

RESEARCH ARTICLE

How fast can raptors see?

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ABSTRACT

Birds, and especially raptors, are highly visual animals. Some of them have the highest spatial resolving power known in the animal kingdom, allowing prey detection at distance. While many raptors visually track fast-moving and manoeuvrable prey, requiring high temporal resolution, this aspect of their visual system has never been studied before. In this study, we estimated how fast raptors can see, by measuring the flicker fusion frequency of three species with different lifestyles. We found that flicker fusion frequency differed among species, being at least 129 Hz in the peregrine falcon, *Falco peregrinus*, 102 Hz in the saker falcon, *Falco cherrug*, and 81 Hz in the Harris's hawk, *Parabuteo unicinctus*. We suggest a potential link between fast vision and hunting strategy, with high temporal resolution in the fast-flying falcons that chase fast-moving, manoeuvrable prey and a lower resolution in the Harris's hawk, which flies more slowly and targets slower prey.

KEY WORDS: Falcon, Flicker fusion frequency, Hawk, Raptor, Temporal resolution, Vision

INTRODUCTION

Vision provides instantaneous and detailed information about the environment (Land and Nilsson, 2012). For an animal to perceive objects of interest, like food or mates, many aspects of vision are important, such as the visual field (the space around the head from which visual information can be gathered), colour perception, contrast sensitivity and spatial resolution (Martin, 2017). Species that forage visually need specialized visual abilities. Birds and especially raptors are believed to be highly dependent on their visual capabilities even though other senses such as olfaction may also be important (Caro et al., 2015; Potier, 2019). For instance, raptors have the highest achromatic (differences only occur in luminance, i.e. the grey level) and chromatic (differences only occur in chromaticity) spatial resolution found among extant animals (Mitkus et al., 2018; Potier et al., 2018; Reymond, 1985).

While many aspects of vision in birds have been studied (e.g. visual fields, colour vision or visual spatial resolution; Martin, 2017), the temporal resolution, i.e. the ability to resolve rapid movements, of bird vision remains poorly known. However, many birds need fast eye sight to perform very quick and precise flight manoeuvres, in order to avoid harmful encounters with stationary objects such as branches, fast-moving predators or flockmates or – in the case of raptors – with fast-flying prey. Each of these tasks requires high resolving power for visual details not only in space but also in time. Temporal resolution has been behaviourally estimated only in domestic

chickens (*Gallus domesticus*: Lisney et al., 2011; Nuboer et al., 1992), rock pigeons (*Columba livia*: Hendricks, 1966), budgerigars (*Melopsittacus undulatus*: Boström et al., 2017; Ginsburg and Nilsson, 1971) and some passerines (Boström et al., 2016; Greenwood et al., 2004). Among these birds, the passerines have the highest temporal resolution, with a maximum of ~140 Hz in the pied flycatcher (*Ficedula hypoleuca*: Boström et al., 2016).

In raptors, while spatial resolution has been estimated in a number of species (Mitkus et al., 2018), temporal resolution has not been studied in any species so far. This is surprising because raptors have different specializations that could be related to high temporal resolving power: (1) raptors have relatively high spatial resolution and can thus benefit from high temporal resolution to reduce motion-induced blur (as has been suggested for insects: Srinivasan and Bernard, 1975); (2) they have a high metabolic rate (Zar, 1968), which is positively correlated to temporal resolution (Healy et al., 2013); (3) they have a deep fovea with steep slopes (Oehme, 1964; Potier et al., 2017b; Walls, 1942), which has been hypothesized to increase temporal acuity (Bringmann, 2019) by more pronounced image distortion (Pumphrey, 1948); and (4) some raptors, such as falcons, fly at surprisingly high speed when diving on fast-moving prey (e.g. 52–58 m s⁻¹ for the gyrfalcon, *Falco rusticolus*: Tucker et al., 1998; theoretically up to 138–174 m s⁻¹ for the peregrine falcon, *Falco peregrinus*: Tucker, 1998), and other species hunt fast-flying prey in complex forest environments. Therefore, we expect raptors to have relatively high temporal resolution which enables them to track fast-moving prey at high speed in complex environments.

In this study, we determined the flicker fusion frequency (FFF), i.e. the frequency at which an intermittent light stimulus appears to be steady, at several light intensities, in order to find the critical flicker fusion frequency (CFF), as an estimate of the maximal temporal resolution in an individual. We studied (1) two species of falconiform raptors, the peregrine falcon (*F. peregrinus* Tunstall 1771) and saker falcon (*Falco cherrug* Gray 1834), both of which fly at high speeds and mostly hunt fast-moving avian prey, and (2) one species of accipitriform raptor, the Harris's hawk [*Parabuteo unicinctus* (Temminck 1824)], which flies at lower speeds and generally hunts slower, terrestrial prey, such as small mammals (Ferguson-Lees and Christie, 2001). We hypothesized that all studied species may have high temporal resolution but, depending on their lifestyle, falcons may have higher temporal resolution than hawks.

MATERIALS AND METHODS

Ethics

This study was conducted under a formal agreement between the animal rearing facility Les Ailes de l'Urga (France) and Lund University (Sweden). In agreement with French law, the birds were handled by their usual trainers under the permit of Les Ailes de l'Urga (national certificate to maintain birds 'Certificat de capacite' delivered to the director of the falconry, Patrice Potier, on 20 June 2006).

