PSYCHOLOGY & NEUROSCIENCE

Psychology & Neuroscience, 2011, 4, 1, 29 - 48
DOI: 10.3922/j.psns.2011.1.005

Comparative neurophysiology of spatial luminance contrast sensitivity

Givago da Silva Souza, Bruno Duarte Gomes and Luiz Carlos L. Silveira

Universidade Federal do Pará, Belém, PA, Brazil

Abstract

The luminance contrast sensitivity function has been investigated using behavioral and electrophysiological methods in many vertebrate species. Some features are conserved across species as a shape of the function, but other features, such as the contrast sensitivity peak value, spatial frequency contrast sensitivity peak, and visual acuity have changed. Here, we review contrast sensitivity across different classes of vertebrates, with an emphasis on the frequency contrast sensitivity peak and visual acuity. We also correlate the data obtained from the literature to test the power of the association between visual acuity and the spatial frequency of the contrast sensitivity function peak. **Keywords:** contrast sensitivity, visual acuity, object vision, animal behavior, psychophysics, visually evoked potentials.

Received 25 May 2011; received in revised form 17 June 2011; accepted 29 June 2011. Available on line 30 June 2011

Spatial vision and contrast sensitivity

The ecological role of vision is mainly related to object localization and identification in a given environment. Vision helps animals search for food, look for sexual partners, avoid predators, and care for their offspring (Ghim & Hodos, 2006). A variety of eye optics designs, photoreceptor matrices, and post-receptoral retinal, tectal, and cortical mechanisms allows for environmental mapping and the neural representation of the visual information available to the animal. A popular hypothesis for visual system evolution relies on the selective pressure to disclose natural camouflage to other living beings (Regan, 2000). According to Regan (2000), five object attributes make it especially visible against its surrounding environment: luminance, texture, movement, color, and binocular disparity. If an object and its surroundings display the same values for these five parameters, then the visual system cannot distinguish one object from another, and the object is perfectly embedded in the environment.

Spatial vision encompasses both the perception of the spatial distribution of light and the perception of object localization in the environment (De Valois & De Valois, 1980). The present review emphasizes findings regarding the visual system processing of spatial luminance distribution at very low contrast levels. Spatial luminance contrast is the relative difference between the brightness of adjacent regions of space (Campbell & Maffei, 1974; Owsley, 2003). Spatial luminance contrast or simultaneous luminance contrast stands in the domain of space, as opposed to temporal luminance contrast or successive luminance contrast, which stands in the domain of time.

Two measurements of luminance contrast are frequently used in spatial vision: contrast threshold and contrast sensitivity. Contrast threshold is a probabilistic measurement that represents the highest contrast for object identification that is equal to chance. Contrast sensitivity is the inverse of contrast threshold. Measuring both contrast threshold and contrast sensitivity is possible using both periodic and non-periodic stimuli, with the former a measurement performed in the spatial frequency domain and the latter a measurement performed in the space domain. Results obtained using spatial and spatial frequency measurements can be converted to each other using a Fourier transformation, provided the system is linear in the range of the conditions studied.

Contrast transfer functions in natural and manmade optical systems

A common way to express visual system performance in the spatial frequency domain is to plot contrast sensitivity as a function of spatial frequency along most

---

Givago da Silva Souza and Luiz Carlos L. Silveira, Universidade Federal do Pará, Núcleo de Medicina Tropical and Instituto de Ciências Biológicas, Belém, Brasil. Bruno Duarte Gomes, Universidade Federal do Pará, Instituto de Ciências Biológicas, Belém, Brasil. Correspondence regarding this article should be directed to: Dr. Givago da Silva Souza, Universidade Federal do Pará, Núcleo de Medicina Tropical, Av. Generalíssimo Deodoro, no 92 (Umarizal), 66055-240 Belém, Pará, Brazil. Phone: +5591-32016819. Fax: +5591-32410032. E-mail: givagosouza@ufpa.br

of the range of spatial frequencies that the visual system sees (i.e., contrast sensitivity function [CSF]; Campbell, 1983). This function allows a quick understanding of the animal's visual system performance both under normal and dysfunctional conditions, displaying both peak contrast sensitivity (i.e., the contrast sensitivity in the range where the visual system is more sensitive) and visual acuity (i.e., the highest spatial frequency that the visual system detects at very high contrast). The CSF peak is a good indicator of the spatial frequencies that are more biologically relevant to the animal, whereas visual acuity represents the spatial resolution of the animal's visual system and the highest spatial frequency that is able to evoke a visual response from the animal. The CSF has a bell shape and can be regarded as dividing the spatial frequency world into two halves. Below the curve are all combinations of spatial frequencies and contrast that are seen by the animal. Above the curve resides the unseen world.

The CSF is the visual psychophysics counterpart of a very well known optical measurement, the Modulation Transfer Function (MTF), which together with the Phase Transfer Function (PTF) results in the more general case, the Optical Transfer Function (OTF; Goodman, 2005). The capacity of any optical system—ranging from a simple lens to a composite optical system made from several lens elements to a very complex photonic system made from many different optical elements combined with image recording devices, such as films, photographic paper, and electronic displays—to transfer information from the object space to the image space or to an image recording device can be described by how much the system attenuates spatial contrast (i.e., modulation transfer) and how much it introduces a phase shift (i.e., phase transfer) for each spatial frequency. This is evaluated by careful measurements of the contrast and phase of a periodic object and its image, followed by quantitative comparisons between the two datasets, thus resulting in the aforementioned MTF and PTF, respectively. Sine wave objects are preferable for this type of experiment because linear optical systems only introduce contrast attenuation with no phase shift for all spatial frequencies. The OTF of an optical system can then be expressed either as the MTF plus PTF as separate real functions of a real variable or as a single complex function of a real variable, with the real variable spatial frequency in both cases. With vision, measuring spatial phase shifts is not very common (Westheimer, 1978), and the CSF that physiologically corresponds to the MTF very often remains as the single measured visual system characteristic (Röhler, 1962; Westheimer, 1963).

Another way to characterize an optical system is to measure its Point Spread Function (PSF; Goodman, 2005; Gubisch, 1967). This is performed by using punctiform objects and recording the amount of blur in the image. A similar measurement can be made using very narrow-line objects. In this case, the resulting function is called a Line Spread Function (LSF), which can then be used to estimate the PSF (Flamant, 1955; Krauskopf, 1962; Westheimer & Campbell, 1962; Campbell & Gubisch, 1966). Both the PSF and LSF are measurements performed in the domain of space, as opposed to the spatial frequency domain where the OTF, MTF, and PTF are measured. A Fourier transformation can then be used to transform the results from one domain to the other. The Fourier theorem establishes that measurements in one domain yield results equal to measurements performed in the related domain followed by Fourier transformation to the first domain, provided the system is linear.

Both spatial frequency and spatial measurements have been used to study visual system contrast transfer. Because the visual system has two very different subsystems, one represented by eye optics and another represented by neural elements (e.g., retinal, subcortical, and cortical), having separate measurements for these two subsystems and measurements for the entire system is desirable. Contrast transfer through the eye optical system has been studied by recording its LSF (Flamant, 1955; Krauskopf, 1962; Westheimer & Campbell, 1962; Campbell & Gubisch, 1966) and MTF (Röhler, 1962; Westheimer, 1963). The eye optical system behaves, in many regards, similarly to manmade optical systems, and the measurement of its LSF or MTF is performed in similar ways and provides equivalent results. The results can then be interpreted using the same rationale. However, an additional practical problem exists when dealing with the eyes of living animals compared with experiments with manmade lenses and optical systems, specifically how to access the image formed by the eye optics. The more common way is called the double-pass method, in which an object is first placed in front of the eye, and its image is formed by the eye optics on the retinal surface. The retinal image is then used as an object by the eye optics, working backward to form a second image outside the eye that can then be measured by the experimenter. Finally, relatively simple mathematics is then used to account for the double-pass and estimate the single-pass effect of the eye optics (Campbell & Gubisch, 1966; Navarro, Artal, & Williams, 1993). Diffraction at the pupil is the main factor that works at very high light levels to degrade the image formed by the eye optics (Campbell & Gubisch, 1966). When the pupil enlarges at progressively lower light levels, diffraction loses importance, and optical aberrations become the main factor that degrades the image formed by the eye optics (Campbell & Gubisch, 1966). The main effect of both diffraction and optical aberrations is an attenuation of image contrast at medium and high spatial frequencies, which can be evaluated by recording the MTF or increasing the light spread in the image of punctiform objects that can be evaluated by recording the PSF or LSF. At intermediate pupil sizes, the eye optics work at optimal conditions to provide a retinal image with minimal blur.

As stated above, the CSF is the psychophysical counterpart of the optical MTF. The CSF has frequently been used to estimate contrast transfer through the entire visual system, comprising both optical and neural subsystems. It has been measured using sine wave gratings placed on a display in front of the subject and recording a behavioral response to determine the contrast threshold for each spatial frequency (Campbell & Green, 1965a; Campbell & Robson, 1968; Robson, 1966; Schade, 1956; Patel, 1966; Van Nes & Bouman, 1967). Additionally, estimating the CSF of the neural part of the visual system is also possible by bypassing the eye optics. This is accomplished by generating a sine wave grating directly on the retina using laser interferometry (Arnulf & Dupuy, 1960; Campbell & Green, 1965a; Westheimer, 1960). The comparison of the eye optics MTF, neural CSF, and CSF of the entire visual system (i.e., optical plus neural parts) made under equivalent conditions from the same animal allows one to distinguish the contribution of each element (i.e., optical and neural) to animal vision. A series of studies by Fergus W. Campbell and colleagues reached the conclusion that the performance of neural elements limits the performance of human vision (Campbell & Green, 1965a; Campbell & Gubisch, 1966; Campbell & Robson, 1968). Experiments in other animals have generally provided similar conclusions (e.g., opossum: Oswaldo-Cruz, Hokoç, & Sousa, 1979; Oswaldo-Cruz, Picanço-Diniz, & Silveira, 1982; Picanço-Diniz, Silveira, & Oswaldo-Cruz, 1983; Silveira, Picanço-Diniz, & Oswaldo-Cruz, 1982).

