Maziarz, 2012). Still, individual feeding bouts only take a few seconds (Podkowa et al., 2019), a time span too short for complete dark-adaptation (Blough, 1956). Despite this, birds seem to use their vision in several behaviours in the nest-cavity. For example, visual cues are likely important for egg localisation during incubation (Avilés et al., 2006), but also for discovering the eggs laid by a nest-parasite (Di Giovanni et al., 2023; Yang et al., 2022); the visual saliency of nestlings have been shown to improve food transfer from parent to nestling (Dugas, 2015; Heeb et al., 2003; Podkowa et al., 2019; Wiebe & Slagsvold, 2009, 2012), but also affect allocation of food between siblings (Bize et al., 2006; Jourdie et al., 2004).

Table 1 Luminance contrast and brightness thresholds in budgerigars

Michelson contrast	**Weber contrast**	**Resolution** degrees (cycles deg^{-1})	**Target or stimulus luminance** cd m^{-2} S+/S-	**Background luminance** cd m^{-2}	**Viewing distance** mm	**Stimulus or target size** degrees	**Stimulus design**	**Reference**
0.29	0.45	9.6 (0.52)	200/110	0.225	12	9.6		Paper III
0.27	0.42	9.6 (0.52)	10.4/6.03	0.018	12	9.6		Paper III
0.37	0.54	9.6 (0.52)	0.68/0.31	0.0008	12	9.6		Paper III
0.26	0.41	9.6 (0.52)	0.190/0.11	0.00024	12	9.6		Paper III
0.09	0.18	–	47*	8.5	1268	3.6		Lind et al. 2013
0.10	–	(1.4)	50/50**	10-11	1268	3.6		Lind et al. 2011
0.07	–	(1.9)	63/63**	8-10	1268	6.7		Haller et al. 2014

**Mean luminance of the S+ and S-

*Mean luminance of the stripes in the grating

A lot of research on the role of vision in brood care has been conducted through experimental manipulation of nest lighting conditions or visual characteristics of nestlings. In many studies, factors such as increase in nestling mass (Bize et al., 2006; Heeb et al., 2003; Jourdie et al., 2004) or parental feeding behaviour (Border et al., 2023; Dugas, 2015; Podkowa et al., 2019) are often used as a proxy for visual discrimination or detection. The visual capacity of birds during rapid decreases in light intensity has never been directly tested.

The experiments in Paper III were designed to find out how well the vision of a cavity-nesting bird, the budgerigar, copes with rapid drops in light intensity, equivalent to what they encountered when entering a nest-cavity. We trained budgerigars to enter a small, dimly lit, chamber, the "decision box", in which they were presented with visual stimuli in a 2AFC trial (see "Stimulus presentation"). The subject left the decision box between each trial to readapt to the higher light level outside.

The stimuli, bright circular targets (9.6° in diameter) on a dark background, were presented under four different lights levels (ranging between 0.47 and 469 lux). We tested the birds' ability to detect a single bright target from the background (the *absolute threshold* for luminance) as well as their the ability to distinguish between two different bright targets (the *difference threshold* for luminance).

Interestingly, the birds more or less always responded already about 1 second after entering the decision box instead of waiting longer for vision to adapt. In passerines, low nest light levels result in reduced feeding efficiency and more time-consuming feeding (Dugas, 2015; Podkowa et al., 2019), likely because of the reduced visual sensitivity prior to full adaptation. We had expected the budgies to take longer to respond to the lowest light levels in our experiment. Although we were unable to show any effect of light level on response times, this does not rule out the presence of such in different contexts. In a 2AFC setting, long decision times are costly, since they result in fewer choices per time unit. Instead, a strategy of making quick, but not always correct, choices can be more cost-effective, especially when it comes to difficult decisions (Drugowitsch et al., 2012). In a feeding context, on the other hand, the more cost-effective strategy is probably to spend a few extra seconds in the nest to secure a safe delivery of food.