Subjects and study site

Three Harris's hawks, two peregrine falcons and one saker falcon participated in the experiments (see Table 1). All birds belong to the

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Table 1. Information on all birds used in the experiment

Order	Common name	Species name	Individual	Sex	Age (years)	Body mass (g)
Falconiformes	Peregrine falcon	<i>Falco peregrinus</i>	Waston	Male	3	530
			Xéros	Male	2	540
			Xélor	Male	2	700
Accipitriformes	Saker falcon	<i>Falco cherrug</i>	Nadja	Female	8	1050
	Harris's hawk	<i>Parabuteo unicinctus</i>	Gypsie	Female	7	1050
			Lancelot	Male	8	750

French falconry park Les Ailes de l'Urga, where they are kept in good health and allowed to fly regularly. They were tested close to their holding aviaries and returned to them immediately after each experimental session. During the period of this study, the birds' body mass was measured every day and maintained at 90% (for falcons) and 95% (for hawks) of the free-feeding body mass. The ratio of experimental body mass to free-feeding body mass was lower in falcons than in hawks because the falcons were parent-reared while the hawks were hand-reared, and therefore more habituated to human presence.

Experimental setup

Experiments were conducted in a room measuring 200×200 cm in area and 220 cm in height. Three walls were made of grey fabric, but the wall on which the stimuli were presented was made from wood and painted in a similar grey colour (Fig. 1). The room was illuminated from above using a white LED lamp that did not flicker (Trådfri LED 1000 lm, IKEA). A diffusion filter (LEE filters 452, Andover, UK) was used to distribute the light evenly in the room. We presented two light stimuli (generated by white LED lamps; Jansjö LED, IKEA), 2 cm in diameter and placed 140 cm above the floor and 115 cm apart from each other, to the birds simultaneously. We used a front-mounted diffusion filter (LEE filters 452) to create even light distribution, and neutral density filters (LEE filters) to generate different intensities. A custom-built circuit (based on an ARDUINO UNO, programmed in open source ARDUINO software IDE, library Tone, and connected via a power transistor to the lamps) was used to generate square wave light stimuli with exact frequencies between 10 and 1000 Hz. A stimulus with a flicker

frequency of 1000 Hz served as the perceptually constant stimulus (hereafter referred to as constant light).

A perch placed under each stimulus allowed access to a hidden hole where a food reward could be given by the experimenter (S.P. for hawks and M.L. for falcons). The birds began each trial from a starting perch, 110 cm above the floor and 180 cm from the stimuli. The stimuli thus had an angular diameter of 0.6 deg when seen from the starting perch.

Behavioural procedure

Experiments were conducted from 10 September 2018 to 11 February 2019. Using operant conditioning and positive reinforcement, we trained each bird individually to discriminate between the constant light as the rewarded stimulus and the flickering light as the unrewarded stimulus (see Boström et al., 2017, for similar procedure). Initially, we trained the bird to fly from the starting perch to the perch in front of the constant light (Fig. 1). During the first 2 days, the food reward was visible and two constant light stimuli were presented, to train the bird to fly to a randomly chosen perch. Then, we started the training with one constant and one flickering light. If the bird made a correct choice and flew to the side presenting the constant light, it received a food reward (a piece of chicken, less than 2 g). If the bird flew to the simultaneously presented lamp flickering at 10 or 20 Hz, it did not receive a reward. The sides of the rewarded and unrewarded stimuli were changed in a pseudo-random order (i.e. the positive stimulus was not presented on the same side for more than three consecutive trials). Thus, during a session of 30 trials, the rewarded stimulus was presented 15 times on each side. When a bird reached 80% correct choices in two



Fig. 1. A female Harris's hawk sitting on the starting perch and making a decision. Note that the bird covers the left stimulus. The hidden hole is just below the visible stimulus. Photo credit: Hervé Colosio.

consecutive sessions of 30 trials each, we considered that it had learnt the task and started test sessions.

Each test session started with five easy trials (unrewarded stimulus flickering at 10 or 20 Hz). After this, we used a 2 up–1 down experimental procedure to increase the frequency of the unrewarded stimulus in steps of 10 Hz until the bird could no longer distinguish the two stimuli. If a bird made two correct choices, we increased the frequency by 10 Hz. If a bird made one incorrect choice, we decreased the frequency by 10 Hz. Closer to the resolution limit of the bird, the same procedure was continued with steps of 5 Hz, 2 Hz and finally 1 Hz until the bird could no longer discriminate the two stimuli; thus, its FFF was reached. To precisely determine the FFF, several frequency reversals in steps of 1 Hz were performed at the threshold frequency (Fig. 2A). The procedure was repeated at five different stimulus luminances [160, 2650, 14,100, 26,400 and 55,500 cd m^{-2} , measured using a photometer (Hagner ScreenMaster, Hagner, Solna, Sweden); Table 2] with two background luminances (0.1 and 2.9 cd m^{-2} ; Table 2). For each luminance, we present the averaged FFF determined in three test sessions. Each bird was tested individually at all light intensities, in random order, but only once per day. We

Table 2. Stimulus and cage illumination for all tests

Stimulus luminance (cd m^{-2})	Background luminance (cd m^{-2})	Cage illuminance (lx)
160	0.1	28
2650	0.1	28
14,100	2.9	1000
26,400	2.9	1000
55,500	2.9	1000

Stimulus luminance was measured using a photometer pointing toward the stimuli. Background luminance was measured 3 cm above the stimuli with the same photometer pointing directly towards the background. Cage luminance was measured 30 cm above the starting perch using the photometer as a luxmeter pointing upward.

determined the CFF as the maximum FFF of a bird at any specific light intensity.

Statistical analyses

All analyses were performed in R (v.3.5.1) using *ggplot2* (<https://CRAN.R-project.org/package=ggplot2>), *lmerTest* (Kuznetsova et al., 2017), *emmeans* (<https://CRAN.R-project.org/package=emmeans>) and *RVAideMemoire* (<https://CRAN.R-project.org/package=RVAideMemoire>) packages. Differences between falcons and hawks in session duration (log transformed) and quantity of food consumed (log transformed) were analysed using linear mixed models with bird identity as random effect following a Gaussian error distribution. We tested for differences in FFF between falcons and hawks at each luminance level, using linear mixed models, following a Gaussian error distribution. Stimulus luminance (log transformed) in interaction with order (falcons versus hawks) was used as a fixed effect and bird identity as a random effect. Pairwise comparisons were obtained using the contrast and Tukey adjustment method. The differences between falcons and hawks in the number of trials per session was analysed using linear mixed models with bird identity as a random effect, following a Poisson error distribution.