The shapes of the eye optics MTFs and visual system CSFs reveal some interesting properties. As expected, the eye optics MTF has a low-pass shape with progressive attenuation in the high spatial frequency range, reaching a cut-off frequency at approximately 60 cycles per degree (cpd; Campbell & Gubisch, 1966). The visual system CSF is band-pass, showing attenuation at high spatial frequencies, similar to the eye optics MTF, plus additional attenuation at low spatial frequencies (Campbell & Green, 1965a; Campbell & Robson, 1968). The attenuation of low spatial frequencies is attributable to visual system neural processing and considered to be related to the lateral inhibition and center-surround organization of the receptive fields of visual system neurons (Enroth-Cugell & Robson, 1966).

Figure 1 shows the several stages of contrast transfer from object generation on a display, such as a cathode ray tube (CRT) display (Figure 1A), modulation transfer through the eye optical elements (Figure 1B), and the end result of contrast transfer through the entire visual system measured behaviorally (Figure 1C). System analysis postulates that system performance depends on the element whose performance is more limited—in this case, the neural part of the visual system.

Vertebrate vision and environmental adaptation

The subphylum Vertebrata (vertebrates) comprises seven classes: Agnatha (jawless fish), Condrichthyes (cartilaginous fish), Osteichthyes (bony fish), Amphibia

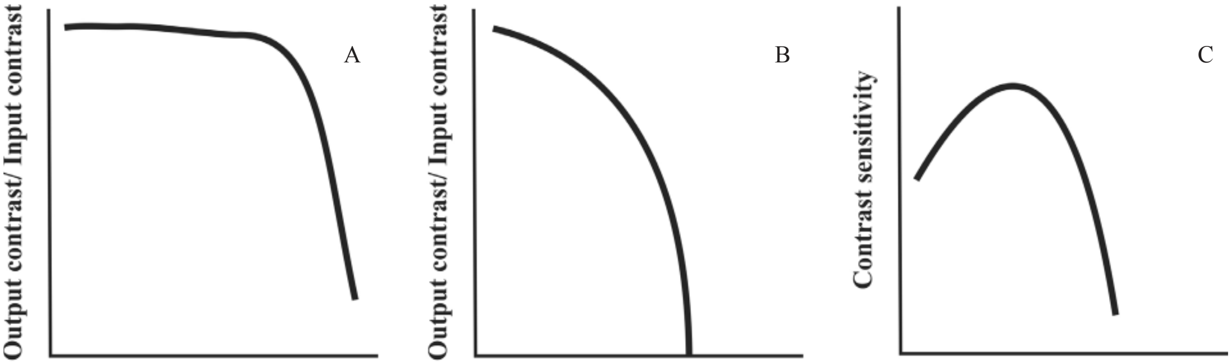

Figure 1. A: The first step in contrast vision is how it arises from the objective world. In this example, sine wave luminance gratings were generated on the screen of a CRT monitor. This type of system is able to represent the luminance modulation of sine wave gratings across a wide range of spatial frequencies that encompass the human visible range. At high spatial frequencies, a progressive contrast loss occurs, which quickly sets the useful range for the modulation of representations on a CRT display. Different physical principles work with different display types, but generally the effect is the same: a low-pass MTF. At low spatial frequencies, the MTF is usually limited only by the display size. **B:** The MTF for the eye optical system taken as a single entity despite the fact that it is composed of several optical elements with different properties. The eye optics MTF is recorded at the eye fundus. It has a low-pass shape, similar to the CRT display MTF, but it transmits a shorter range of high spatial frequencies than it is possible to represent in different displays available to the experimenter**. C:** Contrast transfer of the entire visual system in a human subject obtained using psychophysical methods. The CSF is the result of contrast transfer through a series of elements organized in a cascade that comprise the generation of sine wave gratings on a CRT monitor, high spatial frequency attenuation by the eye optical elements, and both low and high spatial frequency contrast attenuation by neural circuits. As a consequence, the visual system CSF is band-pass.

(amphibians), Reptilia (reptiles), Aves (birds), and Mammalia (mammals). Many features of the vertebrate visual system have been optimized during evolution for appropriate performance in a given set of environmental conditions. Vertebrates occupy terrestrial (both surface and subterranean), aquatic, and aerial environments and interfaces between these compartments. This allows for the evolution of visual systems with different performance for luminance contrast information processing in the spatial frequency domain. The spatial vision of fish, amphibians, reptiles, birds, and mammals has been studied over the years to cover a range of different species to understand the ecological aspects of visual behavior.

Luminance spatial contrast sensitivity of bony fish

The visual response of fish to contrast as a function of spatial frequency has been investigated in several species, some of which are laboratory animals that have been studied for numerous reasons: bluegill sunfish (*Lepomis macrochirus*), zebrafish (*Danio rerio*), medaka or Japanese killifish (*Oryzias latipes*), and goldfish (*Carassius auratus*; Bilotta & Powers, 1991; Haug, Biehlmaier, Mueller, & Neuhauss, 2010; Mueller & Neuhauss, 2010; Northmore & Dvorak, 1979; Northmore, Oh, & Celenza, 2007; Rinner, Rick, & Neuhauss, 2005; Figure 2D). Northmore and Dvorak (1979) and Bilotta and Powers (1991) used Pavlovian conditioning to suppress respiration upon the presentation of a sinusoidal grating. Both works showed that the fish CSF had a band-pass shape for high mean luminance and stationary stimuli. Bilotta and Powers (1991) showed that temporally modulated stimuli or stimuli with low mean luminance changed the CSF shape from band-pass to low-pass. The fish CSF peaks at 0.2-0.3 cpd and has a relatively high cut-off frequency that might provide behavioral visual acuity of 3.2 cpd at high photopic luminance levels (Bilotta & Powers, 1991). Northmore et al. (2007) estimated the contrast sensitivity of fish based on preferential swimming in response to grating stimuli. They found that the CSF had a band-pass shape, peaked at 0.3-0.4 cpd, and had a cut-off frequency of 5-7 cpd.

Rinner et al. (2005) and Haug et al. (2010) used the optokinetic nystagmus response to estimate the contrast sensitivity of larval zebrafish. These studies immobilized zebrafish larvae and then stimulated the larvae with gratings projected onto a cylindrical screen. Fish eye movements were recorded with a camera, and eye angle and velocity were evaluated in real-time. Rinner et al. (2005) found a band-pass CSF that peaked at 0.07-0.08 cpd, with visual acuity of 0.2-0.4 cpd. Haug et al. (2010) found visual acuity of 0.16 cpd. Also using fish optokinetic nystagmus, Mueller and Neuhauss (2010) studied eye velocity as a function of stimulus contrast and spatial frequency in adult zebrafish and medaka. They found that eye velocity quickly changed with low to medium contrast and was saturated at medium to high contrast. Eye velocity as a function of spatial frequency was well described by a band-pass function that peaked at 0.1-0.12 cpd, and zebrafish had slightly higher visual acuity than medaka (0.4 and 0.6 cpd, respectively).

Luminance spatial contrast sensitivity of amphibians

Amphibians have been studied to solve a number of problems in cell biology and visual neuroscience. Some reference studies of vertebrate vision were performed in amphibians (e.g., Hartline, 1938, 1940a, b, c; Lettvin, Maturana, McCulloch, & Pitts, 1959). Despite several works on the single unit properties of neurons located at different sites along the visual pathways and many behavioral studies of amphibian vision, most of these studies have been performed in frogs. Very few studies have focused on contrast sensitivity and visual acuity in vertebrates (Aho, 1997; Manteuffel & Himstedt, 1978). No complete descriptions of the amphibian CSF have been provided. Himstead (1967) and Manteuffel and Himsted (1978) evaluated visual acuity in both aquatic and aerial environments in the smooth newt (*Triturus vulgaris*) by measuring optomotor responses and the single unit responses of neurons located in the optic tectum and thalamus. Aho (1997) estimated the visual acuity of frogs (*Rana pipiens*) using a forced-choice prey-dummy setup. Two dummies were placed in the visual field. Behind the dummies were gratings, but only one of the stimuli drifted. This author found that at high luminance levels, visual acuity reached 2.8 cpd and dropped to approximately 0.7 cpd when the luminance was lowered. He also found, similar to other mammals, a good correlation between behavioral visual acuity and cut-off spatial frequency estimated from the sampling properties of the retinal ganglion cell mosaic. Monroy and Nishikawa (2011) studied the angular head movements of frogs during predatory behavior toward earthworms of different sizes. They found larger angular amplitudes for 2-3 cm prey and a smaller response for both larger-sized prey (low spatial frequencies) and especially smaller-sized prey (high spatial frequencies). This experiment, however informative, was too complex to provide a straightforward description of frog contrast sensitivity and visual acuity. The observed results are doubtless the holistic end product of all of the frog sensory and motor systems working cooperatively.

Luminance spatial contrast sensitivity of reptiles

Similar to amphibians, the study of the luminance spatial contrast sensitivity of reptiles is scarce and has been limited to visual acuity measurements in some species of turtles and snakes (e.g., *Pseudemys scripta elegans* [freshwater turtle], *Caretta caretta* [loggerhead sea turtle], and *Nerodia sipedon pleuralis* [midland banded water snake]; Baker, Gawne, Loop, & Pullman, 2007; Bartol, Musick, & Ochs, 2002; Northmore & Granda, 1991). In turtles, experiments measured visually evoked responses recorded from the optic tectum (Northmore & Granda, 1991) and obtained non-invasive recordings directly from surface electrodes placed on the skin of the animal's head (Bartol et al., 2002). The estimated visual acuity ranged from 4.4-9 cpd (Northmore & Granda, 1991) to 3.9-6.7 cpd (Bartol et al., 2002). Snake visual acuity was estimated to be 4.25 cpd (Baker et al., 2007).

Luminance spatial contrast sensitivity of birds

Birds have very sophisticated vision in the spatial, temporal, and chromatic domains. Bird spatial vision has been extensively studied in several species (Blough & Blough, 1989; Dabrowska, 1975; Fite & Rosenfield-Wessels, 1975; Fox, Lehmkuhle, & Westendorf, 1976; Gaffney & Hodos, 2003; Ghim & Hodos, 2006; Gover, Jarvis, Abeyesinghe, & Wathes, 2009; Harmening, Nikolay, Orlowski, & Wagner, 2009; Hirsch, 1982; Hodos, Miller, & Fite, 1991; Hodos, Ghim, Potocki, Fields, & Storm, 2002; Hodos, Potocki, Ghim, & Gaffney, 2003; Jarvis, Abeyesinghe, McMahon, & Wathes, 2009; Lee, Holden, & Djamgoz, 1997; Martin & Gordon, 1974; Nye, 1968; Over & Moore, 1981; Porciatti, Fontanesi, & Bagnoli, 1989; Reymond & Wolfe, 1981; Reymond, 1985, 1987; Schmid & Wildsoet, 1998; Yamamoto, Furuya, & Watanabe, 2001).