In the absolute threshold experiment, we found a similar threshold (~0.11-0.14 cd m^{-2}) for the three lowest light levels, while it was significantly higher (0.83 cd m^{-2}) for the brightest light level. This confirms that the ambient illuminance has only an indirect role in the light sensitivity of the visual system in budgerigars, which instead adapt to the background luminance of visual stimuli. Although stimulus background luminance differed for all four light levels, the backgrounds at the three lowest levels were likely too dark to affect the birds' luminance sensitivity. As opposed to this, the background at the highest light level reached above their luminance threshold, lowering their light sensitivity compared to the other three levels.

The experiment testing the difference threshold revealed that the budgerigars were close to equally good at detecting luminance contrast (0.41-0.54 Weber contrast) at all four light levels. This result is consistent with Weber's law, suggesting that birds partially adapt to the prevailing luminance already within a second.

The luminance difference thresholds we found in this experiment is notably higher than brightness or luminance contrast thresholds for budgerigars from other studies (Table 1). Fully adapted, and tested in bright light, budgerigars are able to detect static gratings with a 7.1-9.8% Michelson contrast and discriminate between homogenous grey fields with 11% Michelson contrast, the latter being equivalent to a Weber contrast of 0.18 (Haller et al., 2014; Lind et al., 2013; Lind & Kelber, 2011). It is difficult to say to what extent the relatively high luminance difference threshold in our experiments is due to insufficient adaptation and how much is due to other factors. If the spatial stimulus structure had a large impact, the result would likely be more similar to that of our previous study of luminance discrimination in budgerigars, which, like this one, used two homogeneous, spatially separated, grey fields as stimuli (Lind et al., 2013). Background luminance may also have affected the result. The targets in Paper III were significantly brighter than the background (Table 1), which may have impaired visual performance as contrast sensitivity is generally highest when target and background luminance match (Whittle, 1992). A more comprehensive understanding of the role of the adaptation state for the result would have required us to also test the birds under unchanged light conditions. However, this was not possible due to technical difficulties in providing the same high light level throughout the experimental setup.

Differences between budgerigars and cavity nesting passerines

Although with the study in Paper III we had the ambition to study the vision of cavity-nesting birds in general, the results must be interpreted specifically for budgerigars. In fact, there are several differences between the nesting behaviour of budgerigars compared to cavity-nesting passerines, which could reflect the relative importance of different sensory cues. Passerine nestlings vocalize and open their mouths widely in the direction of the parent when they beg for food. Nestlings in species with dark nests have rictal flanges that are larger, brighter, and have a higher contrast to the gape and surrounding, facilitating parental targeting of the mouth when feeding (Aviles et al., 2008; Hunt et al., 2003; Kilner & Davies, 1998). Budgerigar nestlings, on the other hand, do not expand their mouths when begging, nor do they have visually conspicuous rictal flanges. When a budgerigar feed its offspring it grasps its beak, at right angles, and regurgitates seeds directly into the crop.

Due to extreme hatching asynchrony in budgerigars (>2 days between hatchings), nestlings commonly vary greatly in size and development (fig. 12; Stamps et al., 1985). While all nestlings are able to vocalize, the begging behaviour in older nestlings also involves head bobbing, wing flapping and attempts of beak-grasping. Smaller chicks are less mobile and cannot even lift their head the first week after hatching. The female parent still selectively feeds the smallest chick first, often without prior begging, by placing it on its back and grasping its beak (Stamps et al., 1985).

Beak grasping behaviour during feeding is typical of psittacines and suggests that touch plays a prominent role in this context. The touch receptor organ in the upper mandible of psittacines is used to manipulate and explore objects by tactile cues, compensating for the limited vision in the frontal visual field (Martin & Martin, 2020). It is therefore likely that budgerigars use touch more than sight to transfer food to their offspring.

Figure 12. Budgerigar nestlings. Budgerigars hatch asynchronously, and the average age difference between nestlings is about two days. The picture shows three nestlings of different ages, as well as two eggs, belonging to the same clutch.