For all linear mixed models, the best fixed effect structure was selected using the AIC criterion following the method described by Zuur et al. (2009). We inspected the residuals of each model to ensure that they fitted the assumption of linear mixed models following a Gaussian or Poisson error distribution. Throughout the paper, we present the estimates, *t*-values and *P*-values for fixed effects in REML (residual maximum likelihood estimation) models, except for the number of trials, where we present the estimate, *z*-value and *P*-value for fixed effects in ML (maximum likelihood estimation with Laplace approximation) according to the Poisson error distribution (Zuur et al., 2009).

RESULTS

All individuals were highly motivated and participated in the experiment at all intensities. The average number of trials (excluding the five first easy trials) per session was 44 ± 2 (mean \pm s.e.m.) and did not differ between falcons and hawks (estimate = -0.26 ± 0.16 , $z = -1.61$, $P = 0.11$). Within a session, the mean quantity of food consumed was 71 ± 3 g (mean \pm s.e.m.) and did not differ between falcons and hawks (estimate = -0.15 ± 0.15 , d.f. = 6.11, $t = -1.04$, $P = 0.34$). The duration of a session, and therefore the decision time, was significantly higher for falcons than for hawks (falcons: 19.68 ± 1.83 min, hawks: 11.86 ± 0.46 min; estimate = 0.38 ± 0.11 , d.f. = 3.92, $t = 3.50$, $P = 0.03$; see Table S1).

Generally, the peregrine falcons had the highest FFFs, followed by the saker falcon and the Harris's hawks (Fig. 2B). Specifically,

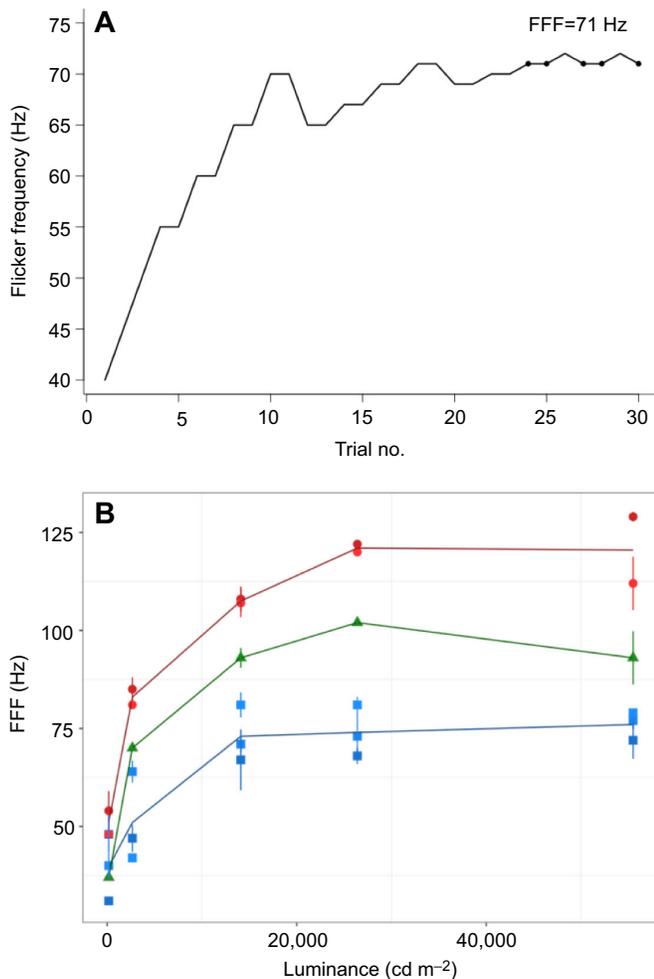


Fig. 2. Flicker fusion frequency (FFF) of falcons and hawks. (A) An example test session at a stimulus luminance 2650 cd m^{-2} with the saker falcon. Each dot corresponds to a correct choice at the FFF determined as 71 Hz. (B) FFF at five stimulus luminances. Blue squares: Harris's hawks ($n=3$); red circles: peregrine falcons ($n=2$); green triangles: saker falcon ($n=1$). Symbols represent means \pm s.d. of individual birds; lines represent species averages.

one Harris's hawk, one peregrine falcon and the saker falcon had their highest FFF (and thus their CFF) at a stimulus luminance of 26,400 cd m⁻² (81, 120 and 102 Hz, respectively; Fig. 2). For the three other individuals, the FFFs increased continuously with luminosity (Fig. 2), and thus the CFF could not be determined. Indeed, for those individuals, the FFF was slightly higher at the highest stimulus luminance of 55,500 cd m⁻² (77 and 75 Hz for the two other Harris's hawks and 129 Hz for the second peregrine falcon) than at 26,400 cd m⁻². The mean FFFs for each species at all luminances are shown in Fig. 2B.

Based on AIC criterion, the best fixed effect structure to explain FFF was the interaction between stimulus luminance and bird order. Indeed, we found a significant interaction between stimulus luminance and bird order for the FFFs (d.f.=4, $\chi^2=26.31$, $P<0.001$). Specifically, falcons had higher FFFs than hawks at high stimulus luminance (luminance 265,000 cd m⁻²: estimate=40.00 ± 7.97, d.f.=7.18, $t=5.02$; $P=0.02$; luminance 55,500 cd m⁻²: estimate=35.33 ± 7.99, d.f.=7.23, $t=4.42$, $P=0.04$). At lower luminance, FFFs of falcons and hawks were similar (all $P>0.10$; see Table S1).