Pigeons (*Columbia livia*) have been widely used in operant conditioned behavior experiments, and their visual system has been the input system of choice in several such experiments mainly because of the high visual acuity of pigeons compared with other commonly studied laboratory vertebrates. Blough (1971) estimated pigeon visual acuity to be 7.5-30 cpd. Hodos et al. (1991) estimated pigeon visual acuity at different ages and found that the youngest individuals (2 years old) had mean visual acuity of 16 cpd, whereas the oldest individuals (10-20 years old) had visual acuity of 2-4 cpd. Blough (1971) and Hodos et al. (2002, 2003) investigated pigeon contrast sensitivity. Blough (1971) used a forced-choice procedure, in which the pigeon had to decide between striped and blank fields to peck. The spatial frequency of the striped field was increased to estimate visual acuity, which ranged from 7.5 to 25.8 cpd. Hodos et al. (2002) used electroretinography and an operant conditioning procedure to estimate the pigeon CSF. They found band-pass functions, but the overall curve was 53% lower for all spatial frequencies when pattern electroretinography was used. The CSF peak was located at a higher spatial frequency, and visual acuity was higher when they used behavioral methods compared with electroretinography (i.e., 0.81 *vs*. 0.68 cpd and 5.23 cpd *vs*. 3.31 cpd, respectively).

The visual system of chickens (*Gallus gallus domesticus*) became quite popular after the famous experiment of experimentally induced myopia in chicks that related this condition to the deprivation of spatial vision during development (Pickett-Seltner, Sivak, & Pasternak, 1988). Over and Moore (1981) found that the visual acuity of 25-day-old chicks was 1.5 cpd. Schmid and Wildsoet (1998) measured the optokinetic response and estimated the visual acuity of 2- to 8-day-old chicks as 6-8 cpd. Jarvis et al. (2009) used a forced-choice procedure, in which the avian response was to peck a correct key. They found that the CSF of adult chickens was higher (approximately 1 cpd), and visual acuity was 7 cpd. Similar results were found by Gover et al. (2009).

The spatial vision of quails (*Coturnix coturnix japonica*) was studied by Lee et al. (1997) using pattern electroretinography. They found that younger quails had higher contrast sensitivity than older quails, especially in the low spatial frequency range. However, visual acuity was similar in young and old quails (5-6 cpd).

The visual systems of other birds, together with commonly used laboratory birds (e.g., pigeons and chickens), have rose scientific interest because of their conspicuous cleverness (e.g., crows), their notorious ability to distinguish their prey at a long distance (e.g., eagles, falcons, and hawks), and their sophisticated nocturnal vision (e.g., owls). Dabrowska (1975) estimated the visual acuity of three different species of crows (*Corvus frugilegus*, *Garrulus glandarius*, and *Coloeus monedula*) and found values near 30 cpd. Fite and Rosenfield-Wessels (1975) estimated the visual acuity of a species of crow (*Cyanocitta cristata*) and found values that ranged from 15 to 19 cpd. Yamamoto et al. (2001) used behavioral methods and estimated the visual acuity of the Japanese jungle crow (*Corvus macrorhyncos*) to be 8.4 cpd.

Reymond and Wolfe (1981) and Reymond (1985) studied the luminance CSF of the eagle (*Aquila audax*) using behavioral methods. They estimated that the eagle CSF had a peak at 1 cpd and visual acuity of 137 cpd at high luminance levels. The behavioral visual acuity of falcons (*Falco sparverius* and *Falco berigora*) was studied by Fox et al. (1976), Hirsch (1982), and Reymond (1987), who found values between 73 and 160 cpd. Gaffney and Hodos (2003) estimated the visual acuity of falcons (*Falco sparverius*) using pattern electroretinography and found a value of 29 cpd. These authors argued that electroretinographic visual acuity is 37% lower than behavioral visual acuity, and with the appropriate corrections they predicted falcon visual acuity of 46 cpd, which was still lower than previous behavioral estimations.

Martin and Gordon (1974) and Fite (1973) estimated owl visual acuity of 7.5-15 cpd. Porciatti, Fontanesi, Raffaelli, & Bagnoli (1989) measured the visual acuity of a species of owl (*Athene noctua*) using pattern electroretinography and found it to be 6 cpd. Martin and Gordon (1974) and Harmening et al. (2009) used behavioral methods to study the contrast sensitivity of three species of owls (*Tyto alba pranticola*, *Strix aluco*, and *Bubo virginianos*). Harmening et al. (2009) found a contrast sensitivity peak of 1-2 cpd and visual acuity of 3-4 cpd.

Ghim and Hodos (2006) used pattern electroretinography to compare the CSF of several bird species, including falcons (*Falco sparvarius*), owls (*Tyto alba*), European starlings (*Sturnus vulgaris*), quails (*Coturnix coturnix japonica*), red-bellied woodpeckers (*Melanerpes carolinus*), and pigeons (*Columbia livia*). They found that these birds had a band-pass CSF that peaked at 3 cpd (falcon), 1-2 cpd (pigeon, starling, and owl), 0.8-1 cpd (quail), and 0.5-0.7 cpd (woodpecker).

Luminance spatial contrast sensitivity of mammals

The measurements of mammalian contrast sensitivity are biologically and evolutionary important. The results in humans can be applied to various subjects, including medicine. Mammals represent a largely diversified and well studied group of vertebrates with different visual system circuitry adapted to many circadian and ecological niches. These animals can process visual information in different ways to make spatially oriented decisions.

Marsupials are among the oldest infraclass mammalian. Their visual system can provide clues about the visual systems of the first mammals. The marsupial CSF was estimated by Silveira et al. (1982) and Hemmi and Mark (1998) using visually evoked potential recordings. Hemmi and Mark (1998) also estimated visual acuity using psychophysical methods. Silveira et al. (1982) studied the vision of opossums (*Didelphis marsupialis*), and Hemmi and Mark (1998) studied the vision of tammar wallabies (*Macropus eugenii*). The mean CSF estimated by Silveira and colleagues had a low-pass profile and visual acuity of 1.25 cpd. However, some animals studied by Silveira and colleagues showed a significant attenuation of contrast sensitivity at the lowest spatial frequencies tested (Silveira, 1980). Hemmi and Mark (1998) found a band-pass electrophysiological CSF that peaked at 0.15 cpd and visual acuity of 2.7 cpd. Tammar wallaby behavioral visual acuity ranged from 4 to 5 cpd.

Several studies measured the visual acuity of bats using behavioral methods. The visual acuity of the little brown bat (*Myotis lucifugus*) was 0.17 cpd, and the visual acuities of the lesser sac-winged bat (*Saccopteryx leptura*; Suthers, 1966), common vampire bat (*Desmodus rotundus*; Manske & Schmidt, 1976), big brown bat (*Eptesicus fuscus*; Bell & Fenton, 1986), and northern bat (*Eptesicus nilssonii*; Rydell & Eklöf, 2003) were 1.43, 1.25, 1, and 1.25 cpd, respectively.

The nervous systems and especially visual systems of cats and small rodents, such as rats, mice, and hamsters, have been extensively investigated. From the 1950s to 1980s, results obtained from the cat visual system were considered easily transferred to the understanding of primate and human vision. This tenet is no longer accepted, but the large amount of data collected from the cat visual system is still very interesting from the point of view of comparative psychology, physiology, and anatomy. Small rodents, which were initially used as one of the more important models for operant behavior experiments, became progressively more used in different laboratories to study various diseases, drug effects, and the knockout of specific genes that govern neural function.

Sinex, Burdette, and Pearlman (1979) applied an optokinetic nystagmus method introduced by Wallman (1975) to study the spatial vision of the house mouse (*Mus musculus*). They investigated the motor response at very low spatial frequencies, such as 0.016 cpd. They found a CSF peak at 0.125 cpd and visual acuity of 0.5 cpd. Birch and Jacobs (1979) estimated the spatial luminance CSF of pigmented and albino rats (*Rattus novergicus*) using a two-forced-choice behavioral task with a display with a homogeneous field and another display with a sinusoidal grating with a range of spatial frequencies and contrasts. For pigmented rats, they found a low-pass CSF peak at 0.12 cpd and visual acuity of 1.2 cpd. For albino rats, they found that the CSF retained the low-pass profile, but contrast sensitivity was lower compared with pigmented rats at all spatial frequencies tested, and visual acuity was less, ranging from 0.34 to 0.43 cpd. The CSFs of pigmented and albino rats showed no fall-off at spatial frequencies as low as 0.12 cpd. Several studies estimated rat behavioral visual acuity as 0.5-1 cpd (Cowey, Henken, & Perry, 1982; Dean, 1981; Lashley, 1938; Linden, Cowey, & Perry, 1983; Wiesenfeld & Branchek, 1976). Legg (1984) was the first to show the fall-off of the rat CSF at low spatial frequencies. He used spatial frequencies lower than 0.12 cpd. Keller, Strasburger, Cerutti, and Sabel (2000) showed a prominent attenuation of contrast sensitivity at spatial frequencies below 0.1 cpd. They found that the CSF peak occurred at 0.1-0.2 cpd.

Other works used visually evoked potentials to estimate the rat CSF (Silveira, Heywood, & Cowey, 1987; Tejada & Tedó, 1998). Silveira et al. (1987) found that the CSF of pigmented rats was band-pass, peaking at 0.1 cpd with a visual acuity of 1.2 cpd. Tejada and Tedó (1998) used an approach similar to Silveira et al. (1987) but used albino rats. They found lower contrast sensitivity at all spatial frequencies compared with those obtained by Silveira et al. (1987) in the pigmented rat, and visual acuity was 0.48 cpd. Despite the methodological differences, a remarkable similarity was found between the results obtained by Birch and Jacobs (1979) and the results obtained by Silveira et al. (1987) and Tejada and Tedó (1998). Prusky, West, & Douglas (2000) compared the visual acuity of rats and mice and found that rats had two-fold higher visual acuity than mice.

The non-invasive visual investigation of cats (*Felis domesticus*) was first conducted by Smith (1936) and later widely investigated in 1970-1980 (Berkley & Watkins, 1973; Bisti & Maffei, 1974; Blake, 1988; Blake, Cool, & Crawford, 1974; Campbell, Maffei, & Piccolino, 1973; Harris, 1978; Pasternak & Merigan, 1981).