Distinguishing between the different chicks in the dark nest surely involves multiple sensory modalities. The vigorous movements made by older nestlings could be a visual signal. But the targeting of the smallest, often passive, nestlings likely involve of additional senses. Unlike most passerines, budgerigar embryos communicate vocally with their parents even before hatching (Berlin & Clark, 1998). Another possible sensory modality is olfaction, which has been reported to be part of the social communication between adult budgerigars (Zhang et al., 2010).

Lastly, budgerigars are probably not guided as much by light conditions as passerines when choosing nestsite. The depth of budgerigar nests has been reported to vary between 26 cm and several meters below the entrance hole (Schrader, 1975; Wyndham, 1981). Passerines build their nests closer to the entrance with a considerably smaller variation (collared flycatcher: 2-38 cm: Maziarz & Wesolowski, 2014; marsh tits Poecile palustris: 8-14 cm, great tits 7-29 cm: Wesolowski & Maziarz, 2012).

Conclusions

In the studies included in this thesis I have explored the abilities of birds, with the budgerigar as my model, to detect and differentiate between single target stimuli. Me and my coauthors found that behavioural measurements of spatial acuity and contrast sensitivity that are based on grating stimuli do not necessarily translate to thresholds for single target stimuli. Although most animals tested are better at resolving single targets compared to gratings, budgerigars appear to be just as good or slightly better at resolving gratings (Paper I and II). The same single target acuity was measured for both for static (Paper I) and semi-randomly moving targets (Paper II). A major contributor to the low target acuity in budgerigars is likely their poor capacity to perceive luminance contrast. Low contrast sensitivity is a general trait in birds, so it is likely that other species also have relatively low target acuity. It would be interesting to find out if single target acuity is equally low in a species that hunt individual prey on the wing (e.g. flycatchers, hobbies, swallows).

Although we did not find any difference in the single target acuity for static and moving targets, an effect of motion in target detection cannot be excluded. Since we only tested one target speed and semi-random movement, we can only draw conclusions regarding these. To more comprehensively investigate the effect of motion on target acuity, different target speeds and types of motion, for example drifting and acceleration, would need to be tested. Furthermore, even if motion does not affect single target acuity, it may well affect the visibility of larger, low contrast, targets. It would also be interesting to find out how motion of a target affects the contrast sensitivity in birds in low light levels. For example, do budgerigar nestlings' head-bobbing and wing flapping also enhance their contrast against the background, besides attracting attention?

In Paper III, we found that budgerigars have about the same contrast sensitivity after a small as after a large decrease in light intensity, indicating that some of their luminance adaptation occurs very quickly. The time course of rapid (milliseconds–minutes) luminance adaptation would be an intriguing study. Such a study would also benefit from including how colour vision is affected by rapid changes in light level. Furthermore, species from separate bird lineages build their nests in cavities and they may well have developed different strategies to cope with rapid light changes. Thus, it would be interesting to explore the visual performance of, for example, a cavity-nesting passerine species in an experiment similar to ours.

Quantification of various aspects of the visual environment of birds in relevant contexts would enable the design of behavioural experiments that can answer ecologically relevant questions. In particular, I believe that more research on potential interactions between spatial and temporal properties of visual stimuli would contribute to a deepened understanding of visual perception in birds.

This thesis has hopefully contributed with a small piece to the puzzle of visual perception and ecology of birds. Although me and my coauthors succeeded in finding answers to some of our original research questions, the experimental results together with various unexpected observations throughout the experimental process, have generated many new questions. I am excited to find out what future studies in this field of research will reveal.

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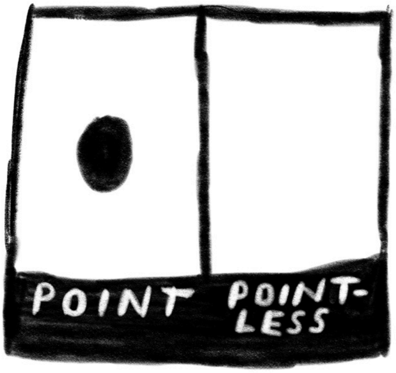

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