For all tested individuals, the FFF was much lower at low light intensities. Indeed, the FFFs were significantly different for different stimulus luminances for both falcons and hawks. Specifically, while FFFs did not differ significantly for the three higher stimulus luminances (14,100, 26,400 and 55,500 cd m⁻²; all $P>0.33$ for falcons and hawks; see Table S1), FFFs at the low luminances (160 and 2650 cd m⁻²) were significantly different from the others (all $P<0.008$ for falcons and hawks; see Table S1). We also found that FFFs were significantly different between the two lower stimulus luminances (160 and 2650 cd m⁻²) for falcons (estimate=-32.44 ± 4.60, d.f.=15.69, $t=-7.05$, $P=0.001$) but not for hawks (estimate=-10.72 ± 4.67, d.f.=16.67, $t=-2.29$, $P=0.44$).

DISCUSSION

Our study is, to our knowledge, the first to investigate the temporal resolution in diurnal birds of prey. Using behavioural experiments, we found that peregrine falcons have a higher temporal resolution of vision than most other vertebrates, but this was not the case for Harris's hawks. These differences in temporal resolution are discussed below in terms of lifestyle and eye physiology; however, we cannot exclude other reasons, such as differences in metabolic rate or body size. Species with high metabolism and small body size have been shown to have higher CFF (Healy et al., 2013). We did not test for a sex difference in temporal resolution as no sex difference in hunting strategies has been reported in the studied species (Ferguson-Lees and Christie, 2001). Furthermore, no sex difference has been reported in the blue tit (but this was not tested by Boström et al., 2016). While the age of individuals was different, there is no or little indication that this should affect temporal resolution (for humans, see Brozek and Keys, 1945, and Ellemberg et al., 1999). Finally, it is important to note that the temporal resolution of vision has been recorded using different methods [electroretinography (ERG), optomotor responses and behavioural assays; see Table 3], and the results obtained with these methods may not be directly comparable (but see Inger et al., 2014). For instance, ERGs produce accurate estimates of the retinal response, which may give higher values than those based on behavioural tests because it excludes potential temporal summation of signals happening at later stages of neuronal processing (Lisney et al., 2012).

Temporal resolution and lifestyle

The airborne (involving high manoeuvrability and sometimes fast-flying abilities) and diurnal lifestyles of birds have been suggested to be linked to high temporal resolution of vision (Boström et al., 2016; Inger et al., 2014). Indeed, the temporal resolution of some

Table 3. Bird species for which flicker fusion frequency (FFF) has been tested

Common name	Species name	Method	Mean CFF	Reference
Great horned owl	<i>Bubo virginianus</i>	ERG	40.0*	Ault and House (1987)
Little owl	<i>Athene noctua</i>	ERG	50.0*	Porciatti et al. (1989)
Zebrafinch	<i>Taeniopygia guttata</i>	Optomotor	55.0	Crozier and Wolf (1941)
House sparrow	<i>Passer domesticus</i>	Optomotor	55.0	Crozier and Wolf (1944)
Domestic chicken	<i>Gallus domesticus</i>	Behavioural	63.5*	Rubene et al. (2010)
Short-eared owl	<i>Asio flammeus</i>	ERG	67.5	Bornschein and Tansley (1961)
Budgerigar	<i>Melopsittacus undulatus</i>	Behavioural	69.4	Ginsburg and Nilsson (1971)
Domestic chicken	<i>Gallus domesticus</i>	Behavioural	71.5*	Jarvis et al. (2002)
Rock pigeon	<i>Columba livia</i>	Behavioural	77.0*	Hendricks (1966)
Harris's hawk	<i>Parabuteo unicinctus</i>	Behavioural	77.7	Present study
Budgerigar	<i>Melopsittacus undulatus</i>	Behavioural	84.2*	Boström et al. (2017)
Domestic chicken	<i>Gallus domesticus</i>	Behavioural	87.0	Lisney et al. (2011)
Rock pigeon	<i>Columba livia</i>	ERG	100.0	Bornschein and Tansley (1961)
European starling	<i>Sturnus vulgaris</i>	ERG	100.0*	Maddocks et al. (2001)
Saker falcon	<i>Falco cherrug</i>	Behavioural	102.0	Present study
Domestic chicken	<i>Gallus domesticus</i>	ERG	104.0	Lisney et al. (2012)
Domestic chicken	<i>Gallus domesticus</i>	Behavioural	105.0	Nuboer et al. (1992)
Brown-headed cowbird	<i>Molothrus ater</i>	ERG	114.7	Ronald et al. (2018)
Peregrine falcon	<i>Falco peregrinus</i>	Behavioural	124.5	Present study
Collared flycatcher	<i>Ficedula albicollis</i>	Behavioural	128.1	Boström et al. (2016)
Blue tit	<i>Cyanistes caeruleus</i>	Behavioural	130.3	Boström et al. (2016)
Pied flycatcher	<i>Ficedula hypoleuca</i>	Behavioural	138.2	Boström et al. (2016)
Rock pigeon	<i>Columba livia</i>	ERG	143.0	Dotd and Wirth (1953)

ERG: electroretinogram recorded from the eye; Optomotor: reaction to a rotation pattern of gratings; Behavioural: dual choice test between a steady and an intermittent stimulus.

Note that critical flicker fusion frequency (CFF) values represent the highest value (when possible) obtained with a given individual. Values are given for non-UV lights only, to make data comparable.

*When FFF continuously increased with luminance for some individuals, the highest FFF is given.

species of birds including the domestic chicken, the rock pigeon, the blue tit (*Cyanistes caeruleus*), the collared flycatcher (*Ficedula albicollis*) and the pied flycatcher, exceeds the range of CFFs recorded in other vertebrates (see Table 3 and Inger et al., 2014, for a list of FFF data of vertebrates).