Smith (1936) found behaviorally that cats could distinguish between horizontally and vertically oriented luminance contrast stripes. This finding allowed researchers, during the 1960s, to relate neural substrates in the retina or visual cortex to psychophysical findings in cats. Enroth-Cugell and Robson (1966) found that the visual acuity of retinal ganglion cells in cats was 5.5 cpd, whereas Campbell and colleagues (Campbell, Cooper, & Enroth-Cugell, 1969) performed the same investigation in thalamic and cortical cells and found visual acuity of 4 cpd.

Campbell et al. (1973) estimated the CSF in anaesthetized cats using visually evoked potential as the investigation method. The cat CSF peaked at 0.2 cpd, and visual acuity ranged from 15 to 20 cpd. Harris (1978) used visually evoked potentials to estimate the CSF of awake cats, which peaked at 0.4 cpd, and visual acuity was approximately 10 cpd. Bisti and Maffei (1974) and Blake et al. (1974) used behavioral methods, in which the cat had to push a pedal when it detected the gratings. Both studies found a CSF that peaked at 0.4 cpd, but visual acuity was approximately 5 cpd (Blake et al., 1974) and 10 cpd (Bisti & Maffei, 1974). Berkley and Watkins (1973) estimated visual acuity using visually evoked potentials, which ranged from 3 to 6 cpd. Pasternak and Merigan (1981) studied the effects of stimulus mean luminance on the cat CSF. The cats were trained under a two-forced-choice paradigm to discriminate vertical sinusoidal gratings from homogeneous fields of equal mean luminance. They found that the CSF profile changed from low-pass to band-pass as the mean luminance decreased. The CSFs peaked at 0.6 cpd and 0.15 cpd at high and low mean luminance, respectively. Visual acuity was approximately 4 cpd at high mean luminance and approximately 1 cpd at low mean luminance.

The spatial vision of other mammals has been investigated. Pak (1984) estimated the pigmented rabbit CSF, which peaked at 0.35 cpd, with visual acuity of 3 cpd. Vaney (1980) measured the visual acuity of wild European rabbits, which ranged from 1.6 to 2.5 cpd. The visual acuity of dogs that were subjected to neuromuscular block was 11.6 cpd and 12.6 cpd, estimated by electroretinography and visually evoked potentials, respectively. Hanke, Scholtyseek, Hanke, and Dehnhardt (2011) studied the contrast sensitivity of harbor seals (*Phoca vitulina*). They found a CSF peak at 0.7 cpd and visual acuity of 2-3 cpd. Weiffen, Moller, Mauck, and Dehnhardt (2006) measured the underwater visual acuity of harbor seals at different levels of water turbidity. They found a linear loss of visual acuity as turbidity increased. Timney and Keil (1992) estimated the visual acuity of horses to be 23.3 cpd, and Rehkämper, Perrey, Werner, Opfermann-Rüngeler, and Görlach (2000) found that cattle visual acuity for vertical lines was 2.6 cpd and for horizontal lines was 1.6 cpd.

Jacobs, Blakeslee, McCourt, and Tootell (1980) estimated the CSF of ground squirrels, which peaked at 0.7-0.8 cpd, with visual acuity of 4 cpd. Jacobs, Birch, and Blakeslee (1982) compared the CSF of three different species of tree squirrels (western gray squirrel, *Sciurus griseus*; fox squirrel, *Sciurus niger*; eastern gray squirrel, *Sciurus carolinensis*). No difference in the CSF was found between these species. The squirrel CSF peaked at 0.5 cpd, and visual acuity was 1.8-3.8 cpd.

The study of spatial contrast sensitivity in primates is a hot field of spatial vision investigation. The large amount of data obtained from primates has occurred because of their similarity to humans. Petry, Fox, and Casagrande (1984) estimated the CSF of prosimians tree shrew (*Tupaia belangeri*) using a forced-choice discrimination task. Two of the three specimens had a CSF peak at 0.7 cpd and visual acuity of approximately 2-2.4 cpd, whereas the third specimen had a CSF peak at 0.3 cpd and visual acuity of 1.25 cpd. Similar experiments were performed with galagos (*Galago crassicaudatus*; Langston, Casagrande, & Fox, 1986), southern pig-tailed macaques (*Macaca nemestrina*; De Valois, Morgan, & Snodderly, 1974; Merigan, Pasternak, & Zehl, 1981), crab-eating macaques (*Macaca fascicularis*; De Valois et al., 1974), owl monkeys (*Aotus trivirgatus*; Jacobs, 1977), and squirrel monkeys (*Saimiri sciureus* Merigan, 1976). The results obtained from *Macaca* and *Saimiri* were not different. Their CSFs peaked at 3-5 cpd, with visual acuity of 30-40 cpd (De Valois et al., 1974; Merigan, 1976). The owl monkey CSF peaked at 2-3 cpd, with visual acuity of 12-15 cpd (Jacobs, 1977). The galago CSF peaked at 0.7-0.9 cpd, with visual acuity of 3-4 cpd (Langston et al., 1986). Bonds, Casagrande, Norton, and DeBruyn (1987) also estimated the galago CSF using visually evoked potentials, and their results were slightly different from Langston et al. (1986). Bonds at al. (1987) found a CSF peak at 0.2-0.4 cpd and visual acuity of 1.6-3 cpd.

The spatial luminance CSF in humans (*Homo sapiens*) was first investigated by Schade (1956). During the 1960s and 1970s, a series of studies was performed that unveiled important aspects of human vision using psychophysical and non-invasive electrophysiological methods (Atkinson & Campbell, 1974; Bain & Kulikowski, 1976; Blakemore & Campbell, 1969a, b; Blakemore, Carpenter, & Georgeson, 1970; Campbell & Gubisch, 1966; Campbell & Green, 1965a, b; Campbell & Gregory, 1960a, b; Campbell, Howell, & Robson, 1971; Campbell, Kulikowski, & Levinson, 1966; Campbell & Kulikowski, 1966; Campbell & Kulikowski, 1971; Campbell & Kulikowski, 1972; Campbell & Maffei, 1970; Campbell, Nachmias, & Jukes, 1970; Campbell & Robson, 1968; Campbell et al., 1969; Gubisch, 1967; King-Smith & Kulikowski, 1973a, b; King-Smith & Kulikowski, 1975; Kulikowski, 1978; Kulikowski, 1971a, b; Kulikowski, Abadi, & King-Smith, 1973; Kulikowski & Campbell, 1971; Kulikowski & King-Smith, 1973; Kulikowski & Tolhurst, 1973; Maffei & Campbell, 1970; Robson, 1966; Tolhurst, 1972a, b; Tolhurst, 1973; Tolhurst & Hart, 1972; Wood & Kulikowski, 1978). The legacy of these studies, in addition to those performed in animals using invasive and non-invasive methods, elicited a theory of visual processing by parallel channels that were responsible for detecting narrow bands of spatial frequencies that together represent the CSF. The human