Acknowledging the relatively small dataset (but intra-specific variation among individuals appears to be lower than inter-specific variation; see Lisney et al., 2011; Boström et al., 2016), our results show some diversity in the temporal resolution among raptors. We found a higher temporal resolution in falcons, species that have positively selected genes for photoresponse recovery and/or light adaption, which may contribute to high temporal resolution (Wu et al., 2016). In particular, the highest temporal resolution was found in the peregrine falcon, which is known to be the fastest-flying animal in the world. This species can dive theoretically at 138–174 m s⁻¹ (Tucker, 1998), with a recorded speed of up to 96 m s⁻¹ for a captive individual (recorded by falconer Patrick Morel on a female peregrine using a Microsensory RTS mini device). It hunts fast-escaping and manoeuvrable prey, such as shorebirds, passerines and pigeons (Drewitt and Dixon, 2008; Ward and Laybourne, 1985). By contrast, the temporal resolution of the Harris's hawk was considerably lower. This species flies at lower speed and forages mainly on mammals such as rodents, rabbits and hares, which are not as fast and manoeuvrable as the flying prey of falcons (Figueroa and González-Acuña, 2006). Our results are in agreement with the suggestion (Boström et al., 2017) that fast-flying species aiming for fast-moving prey have a high temporal resolution. For these species, high temporal resolution should be important because they need to rapidly integrate information (Laughlin and Weckström, 1993) for essential tasks such as pattern recognition

(Srinivasan and Lehrer, 1984), motion vision (Healy et al., 2013) and depth perception (Martin, 2017). However, behavioural assays have shown that Harris's hawks have similar temporal resolution to that of chickens (Jarvis et al., 2002; Lisney et al., 2011), which forage on seeds. This could suggest that high temporal resolution may also be essential for other behaviours, such as predator avoidance (e.g. looming escape; de Vries and Clandinin, 2012).

Temporal resolution and fovea

One of the functions of the bird fovea that have been debated for almost 80 years (Bringmann, 2019) is its contribution to image fixation by improving the sensitivity to movements (Pumphrey, 1948). Pumphrey (1948) has proposed that species possessing a deep fovea with steep slopes may fixate prey more accurately. Indeed, deeper foveas with steeper slopes distort the image more strongly, possibly making motion detection, and therefore temporal resolution, more efficient compared with shallower foveas (with shallower slopes). According to this hypothesis, one could expect that species that forage on fast-moving prey possess a deeper fovea with steeper slopes to allow for better fixation of the prey, compared with species hunting slow-moving prey. We found no evidence for this hypothesis. By contrast, the species with the lowest temporal resolution, the Harris's hawk, has a deeper fovea with steeper slopes than the species with the highest temporal resolution, the peregrine falcon (Mitkus et al., 2017; Potier et al., 2016, 2017a). One possible explanation for this might be that the deep-foveated birds, with steeper slopes and a small region of high visual acuity, are more likely to foveate accurately, and therefore experience lower slip velocities whilst fixating a target. Consequently, they may not require high temporal resolution to mitigate motion-induced blur.

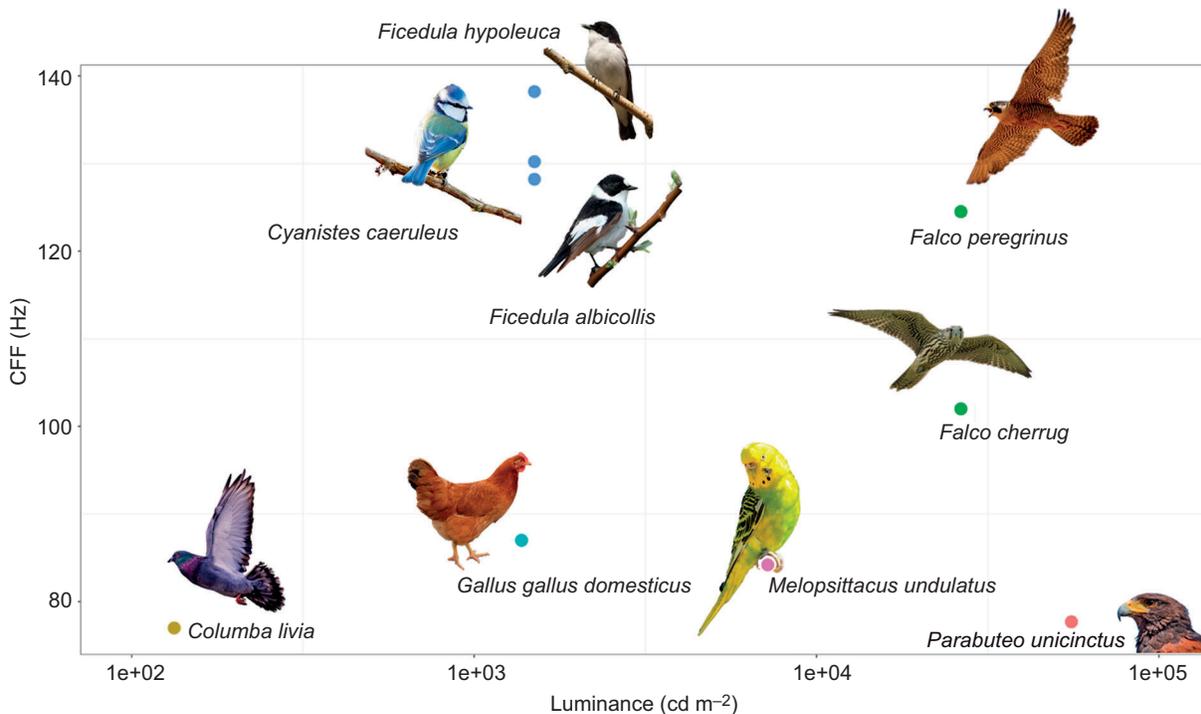


Fig. 3. Critical flicker fusion frequency (CFF) of bird species tested behaviourally, as a function of stimulus luminance. Note that the luminance scale here is logarithmic. Each dot represents the average CFF per bird species. Different coloured symbols represent different bird orders (brown: Columbiformes; turquoise: Galliformes; blue: Passeriformes; pink: Psittaciformes; green: Falconiformes; red: Accipitriformes). References: rock pigeon (*Columba livia*) – Hendricks (1966); domestic chicken (*Gallus gallus domesticus*) – Lisney et al. (2012); collared flycatcher (*Ficedula albicollis*), pied flycatcher (*Ficedula hypoleuca*) and blue tit (*Cyanistes caeruleus*) – Boström et al. (2016); budgerigar (*Melopsittacus undulatus*) – Boström et al. (2017); peregrine falcon (*Falco peregrinus*), saker falcon (*Falco cherrug*) and Harris's hawk (*Parabuteo unicinctus*) – present study.

The dependence of motion-induced blur on spatial and temporal acuity of vision has been modelled in Srinivasan and Bernard (1975). More comparative studies are needed to explore whether foveal shape may be related to temporal resolution.

Luminance and lifestyle

Raptors are considered to be highly adapted to see well and perform visual tasks in bright daylight (Mitkus et al., 2018). Indeed, their spatial resolution decreases significantly at low light levels (Reymond, 1985). Our study is the first to investigate temporal resolution at very high luminance in birds. Indeed, previous studies did not test temporal resolution with stimuli of luminances higher than 7500 cd m⁻² (Boström et al., 2016, 2017). In our study, the highest FFF of all species was found at very high luminances of more than 25,000 cd m⁻² (Fig. 3). Thus, raptors have high temporal resolution only at very high light intensities. A recent study on visually related genes indicated that the transduction genes should favour fast vision in falcons (Wu et al., 2016). Furthermore, similar to owls but unlike accipitriforms, falcons also harboured one positively selected dim-light vision gene (Wu et al., 2016), and peregrine falcons have been observed hunting at low light levels (DeCandido and Allen, 2006), suggesting high temporal resolution at low light levels. However, our experiment revealed that falcons (falconiforms) have high temporal resolution only under very bright light conditions. With low stimulus intensities, their FFF was similar to that of hawks (accipitriforms).

Increasing welfare of raptors in captivity

It is well accepted that flicker of artificial lights used in their enclosures can be detected by captive birds (Greenwood et al., 2004) and may affect their behaviour, such as mate choice (Evans et al., 2006), induce physiological stress (Maddocks et al., 2001; Evans et al., 2012) and potentially have an impact on visual performance, as shown in mice (Yu et al., 2011). In many countries, raptors are kept for purposes such as falconry or display, which can be essential for raptor conservation and research (Kenward, 2009; Potier, 2016). While most raptors are kept in outdoor aviaries, indoor aviaries using artificial lighting are also used for reproduction (Nelson, 1972). Our study provides evidence that bright artificial illumination flickering at 100 Hz (common in Europe) or 120 Hz (USA) may not be suitable in enclosures for raptors, specifically falcons. As we used small stimuli, the FFF may be higher with larger stimuli (Kalloniatis and Luu, 2007). Therefore, when raptors are kept under bright artificial illumination, we suggest the use of lamps with higher flicker frequencies or no flicker at all.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: S.P., M.P., A.K.; Methodology: S.P., M.P., A.K.; Software: M.P.; Validation: S.P., A.K.; Formal analysis: S.P.; Data curation: S.P., M.L.; Writing - original draft: S.P.; Writing - review & editing: S.P., M.P., A.K.; Supervision: S.P., A.K.; Funding acquisition: S.P., A.K.

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Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.209031.supplemental>