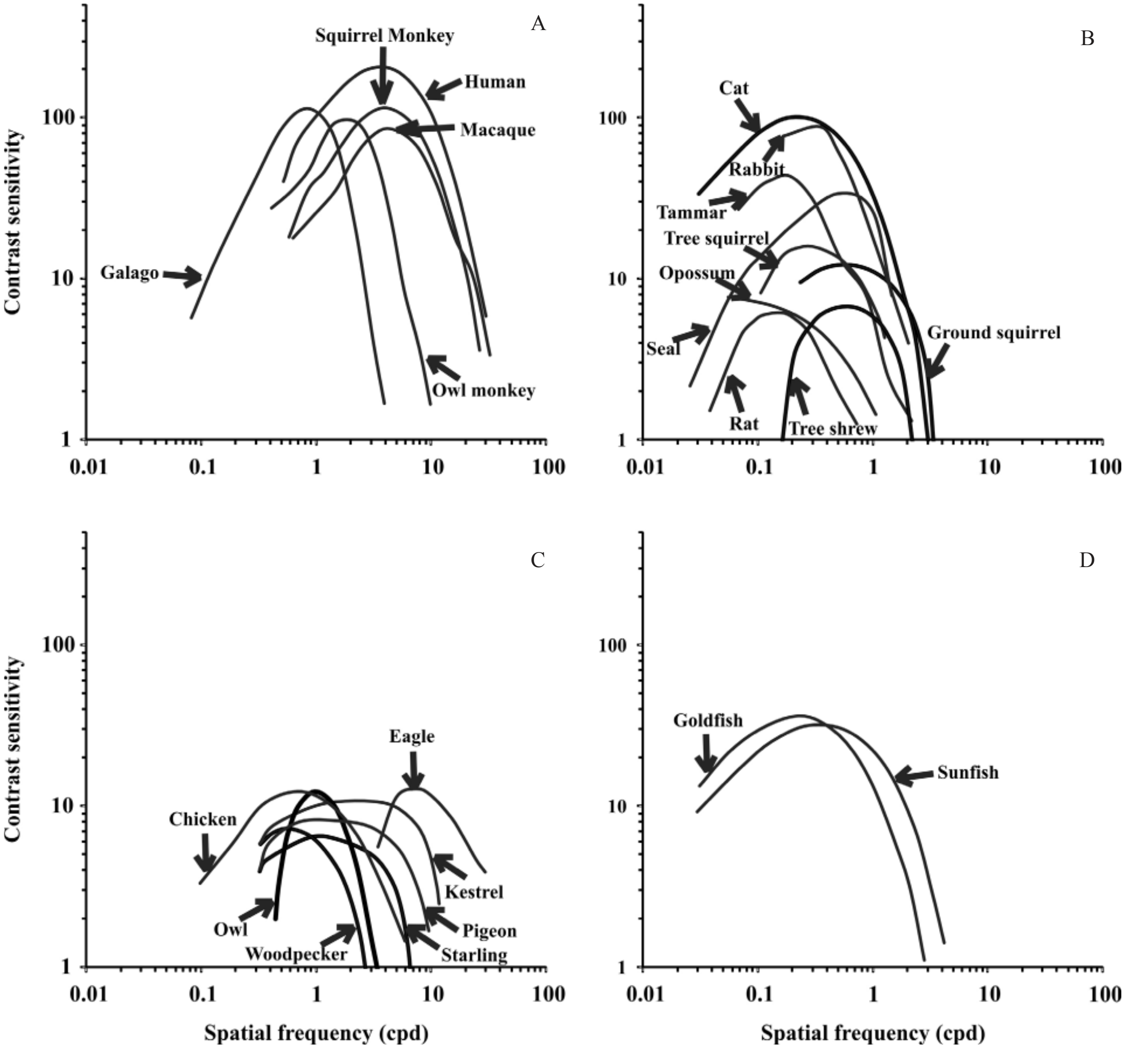

Figure 2. Comparison between contrast sensitivity functions (CSFs) obtained from several vertebrates using various behavioral and electrophysiological methods. **A:** Primates, including the CSFs from humans (Campbell & Robson, 1968), macaques (De Valois et al., 1974), owl monkeys (Jacobs, 1977), squirrel monkeys (Merigan, 1976), and galagos (Langston et al., 1986). **B:** Other mammals, including the CSFs from cats (Blake et al., 1974), ground squirrels (Jacobs et al., 1980), opossums (Silveira et al., 1982), tree squirrels (Jacobs et al., 1982), rabbits (Pak, 1984), tree shrews (Petry et al., 1984), tammar wallabies (Hemmi & Mark, 1998), rats (Keller et al., 2000), and seals (Hanke et al., 2011). **C:** Birds, including the CSFs from eagles (Reymond & Wolfe, 1981), woodpeckers (Ghim & Hodos, 2006), starlings (Ghim & Hodos, 2006), kestrels (Ghim & Hodos, 2006), pigeons (Ghim & Hodos, 2006), owls (Harmening et al., 2009), and chickens (Jarvis et al., 2009). **D:** Fish, including the CSFs from goldfish (Northmore & Dvorak, 1979) and sunfish (Northmore et al., 2007).

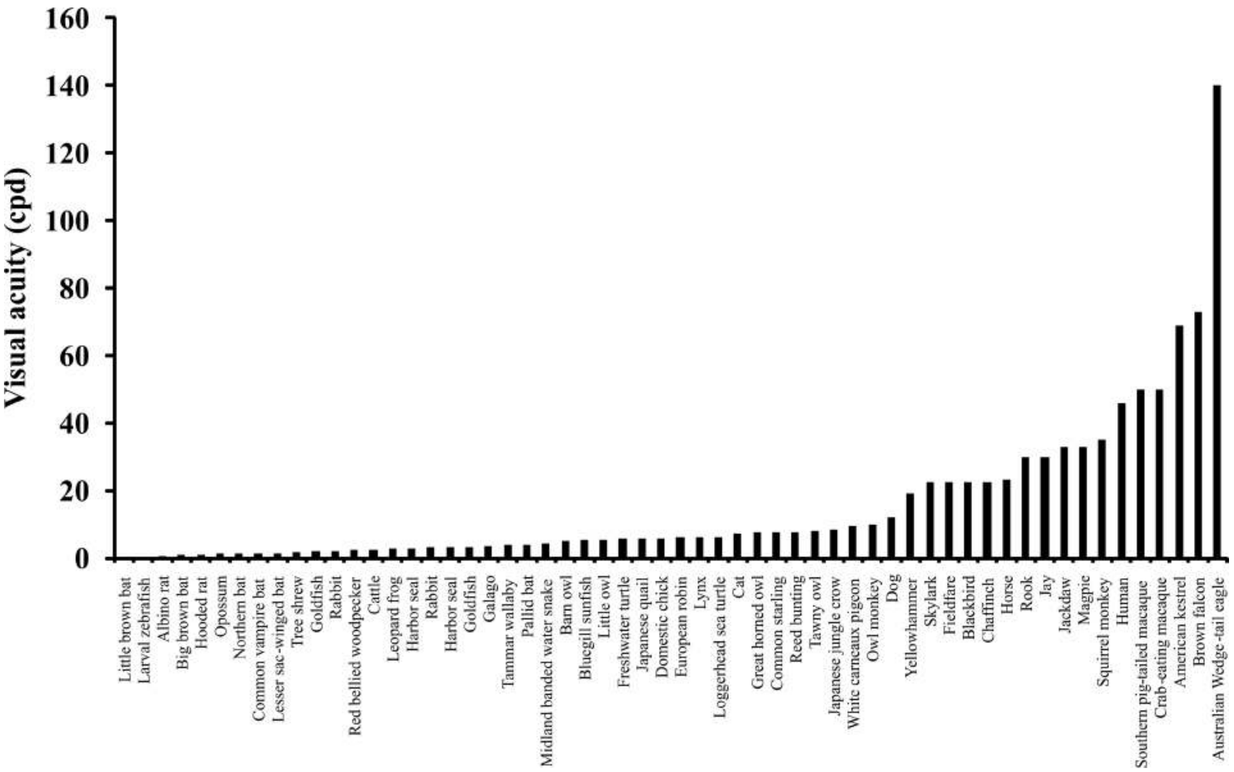

Figure 3. Crescent-ordered list of the visual acuity of different species. We estimated a mean value of visual acuity for species whose visual acuity was investigated in many studies under similar conditions. See Table 1 for references.

CSF in photopic conditions peaks at 2-6 cpd and falls off at low and high spatial frequencies. Visual acuity can reach 60 cpd using foveal vision.

Fundamental theory of the spatial luminance contrast sensitivity function

Some features of spatial CSFs are shared by all species. The CSFs described above show a spatial frequency range with high contrast sensitivity that decreases at lower and higher spatial frequencies. This band-pass profile of the function can be altered by other parameters, such as mean luminance and temporal frequency. Non-linear mechanisms involved in the receptive field at different levels of the visual system should be present in different species to generate similar CSF patterns.

Other features of the CSF are very different among species. They widely depend on the morphophysiological organization of the different visual systems. Some characteristics, such as eye optics, the photoreceptor mosaic, the density of retinal neurons, post-receptoral mechanisms, and the number of neurons at different stages of visual processing, have been selected in each species that together contribute to the generation of different contrast sensitivity peaks, spatial frequency peaks, and visual acuity (Hughes, 1977; Jacobs et al., 1982).

Figure 2 shows the CSFs of several species. We can observe the similar shapes and different positions of the contrast sensitivity and spatial frequency coordinates. Figure 3 shows a crescent order of visual acuity in different species. The data presented in Figure 3 show the average of several studies for each species under similar experimental conditions. The species with the highest visual acuity are bird raptors and primates. Both groups are diurnal, and they have very large eyes. Higher visual acuity can be supported in large eyes by spreading the image over a large number of receptors (Fite & Rosenfield-Welles, 1975; Hughes, 1977; Reymond, 1985; Ross, 2000; Schultz, 1940; Troilo, Howland, & Judge, 1993). In large eyes, the contrast of the image decreases, but this impairment is compensated for by the amount of light that enters the eyes of diurnal animals. Both groups also have high foveal neuronal densities (Andrade da Costa & Hokoç, 2000; Curcio, Sloan, Kalina, & Hendrikson, 1990; DeBruyn, Wise, & Casagrande, 1980; Fite & Rosenfield-Welles, 1975; Reymond, 1985; Troilo et al., 1993; Wikler, & Rakic, 1990; Yamada, Marshak, Silveira, & Casagrande, 1998; Yamada, Silveira, Perry, & Franco, 2001). This high visual acuity has been associated with the ability to locate prey or predators from long distances (Tisdale & Fernández-Juricic, 2009). Most primates have other adaptations, such as the absence of tapeta lucida, no vessels in the central retina, and short-wavelength filters that support high visual acuity (Dartnall et al., 1965; Martin, 1990). The specialization of the primate visual nervous system to detect small details is very significant. Even in nocturnal primates, such as the nocturnal pattern activity of the owl monkey (*Aotus*), visual acuity reaches approximately

10 cpd (Jacobs, 1977). Compared with other primates, owl monkeys have poor vision, but compared with other large-eye mammals, *Aotus* has better visual acuity or visual acuity that is as good as horses, cats, and even some diurnal birds. Another primate example of nervous system specialization is *Callithrix jacchus*. Even with small eyes, it has an estimated visual acuity of 30 cpd, which is higher than other mammals with larger eyes (Troilo et al., 1993). The visual acuity of *Callithrix* has not been estimated using behavioral methods, but rather from the microanatomy of the retina, which is similar to other primates and matches the behavioral results (Curcio et al., 1990; Andrade da Costa & Hokoç, 2000; Yamada et al., 2001).

Natural selection acts in the visual system to not only increase visual acuity. Visual acuity is only the maximum spatial frequency of detection at high contrast (i.e., the last point of CSF). Visual acuity likely co-evolves with other factors that are more important to the survival of the species. Many studies have associated visual acuity with other visual features that emphasize how other features converge to increase visual acuity (Kay & Kirk, 2000; Kiltie, 2000; Kirk & Kay, 2004). Other spatial frequencies could be ecologically more important than visual acuity in the recognition of other individuals from the same species or group or in finding prey or food in a low-contrast environment. The main spatial frequency range to be naturally selected would reasonably be the spatial frequency range of the CSF peak, and all other optical and neural changes may be associated with that selection. We tested the relationship between the spatial frequency of the CSF peak and visual acuity (Figure 4). We found a good correlation ($R^2 = .91$) using an exponential model, suggesting that both parameters may co-evolve. Small changes in the spatial frequency of the CSF peak are related to small changes in visual acuity until a range of 1-2 cpd for the spatial frequency of the CSF peak. After 1-2 cpd, the rate of change of visual acuity increases for each change in the spatial frequency of the CSF peak. Our analysis suggests that after the establishment of neural circuitry selected to be tuned for a spatial frequency, its high spatial frequency cut-off would also be automatically selected. The reason why the rate of change of visual acuity increases after a CSF peak at 1-2 cpd is still unclear. Other comparisons between the spatial frequency of the CSF peak and other optical and neural factors could be made to support our hypothesis.

Table 1 summarizes the data from the literature regarding the spatial frequency of the CSF peak, contrast sensitivity value at the CSF peak, and visual acuity. This table may be useful for the study of vertebrate contrast sensitivity.

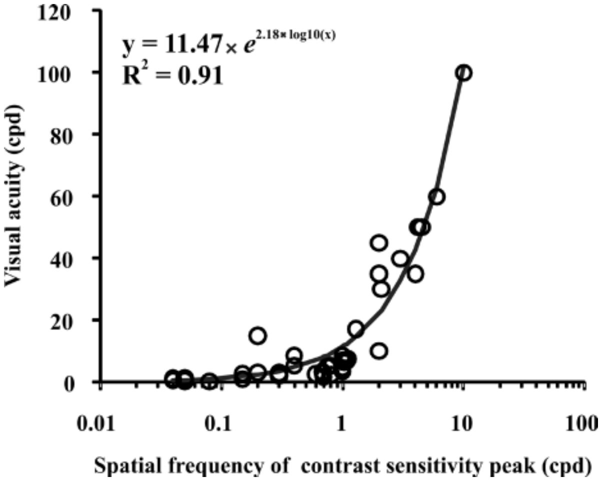

Figure 4. Correlation between the spatial frequency of the contrast sensitivity peak and visual acuity in the species listed in Table 1. The dataset is well described by an exponential function.

Table 1. Contrast sensitivity and visual acuity of different species studied by psychophysics, electrophysiology, and optokinetic responses.

Common name	Binomial nomenclature	Method	Peak Value (*)	Visual acuity (cpd)	Reference
Osteichthyes					
Goldfish	*Carassius auratus*	PsyPhy	40 (0.3)	2	Northmore & Dvorak, 1979
Goldfish	*Carassius auratus*	PsyPhy	100 (0.2)	3.2	Billota & Powers, 1991
-	*Asprotilapia leptura*	OKR	-	2.6	Dobberfuhl, Ullmann, & Shumway (2005)
-	*Xenotilapia spilotera*	OKR	-	0.59	Dobberfuhl et al. (2005)
-	*Xenotilapia flavipinnis*	OKR	-	0.59	Dobberfuhl et al. (2005)
Zebrafish (larval)	*Danio rerio*	OKR	(0.08)	0.3	Rinner et al., 2005

Table 1. *Continue*

Common name	Binomial nomenclature	Method	Peak Value (*)	Visual acuity (cpd)	Reference
Bluegill sunfish	*Lepomis macrochirus*	PsyPhy	40 (0.4)	5.25	Northmore et al., 2007
Zebrafish (larval)	*Danio rerio*	OKR	-	0.16	Haug et al., 2010
Amphibia					
Leopard frog	*Rana pipiens*	PsyPhy	-	2.8	Aho (1996)
Reptilia					
Freshwater turtle	*Pseudemys script elegans*	VECP	-	5.6	Northmore & Granda (1991)
Loggerhead sea turtle	*Caretta caretta*	VECP	-	6.1	Bartol et al. (2002)
Midland banded water snake	*Nerodia sipedon pleuralis*	VECP	-	4.25	Baker et al. (2007)
Aves					
Chick	*Gallus gallus domesticus*	PsyPhy	-	14	Johnson (1914)
Pigeon	*Columbia livia*	PsyPhy	-	14	Hamilton & Goldstein (1933)
Blackbird	*Turdus merula*	PsyPhy	-	22.5	Donner (1951)
Chaffinch	*Fringilla coelebs*	PsyPhy	-	22.5	Donner (1951)
European robin	*Erithacus rubeculus*	PsyPhy	-	6	Donner (1951)
Fieldfare	*Turdus pilaris*	PsyPhy	-	22.5	Donner (1951)
Reed bunting	*Emberiza schoeniclus*	PsyPhy	-	7.8	Donner (1951)
Skylark	*Aulada arvensis*	PsyPhy	-	22.5	Donner (1951)
Yellowhammer	*Emberiza citrinella*	PsyPhy	-	19.1	Donner (1951)
Pigeon	*Columbia livia*	PsyPhy	-	13	Blough (1971)
Great horned owl	*Bubo virginianus*	PsyPhy	-	7.5	Fite (1973)
Tawny owl	*Strix aluco*	PsyPhy	-	8	Martin & Gordon (1974)
Jackdaw	*Coloeus monedula*	-	-	33	Dabrowska (1975)
Jay	*Garrulus glandarius*	-	-	30	Dabrowska (1975)

Table 1. *Continue*

Common name	Binomial nomenclature	Method	Peak Value (*)	Visual acuity (cpd)	Reference
Magpie	*Pica pica*	-	-	33	Dabrowska (1975)
Rook	*Corvus frugileus*	-	-	30	Dabrowska (1975)
Australian wedge-tailed eagle	*Aquila audax*	PsyPhy	16 (10)	100	Reymond & Wolfe (1981)
Domestic chick	*Gallus gallus domesticus*	PsyPhy	-	1.5	Over & Moore (1981)
American kestrel	*Falco sparverius*	PsyPhy	-	40	Hirsch (1982)
Wedge-tailed eagle	*Aquila audax*	PsyPhy	-	140	Reymond (1985)
American kestrel	*Falco sparverius*	PsyPhy	-	160	Fox et al. (1976)
Brown falcon	*Falco berigora*	PsyPhy	-	73	Reymond (1987)
Little owl	*Athene noctua*	ERG	-	5	Porciatti et al. (1989)
Little owl	*Athene noctua*	VECP	-	6	Porciatti et al. (1990)
White Carneaux pigeon	*Columbia livia*	PsyPhy	-	16	Hodos et al. (1991)
Japanese quail	*Coturnix coturnix japonica*	PsyPhy	-	6.8	Hodos et al. (1991)
Pigeon	*Columbia livia*	ERG	-	18	Porciatti,Hodos, Signorini, & Bramanti (1991)
Japanese quail	*Coturnix coturnix japonica*	ERG	7 (1)	4.5	Lee et al. (1997)
White leghorn new domestic chick	*Gallus gallus domesticus*	OKR	10 (1)	8.6	Schmid, & Wildsoet (1998)
Japanese jungle crow	*Corvus macrorhyncos*	PsyPhy	-	8.4	Yamamoto et al. (2001)
White Carneaux pigeon	*Columbia livia*	ERG	4.6 (0.68)	3.31	Hodos et al. (2002)
White Carneaux pigeon	*Columbia livia*	PsyPhy	9.9 (0.81)	5.23	Hodos et al. (2002)
American kestrel	*Falco sparverius*	ERG	-	46	Gaffney & Hodos (2003)
American kestrel	*Falco sparvarius*	ERG	10.7 (2.09)	30.1	Ghim & Hodos (2006)
Barn owl	*Tyto alba*	ERG	6 (1.08)	6.98	Ghim & Hodos (2006)
Common starling	*Sturnus vulgaris*	ERG	6.2 (1.11)	7.56	Ghim & Hodos (2006)

Table 1. *Continue*

Common name	Binomial nomenclature	Method	Peak Value (*)	Visual acuity (cpd)	Reference
Japanese quail	*Coturnix coturnix japonica*	ERG	9.8 (1.03)	6.38	Ghim & Hodos (2006)
Red-bellied Woodpecker	*Melanerpes carolinus*	ERG	6.7 (0.81)	2.29	Ghim & Hodos (2006)
White Carneaux Pigeon	*Columbia livia*	ERG	8 (1.29)	17.17	Ghim & Hodos (2006)
Barn owl	*Tyto alba pranticola*	PsyPhy	12 (1)	3.43	Harmening et al. (2009)
Domestic chick	*Gallus gallus domesticus*	PsyPhy	-	6.5	Gover et al. (2009)
Domestic chick	*Gallus gallus domesticus*	PsyPhy	10 (1)	7	Jarvis et al. (2009)
Mammalia					
Capuchin monkey	*Cebus monkey*	PsyPhy	-	63	Johnson (1914)
Pigmented rat	*Ratus novergicus*	PsyPhy	-	1.7	Lashley (1930)
Albino rat	*Rattus novergicus*	PsyPhy	-	0.57	Lashley (1930)
Chimpanzee	*Pan trogloditys*	PsyPhy	-	65	Spence (1934)
Rhesus monkey	*Macaca mulatta*	PsyPhy	-	67	Weinstein & Grether (1940)
Human	*Homo sapiens*	PsyPhy	200 (6)	60	Campbell, & Green (1965a)
Human	*Homo sapiens*	PsyPhy	200 (3)	40	Robson (1966)
Lesser sac-winged Bat	*Saccopteryx leptura*	PsyPhy	-	1.43	Suthers (1966)
Little brown bat	*Myotis lucifugus*	PsyPhy	-	0.17	Suthers (1966)
Stumptail macaque	*Macaca arctoides*	PsyPhy	-	42.8	Yarczower, Wolbarsht, Galloway, Fligsten, & Malcolm (1966)
Rhesus macaque	*Macaca mulatta*	PsyPhy	-	53	Cowey & Ellis (1967)
Rabbit	*Oryctolagus cuniculus*	PsyPhy	-	6	Van Hof (1967)
Deermice	*Peromyscus californicus*	PsyPhy	-	1.57	Rahmann, Rahman, & King (1968)
Deermice	*Peromyscus maniculatus gracilis*	PsyPhy	-	1.5	Rahmann et al. (1968)

Table 1. *Continue*

Common name	Binomial nomenclature	Method	Peak Value (*)	Visual acuity (cpd)	Reference
Deermice	*Peromyscus maniculatus bairdii*	PsyPhy	-	1.25	Rahmann et al. (1968)
Deermice	*Peromyscus polionotus*	PsyPhy	-	0.5	Rahmann et al. (1968)
Deermice	*Peromyscus floridanus*	PsyPhy	-	0.9	Rahmann et al. (1968)
Human	*Homo sapiens*	PsyPhy	550 (2)	45	Campbell & Robson (1968)
Human	*Homo sapiens*	VECP	250 (2)	35	Campbell & Maffei (1970)
Harbor seal	*Phoca vitulina*	PsyPhy	-	3.6	Schusterman & Balliet (1970a)
Stellar sea lion	*Eumetopias jubata*	PsyPhy	-	4.2 (underwater)	Schusterman & Balliet (1970a)
California sea lion	*Zalophus californicus*	PsyPhy	-	5.7	Schusterman & Balliet (1970b)
Asian clawless otter	*Amblionyx cinerea*	PsyPhy	-	2.2	Balliet & Schusterman (1971)
Pacific white-sided dolphin	*Lagenorrhyncus obliquidens*	PsyPhy	-	5	Spong & White (1971)
Killer whale	*Orcinus orca*	PsyPhy	-	11	White, Cameron, Spong, & Bradford (1971)
Cat	*Felis catus*	VECP	-	4.5	Berkley & Watkins (1973)
Cat	*Felis catus*	VECP	120 (0.2)	15	Campbell et al. (1973)
Bottlenose dolphin	*Tursiops truncates*	PsyPhy	-	3.3	Pepper & Simmons (1973)
Cat	*Felis catus*	PsyPhy	-	6	Blake et al. (1974)
Crab-eating macaque	*Macaca fascicularis*	PsyPhy	100 (4.2)	50	De Valois et al. (1974)
Human	*Homo sapiens*	PsyPhy	200 (4.5)	50	De Valois et al. (1974)
Mink	*Mustela vison*	PsyPhy	-	4 (air) 1.93 (underwater)	Sinclair, Dunstone, & Poole (1974)
Bottlenose dolphin	*Tursiops truncatus*	PsyPhy	-	2.5 (air) 3.8 (water)	Herman, Peacock, Yunker, & Madsen (1975)
Cat	*Felis catus*	PsyPhy	-	9	Jacobson, Franklin, & McDonald (1976)
Common vampire bat	*Desmodus rotundus*	PsyPhy	-	1.25	Manske & Schmidt (1976)