References

- Ault, S. J. and House, E. W. (1987). Electroretinographic responses of the great horned owl (*Bubo virginianus*). *J. Raptor Res.* **21**, 147-152.
- Bornschein, H. and Tansley, K. (1961). Elektretinogramm und netzhautstruktur der Sumpfohreule (*Asio flammeus*). *Experientia* **17**, 185-187. doi:10.1007/BF02160375
- Boström, J. E., Dimitrova, M., Canton, C., Håstad, O., Qvarnström, A. and Ödeen, A. (2016). Ultra-rapid vision in birds. *PLoS ONE* **11**, e0151099. doi:10.1371/journal.pone.0151099
- Boström, J. E., Haller, N. K., Dimitrova, M., Ödeen, A. and Kelber, A. (2017). The flicker fusion frequency of budgerigars (*Melopsittacus undulatus*) revisited. *J. Comp. Physiol. A* **203**, 15-22. doi:10.1007/s00359-016-1130-z
- Bringmann, A. (2019). Structure and function of the bird fovea. *Anat. Histol. Embryol.* **48**, 177-200. doi:10.1111/ah.12432
- Brozek, J. and Keys, A. (1945). Changes in flicker-fusion frequency with age. *J. Consult. Psychol.* **9**, 87. doi:10.1037/h0053488
- Caro, S. P., Balthazart, J. and Bonadonna, F. (2015). The perfume of reproduction in birds: chemosignaling in avian social life. *Horm. Behav.* **68**, 25-42. doi:10.1016/j.jybeh.2014.06.001
- Crozier, W. J. and Wolf, E. (1941). The simplex flicker threshold contour for the zebra finch. *J. Gen. Physiol.* **24**, 625-633. doi:10.1085/jgp.24.5.625
- Crozier, W. J. and Wolf, E. (1944). Flicker response contours for the sparrow, and the theory of the avian pecten. *J. Gen. Physiol.* **27**, 315-324. doi:10.1085/jgp.27.4.315
- de Vries, S. E. J. and Clandinin, T. R. J. C. B. (2012). Loom-sensitive neurons link computation to action in the *Drosophila* visual system. *Curr. Biol.* **22**, 353-362. doi:10.1016/j.cub.2012.01.007
- DeCandido, R. and Allen, D. (2006). Nocturnal hunting by peregrine falcons at the empire state building, New York City. *Wilson J. Ornithol.* **118**, 53-58. doi:10.1676/1559-4491(2006)118[0053:NHBPPA]2.0.CO;2
- Doty, E. and Wirth, A. (1953). Differentiation between rods and cones by flicker electroretinography in pigeon and guinea pig. *Acta Physiol. Scand.* **30**, 80-89. doi:10.1111/j.1748-1716.1954.tb01076.x
- Drewitt, E. J. and Dixon, N. (2008). Diet and prey selection of urban-dwelling Peregrine Falcons in southwest England. *Br. Birds* **101**, 58-67.
- Elleberg, D., Lewis, T. L., Liu, C. H. and Maurer, D. (1999). Development of spatial and temporal vision during childhood. *Vision Res.* **39**, 2325-2333. doi:10.1016/S0042-6989(98)00280-6
- Evans, J. E., Cuthill, I. C. and Bennett, A. T. D. (2006). The effect of flicker from fluorescent lights on mate choice in captive birds. *Anim. Behav.* **72**, 393-400. doi:10.1016/j.anbehav.2005.10.031
- Evans, J. E., Smith, E. L., Bennett, A. T. D., Cuthill, I. C. and Buchanan, K. L. (2012). Short-term physiological and behavioural effects of high- versus low-frequency fluorescent light on captive birds. *Anim. Behav.* **83**, 25-33. doi:10.1016/j.anbehav.2011.10.002
- Ferguson-Lees, J. and Christie, D. A. (2001). *Raptors of the World*. A&C Black.
- Figuroa, R. A. R. and González-Acuña, D. (2006). Prey of the Harris's Hawk (*Parabuteo unicinctus*) in a suburban area of southern Chile. *J. Raptor Res.* **40**, 164-169. doi:10.3356/0892-1016(2006)40[164:POTHHP]2.0.CO;2
- Ginsburg, N. and Nilsson, V. (1971). Measuring flicker threshold in the budgerigar. *J. Exp. Anal. Behav.* **15**, 189-192. doi:10.1901/j.1971.15-189
- Greenwood, V. J., Smith, E. L., Goldsmith, A. R., Cuthill, I. C., Crisp, L. H., Walter-Swan, M. B. and Bennett, A. T. D. (2004). Does the flicker frequency of fluorescent lighting affect the welfare of captive European starlings? *Appl. Anim. Behav. Sci.* **86**, 145-159. doi:10.1016/j.applanim.2003.11.008
- Healy, K., McNally, L., Ruxton, G. D., Cooper, N. and Jackson, A. L. (2013). Metabolic rate and body size are linked with perception of temporal information. *Anim. Behav.* **86**, 685-696. doi:10.1016/j.anbehav.2013.06.018
- Hendricks, J. (1966). Flicker thresholds as determined by a modified conditioned suppression procedure. *J. Exp. Anal. Behav.* **9**, 501-506. doi:10.1901/j.1966.9-501
- Inger, R., Bennie, J., Davies, T. W. and Gaston, K. J. (2014). Potential biological and ecological effects of flickering artificial light. *PLoS ONE* **9**, e98631. doi:10.1371/journal.pone.0098631
- Jarvis, J. R., Taylor, N. R., Prescott, N. B., Meeks, I. and Wathes, C. M. (2002). Measuring and modelling the photopic flicker sensitivity of the chicken (*Gallus g. domesticus*). *Vision Res.* **42**, 99-106. doi:10.1016/S0042-6989(01)00268-1
- Kalloniatis, M. and Luu, C. (2007). Temporal resolution. In *The Organization of the Retina and Visual System* (ed. H. Kolh, R. Nelson, E. Fernandez and B. Jones). Salt Lake City, UT: University of Utah Health Sciences Center.
- Kenward, R. E. (2009). Conservation values from falconry. In *Recreational Hunting, Conservation and Rural Livelihoods: Science and Practice* (ed. B. Dickson, J. Hutton and B. Adams), pp. 181-196. Wiley-Blackwell.
- Kuznetsova, A., Brockhoff, P. B. and Christensen, R. H. B. (2017). lmerTest package: tests in linear mixed effects models. *J. Stat. Softw.* **82**. doi:10.18637/jss.v082.i13
- Land, M. F. and Nilsson, D.-E. (2012). *Animal Eyes*. Oxford University Press.
- Laughlin, S. and Weckström, M. (1993). Fast and slow photoreceptors—a comparative study of the functional diversity of coding and conductances in the Diptera. *J. Comp. Physiol. A* **172**, 593-609. doi:10.1007/BF00213682