Table 1. *Continue*

Common name	Binomial nomenclature	Method	Peak Value (*)	Visual acuity (cpd)	Reference
Squirrel monkey	*Saimiri sciureus*	PsyPhy	150 (4)	35	Merigan (1976)
Pigmented rat	*Rattus novergicus*	PsyPhy	-	0.5	Wiesenfeld, & Branchek (1976)
Owl monkey	*Aotus trivirgatus*	PsyPhy	90 (2)	10	Jacobs (1977)
Cat	*Felis catus*	VECP	120 (0.4)	8.5	Harris (1978)
Albino rat	*Rattus novergicus*	PsyPhy	11 (0.05)	0.4	Birch & Jacobs (1979)
Pigmented rat	*Rattus novergicus*	PsyPhy	25 (0.05)	1.2	Birch & Jacobs (1979)
House mouse	*Mus musculus*	OKR	0.91 (0.125)	0.5	Sinex et al. (1979)
Golden hamster	*Mesocricetus auratus*	PsyPhy	-	0.35	Emerson (1980)
California ground squirrel	*Speromphilus beecheyi*	PsyPhy	- (0.7)	4 cpd	Jacobs et al. (1980)
Rabbit	*Oryctolagus cuniculus*	PsyPhy	-	2	Vaney (1980)
Ring-tailed lemur	*Lemur catta*	PsyPhy	-	7 cpd	Neuringer, Kosobud, & Cochrane (1981)
Cat	*Felis catus*	PsyPhy	60 (0.6)	2.6	Pasternak & Merigan (1981)
Tree squirrel	*Sciurus griseus* *Sciurus niger* *Sciurus carolensis*	PsyPhy	30 (0.5)	3.8	Jacobs et al. (1982)
Opossum	*Didelphis marsupialis*	VECP	8 (0.05)	1.25	Silveira et al. (1982)
Meerkat	*Suricata suricata*	PsyPhy	-	6.3	Moran, Timney, Sorensen, & Desrochers (1983)
Dog	*Canis lupus familiaris*	VECP	-	12.59	Odom, Bromberg, & Dawson (1983)
Dog	*Canis lupus familiaris*	ERG	-	11.61	Odom et al. (1983)
Rabbit	*Oryctolagus cuniculus*	VECP	100 (0.3)	3	Pak (1984)
Tree shrew	*Tupaia belangeri*	PsyPhy	9 (0.7)	1.8	Petry et al. (1984)
Human	*Homo sapiens*	PsyPhy	250 (2)	35	Mullen (1985)
Big brown bat	*Eptesicus fuscus*	PsyPhy	-	1	Bell, & Fenton (1986)
Pallid bat	*Antrozous pallidus*	PsyPhy	-	4	Bell, & Fenton (1986)

Table 1. *Continue*

Common name	Binomial nomenclature	Method	Peak Value (*)	Visual acuity (cpd)	Reference
Greater galago	*Galago crassicaudatus*	PsyPhy	120 (0.75)	5	Langston et al. (1986)
Bush baby	*Otolemur crassicaudatus*	PsyPhy	-	6	Langston et al. (1986)
Northern native cat	*Dasyurus hallucatus*	PsyPhy	-	2.8	Harman, Nelson, Crewther, & Crewther (1986)
Greater galago	*Galago crassicaudatus*	VECP	35 (0.3)	2.3	Bonds et al. (1987)
Lesser galago	*Galago senegalensi*	VECP	35 (0.3)	2.3	Bonds et al. (1987)
Pigmented rat	*Rattus novergicus*	VECP	30 (0.04)	1.18	Silveira et al. (1987)
Lynx	*Lynx europea*	VECP	-	6	Maffei, Fiorentini, & Bisti (1990)
Horse	*Equus ferus caballus*	PsyPhy	-	23.3	Timney & Keil (1992)
Tammar wallaby	*Macropus eugenii*	VECP	60 (0.15)	2.7	Hemmi & Mark (1998)
Tammar wallaby	*Macropus eugenii*	PsyPhy	-	4.8	Hemmi & Mark (1998)
Albino rat	*Rattus novergicus*	VECP	20 (0.04)	0.48	Tejada & Tedó (1998)
Hooded rat	*Rattus novergicus*	PsyPhy	6.3 (0.15)	0.9	Keller et al. (2000)
Long Evans rat	*Rattus novergicus*	PsyPhy	-	1	Prusky et al. (2000)
Cattle	*Bos primigenius*	PsyPhy	-	2.6	Rehkämper et al. (2000)
Bactrian camel	*Camelus bactrius*	PsyPhy	-	10	Harman, Dann, Ahmat, Macuda, Johnston, & Timney (2001)
Northern bat	*Eptesicus nilssonii*	PsyPhy	-	1.25	Rydell & Eklöf (2003)
Harbor seal	*Phoca vitulina*	OKR	-	2.9	Hanke, Kröger, Siebert, & Dehnhardt (2008)
Pig	*Sus domestica*	PsyPhy	-	0.03	Zonderland, Cornelissen, Wolthuis-Fillerup, & Spoolder (2008)
Blue-eyed black lemur	*Eulemur macaco flavifrons*	PsyPhy	-	5.1	Veilleux, & Kirk (2009)
Harbor seal	*Phoca vitulina*	PsyPhy	40 (0.7)	3	Hanke et al. (2011)

Note: * Contrast sensitivity peak value at the spatial frequency indicated between brackets in cycles per degree. PsyPhy, data obtained using psychophysics. OKR , data obtained by recording of the optokinetic motor response. VECP, data obtained by recording the visually evoked cortical potential pattern. ERG, data obtained by recording the pattern electroretinogram.

Acknowledgements

The authors dedicate this work to Eduardo Oswaldo Cruz, physician, physiologist, and visual neuroscientist, who was awarded the 2009 Brazilian Neuroscience Medal. Supported by: FINEP IBN Net; CNPq-PRONEX/FAPESPA #2268 and #316799/2009; CNPq #476744/2009-1, #620037/2008-3, and #475860/2010-1; and CAPES-PROCAD #182/2007. LCLS is a CNPq research fellow. LCLS would like to thank Eduardo Oswaldo Cruz, who guided him through the first steps of his scientific career and taught him all that matters about Physiological Optics and Visual Neuroscience.

References

Aho, A.C. (1997). The visual acuity of the frog (*Rana pipiens*). *Journal of Comparative Physiology A*, *180*, 19-24.

Andrade da Costa, B.L.S, & Hokoç, J.N. (2000). Photoreceptor topography of the retina in the New World Monkey *Cebus apella*. *Vision Research*, *40*, 2395-2409.

Arnulf, A., & Dupuy, O. (1960). La transmission des contrastes par le systeme optique de l'oeil et les seuils des contrastes retiniens. *Comptes Rendue de L'Academie des Sciences Paris*, *250*, 2757-2759.

Atkinson, J., & Campbell, F.W. (1974). The effect of phase on the perception of compound gratings. *Vision Research*, *14*, 159-162.

Bain, R., & Kulikowski, J.J. (1976). Contrast thresholds for pattern and movement detection evaluated by evoked potentials. *Journal of Physiology (London)*, *259*, 34P-35P.

Baker, R.A., Gawne, T.J., Loop, M.S., & Pullman, S. (2007). Visual acuity of the midland banded water snake estimated from evoked telencephalic potentials. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, *193*, 865-870.

Balliet, R.F., & Schusterman, R.J. (1971). Underwater and aerial visual acuity in the Asian "clawless" otter (*Amblionyx cineria cineria*). *Nature*, *234*, 305-306.

Bartol, S.M., Musick, J.A., & Ochs, A.L. (2002). Visual acuity thresholds of juvenile loggerhead sea turtles (*Caretta caretta*): an electrophysiolocal approach. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, *187*, 953-960.

Bell, G.P., & Fenton, M.B. (1986). Visual acuity, sensitivity and binocularity in a gleaning insectivorous bat, *Macrotus californicus* (Chiroptera: Phyllostomidae). *Animal Behaviour*, 34, 409-414.

Berkley, M.A., & Watkins, D.W. (1973). Grating resolution and refraction in the cat estimated from evoked cerebral potentials. *Vision Research*, *13*, 403-415.

Bilotta, J., & Powers, M.K. (1991). Spatial contrast sensitivity of goldfish: mean luminance, temporal frequency and a new psychophysical technique. *Vision Research*, *31*, 577-585.

Birch, D., & Jacobs, G.H. (1979). Spatial contrast sensitivity in albino and pigmented rats. *Vision Research*, *19*, 933-937.

Bisti, S., & Maffei, L. (1974). Behavioural contrast sensitivity of the cat in various visual medians. *Journal of Physiology (London)*, *241*, 201-210.

Blake, R. (1988). Cat spatial vision. *Trends in Neurosciences*, *11*, 78-83.

Blake, R., Cool, S.J., & Crawford, M.L.J. (1974). Visual resolution in the cat. *Vision Research*, *14*, 1211-1217.

Blakemore, C., & Campbell, F.W. (1969a). Adaptation to spatial stimuli. *Journal of Physiology (London)*, *200*, 11P-13P.

Blakemore, C., & Campbell, F.W. (1969b). On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. *Journal of Physiology (London)*, *203*, 237-260.

Blakemore, C., Carpenter, R.H., & Georgeson, M.A. (1970). Lateral inhibition between orientation detectors in the human visual system. *Nature*, *228*, 37-39.

Blough, P.M. (1971). The visual acuity of the pigeon for distant targets. *Journal of the Experimental Analysis of Behavior*, *15*, 57-67.

Blough, P.M., & Blough, D.S. (1989). Visual effects of opiates in pigeons: II. Contrast sensitivity to sinewave gratings. *Psychopharmacology*, *97*, 85-88.