- Lisney, T. J., Rubene, D., Rózsa, J., Løvlie, H., Håstad, O. and Ödeen, A.** (2011). Behavioural assessment of flicker fusion frequency in chicken *Gallus gallus domesticus*. *Vision Res.* **51**, 1324-1332. doi:10.1016/j.visres.2011.04.009
- Lisney, T. J., Ekesten, B., Tauson, R., Håstad, O. and Ödeen, A.** (2012). Using electroretinograms to assess flicker fusion frequency in domestic hens *Gallus gallus domesticus*. *Vision Res.* **62**, 125-133. doi:10.1016/j.visres.2012.04.002
- Maddocks, S. A., Goldsmith, A. R. and Cuthill, I. C.** (2001). The influence of flicker rate on plasma corticosterone levels of European starlings, *Sturnus vulgaris*. *Gen. Comp. Endocrinol.* **124**, 315-320. doi:10.1006/gcen.2001.7718
- Martin, G. R.** (2017). *The Sensory Ecology of Birds*. Oxford University Press.
- Mitkus, M., Olsson, P., Toomey, M. B., Corbo, J. C. and Kelber, A.** (2017). Specialized photoreceptor composition in the raptor fovea. *J. Comp. Neurol.* **525**, 2152-2163. doi:10.1002/cne.24190
- Mitkus, M., Potier, S., Martin, G. R., Duriez, O. and Kelber, A.** (2018). Raptor vision. *Oxford Research Encyclopedia of Neuroscience*. Retrieved 11 Dec 2019, from <https://oxfordre.com/neuroscience/view/10.1093/acrefore/9780190264086.001.0001/acrefore-9780190264086-e-232>.
- Nelson, R.** (1972). On photoperiod and captivity breeding of northern peregrines. *Raptor Res.* **6**, 57-72.
- Nuboer, J. F. W., Coemans, M. A. J. M. and Vos, J. J.** (1992). Artificial lighting in poultry houses: are photometric units appropriate for describing illumination intensities? *Br. Poult. Sci.* **33**, 135-140. doi:10.1080/00071669208417450
- Oehme, H.** (1964). Vergleichende Untersuchungen an Greifvogeläugeln. *Z. Morph. Ökol. Tiere* **53**, 618-635. doi:10.1007/BF00407730
- Porciatti, V., Fontanesi, G. and Bagnoli, P.** (1989). The electroretinogram of the little owl (*Athene noctua*). *Vision Res.* **29**, 1693-1698. doi:10.1016/0042-6989(89)90151-X
- Potier, S.** (2016). Ecologie sensorielle des rapaces: vision et olfaction. *PhD thesis*, Lund University.
- Potier, S.** (2019). Olfaction in raptors. *Zool. J. Linn. Soc.*, zlz121. doi:10.1093/zoolin/zlz121
- Potier, S., Bonadonna, F., Kelber, A., Martin, G. R., Isard, P.-F., Dulaurent, T. and Duriez, O.** (2016). Visual abilities in two raptors with different ecology. *J. Exp. Biol.* **219**, 2639-2649. doi:10.1242/jeb.142083
- Potier, S., Bonadonna, F., Martin, G. R., Isard, P.-F., Dulaurent, T., Mentek, M. and Duriez, O.** (2017a). Visual configuration of two species of Falconidae with different foraging ecologies. *Ibis* **160**, 54-61. doi:10.1111/ibi.12528
- Potier, S., Mitkus, M., Bonadonna, F., Duriez, O., Isard, P.-F., Dulaurent, T., Mentek, M. and Kelber, A.** (2017b). Eye size, fovea, and foraging ecology in accipitriform raptors. *Brain Behav. Evol.* **90**, 232-242. doi:10.1159/000479783
- Potier, S., Mitkus, M. and Kelber, A.** (2018). High resolution of colour vision, but low contrast sensitivity in a diurnal raptor. *Proc. R. Soc. B* **285**, 20181036. doi:10.1098/rspb.2018.1036
- Pumphrey, R.** (1948). The theory of the fovea. *J. Exp. Biol.* **25**, 299-312.
- Reymond, L.** (1985). Spatial visual acuity of the eagle *Aquila audax*: a behavioural, optical and anatomical investigation. *Vision Res.* **25**, 1477-1491. doi:10.1016/0042-6989(85)90226-3
- Ronald, K. L., Fernández-Juricic, E. and Lucas, J. R.** (2018). Mate choice in the eye and ear of the beholder? Female multimodal sensory configuration influences her preferences. *Proc. R. Soc. B* **285**, 20180713. doi:10.1098/rspb.2018.0713
- Rubene, D., Håstad, O., Tauson, R., Wall, H. and Ödeen, A.** (2010). The presence of UV wavelengths improves the temporal resolution of the avian visual system. *J. Exp. Biol.* **213**, 3357-3363. doi:10.1242/jeb.042424
- Srinivasan, M. V. and Bernard, G. D.** (1975). The effect of motion on visual acuity of the compound eye: A theoretical analysis. *Vision Res.* **15**, 515-525. doi:10.1016/0042-6989(75)90029-2
- Srinivasan, M. V. and Lehrer, M.** (1984). Temporal acuity of honeybee vision: behavioural studies using moving stimuli. *J. Comp. Physiol. A* **155**, 297-312. doi:10.1007/BF00610583
- Tucker, V. A.** (1998). Gliding flight: speed and acceleration of ideal falcons during diving and pull out. *J. Exp. Biol.* **201**, 403-414.
- Tucker, V. A., Cade, T. and Tucker, A. E.** (1998). Diving speeds and angles of a gyrfalcon (*Falco rusticolus*). *J. Exp. Biol.* **201**, 2061-2070.
- Walls, G. L.** (1942). *The Vertebrate Eye and Its Adaptive Radiation*. New York: Hafner Publishing Co (Fascimile of 1942 Edition).
- Ward, F. P. and Laybourne, R. C.** (1985). A difference in prey selection by adult and immature peregrine falcons during autumn migration. *ICBP Technical Publication* **5**, 303-309.
- Wu, Y., Hadly, E. A., Teng, W., Hao, Y., Liang, W., Liu, Y. and Wang, H.** (2016). Retinal transcriptome sequencing sheds light on the adaptation to nocturnal and diurnal lifestyles in raptors. *Sci. Rep.* **6**, 33578. doi:10.1038/srep33578
- Yu, Y., Chen, H., Tuo, J. and Zhu, Y.** (2011). Effects of flickering light on refraction and changes in eye axial length of C57BL/6 mice. *Ophthalmic Res.* **46**, 80-87. doi:10.1159/000323179
- Zar, J. H.** (1968). Standard metabolism comparisons between orders of birds. *The Condor* **70**, 278-278. doi:10.2307/1366710
- Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A. and Smith, G. M.** (2009). *Mixed Effects Models and Extensions in Ecology with R*. Springer Science & Business Media.