Bonds, A.B., Casagrande, V.A., Norton, T.T., & DeBruyn, E.J. (1987). Visual resolution and sensitivity in a nocturnal primate (*Galago*) measured with visual evoked potentials. *Vision Research*, *27*, 845-857.

Campbell, F.W. (1983). Why do we measure contrast sensitivity? *Behavioural Brain Research*, *10*, 87-97.

Campbell, F.W., Cooper, G.F., & Enroth-Cugell, C. (1969). The spatial selectivity of the visual cells of the cat. *Journal of Physiology (London)*, *203*, 223-235.

Campbell, F.W., & Maffei, L. (1970). Electrophysiological evidence for the existence of orientation and size detectors in the human visual system. *Journal of Physiology (London)*, *207*, 635-652.

Campbell, F.W., & Green, D.G. (1965a). Optical and retinal factors affecting visual resolution. *Journal of Physiology (London)*, *181*, 576-593.

Campbell, F.W., & Green, D.G. (1965b). Monocular versus binocular visual acuity. *Nature*, *208*, 191-192.

Campbell, F.W., & Gregory, A.H. (1960a). Effect of size of pupil on visual acuity. *Nature*, *187*, 1121-1123.

Campbell, F.W., & Gregory, A.H. (1960b). The spatial resolving power of the human retina with oblique incidence. *Journal of the Optical Society of America*, *50*, 831.

Campbell, F.W., & Gubish, R.W. (1966). Optical quality of human eye. *Journal of Physiology (London)*, *186*, 558-578.

Campbell, F.W., Howell, E.R., & Robson, J.G. (1971). The appearance of gratings with and without the fundamental Fourier component. *Journal of Physiology (London)*, *217*, 17P-18P.

Campbell, F.W., & Kulikowski, J.J. (1966). Orientational selectivity of the human visual system. *Journal of Physiology (London)*, *187*, 437-445.

Campbell, F.W., Kulikowski, J.J., & Levinson, J. (1966). The effect of orientation on the visual resolution of gratings. *Journal of Physiology (London)*, *187*, 427-436.

Campbell, F.W., & Kulikowski, J.J. (1971). Electrophysiological measure of the psychophysical contrast threshold. *Journal of Physiology (London)*, *217*, 54P-55P.

Campbell, F.W., & Kulikowski, J.J. (1972). Visual evoked potential as a function of contrast of a grating pattern. *Journal of Physiology (London)*, *222*, 345-356.

Campbell, F.W., & Maffei, L. (1974). Contrast and spatial frequency. *Scientific American*, *231*, 106-114.

Campbell, F.W., Maffei, L., & Piccolino, M. (1973). The contrast sensitivity of the cat. *Journal of Physiology (London)*, *229*, 719-731.

Campbell, F.W., Nachmias, J., & Jukes, J. (1970). Spatial-frequency discrimination in human vision. *Journal of the Optical Society of America*, *60*, 555-559.

Campbell, F.W., & Robson, J.G. (1968). Application of Fourier analysis to the visibility of gratings. *Journal of Physiology (London)*, *197*, 551-566.

Cowey, A., & Ellis, C.M. (1967). Visual acuity of rhesus and squirrel monkeys. *Journal of Comparative and Physhiological Psychology*, *64*, 80-84.

Cowey, A., Henken, D.B., & Perry, V.H. (1982). Effects on visual acuity of neonatal or adult tectal ablation in rats. *Experimental Brain Research*, *48*, 149-152.

Curcio, C.A., Sloan, K.R., Kalina, R.E., & Hendrikson, A.E. (1990). Human photoreceptor topography. *Journal of Comparative Neurology*, *292*, 497-523.

Dabrowska, B. (1975). Investigations on visual acuity of some corvine species. *Folia Biologica*, *23*, 311-332.

Dartnall, H.J.A., Arden, G.B., Ikeda, H., Luck, C.P., Rosenberg, M.E., Pedler, C.M.H., & Tansley (1965). Anatomical, electrophysiological and pigmentary aspects of vision in the bush baby: an interpretative study. *Vision Research*, *5*, 399-424.

Dean, P. (1981). Visual pathways and acuity in hooded rats. *Behavioural Brain Research*, *3*, 239-271.

DeBruyn, E.J., Wise, V.L., & Casagrande, V.A. (1980). The size and topographic arrangement of retinal ganglion cells in the galago. *Vision Research*, *20*, 315-327.

De Valois, R.L., & De Valois, K.K. (1980). Spatial vision. *Annual Review of Psychology*, *31*, 309-341.

De Valois, R.L., Morgan, H., & Snodderly, D.M. (1974). Psychophysical studies of monkey vision: 3. Spatial luminance contrast sensitivity tests of macaque and human observers. *Vision*

Research, *14*, 75-81.

Donner, K. (1951). The visual acuity of some passerine birds. *Acta Zoologica Fennica*, *66*, 3-33.

Dobberfuhl, A.P., Ullmann, J.F., & Shumway, C.A. (2005). Visual acuity, environmental complexity, and social organization in African cichlid fishes. *Behavioral Neuroscience*, 119, 1648-1655.

Emerson, V.F. (1980). Grating acuity of the golden hamster: the effects of stimulus orientation and luminance. *Experimental Brain Research*, *38*, 43-52.

Enroth-Cugell, C., & Robson, J.G. (1966). The contrast sensitivity of retinal ganglion cells of the cat. *Journal of Physiology (London)*, *187*, 517-552.

Fite, K.V. (1973). Anatomical and behavioral correlates of visual acuity in the Great Horned Owl. *Vision Research*, 13, 219-230.

Fite, K.V., & Rosenfield-Wessels, S. (1975). A comparative study of deep avian foveas. *Brain, Behavior and Evolution*, *12*, 97-115.

Flamant, F. (1955). Étude de la répartition de lumière dans l'image rétinienne d'une fente. *Revue d'Optique, Théorique et Instrumentale*, *34*, 433-459.

Fox, R., Lehmkuhle, S.W., & Westendorf, D.H. (1976). Falcon visual acuity. *Science*, *192*, 263-265.

Gaffney, M.F., & Hodos, W. (2003). The visual acuity and refractive state of the American kestrel (*Falco sparverius*). *Vision Research*, *43*, 2053-2059.

Ghim, M.M., & Hodos, W. (2006). Spatial contrast sensitivity of birds. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, *192*, 523-534.

Goodman, J.W. (2005). *Introduction to Fourier Optics*. Englewood, CO: Roberts & Company.

Gover, N., Jarvis, J.R., Abeyesinghe, S.M., & Wathes, C.M. (2009). Stimulus luminance and the spatial acuity of domestic fowl (*Gallus g. domesticus*). *Vision Research*, *49*, 2747-2753.

Gubisch, R.W. (1967). Optical performance of the human eye. *Journal of the Optical Society of America*, *57*, 407-415.

Hamilton, W.F., & Goldstein, J.L. (1933). Visual acuity and accommodation in the pigeon. *Journal of Comparative Psychology*, *15*, 193-197.

Hanke, F. D., Kröger, R. H. H., Siebert, U, & Dehnhardt , G.(2008). Multifocal lenses in a monochromat: the harbour seal. *Journal of Experimental Biology,* 211, 3315–3322.

Hanke, F.D., Scholtyseek, C., Hanke, W., & Dehnhardt G. (2011). Contrast sensitivity in a harbor seal (*Phoca vitulina*). *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, *197*, 203-210.

Harman, A., Dann, J., Ahmat, A., Macuda, T., Johnston, K., & Timney, B. (2001). The retinal ganglion cell layer and visual acuity of the camel. *Brain, Behaviour and Evolution*, 58, 15-27.

Harman, A.M., Nelson, J.E., Crewther, S.G., & Crewther, D.P. (1986). Visual acuity of the northern native cat (*Dasyurus hallucatus*): behavioural and anatomical estimates. *Behavioural Brain Research*, *22*, 211-216.

Harmening, W.M, Nikolay, P., Orlowski, J., & Wagner, H. (2009). Spatial contrast sensitivity and grating acuity of barn owls. *Journal of Vision*, *9*, 13.

Harris, L.R. (1978). Contrast sensitivity and acuity of a conscious cat measured by the occipital evoked potential. *Vision Research*, *18*, 175-178.

Hartline, H.K. (1938). The response of single optic nerve fibers of the vertebrate eye to illumination of the retina. *American Journal of Physiology*, *121*, 400-415.

Hartline, H.K. (1940a). The receptive field of optic nerve fibers. *American Journal of Physiology*, *130*, 690-699.

Hartline, H.K. (1940b). The effects of spatial summation in the retina on the excitation of the fibers of the optic nerve. *American Journal of Physiology*, *130*, 700-711.

Hartline, H.K. (1940c). The nerve messages in the fibers of the visual pathway. *Journal of the Optical Society of America*, *30*, 239-247.

Haug, M.F., Biehlmaier, O., Mueller, K.P., & Neuhauss, C.F. (2010). Visual acuity in larval zebrafish: behavior and histology. *Frontiers in Zoology*, *7*, 1-8.

Hemmi, J.M., & Mark, R.F. (1998). Visual acuity, contrast sensitivity and retinal magnification in a marsupial, the tammar wallaby (*Macropus eugenii*). *Journal of Comparative Physiology A*, *183*, 379-387.

Herman, L.M., Peacock, M.F., Yunker, M.P., & Madsen, C.J. (1975). Bottle-nosed dolphin: double-slit pupil yields equivalent aerial and underwater diurnal acuity. *Science*, *189*, 650-652.

Himstedt, W. (1967). Experimentelle analyse der optischen sinnesleistungen im beutefangverhalten der einheimischert urodelen. *Zoologische Jahrbücher, Abteilung für Allgemeine Zoologie und Physiologie der Tiere, Jena*, *73*, 281-320.

Hirsch, J. (1982). Falcon visual sensitivity to grating contrast. *Nature*, 300, 57-58.

Hodos, W., Ghim, M.M., Potocki, A., Fields, J.N., & Storm, T. (2002). Contrast sensitivity in pigeons: a comparison of behavioral and pattern ERG methods. *Documenta Ophthalmologica*, *104*, 107-118.

Hodos, W., Miller, R.F., & Fite, K.V. (1991). Age-dependent changes in visual acuity and retinal morphology in pigeons. *Vision Research*, *31*, 669-677.

Hodos, W., Potocki, A., Ghim, M., & Gaffney, M. (2003). Temporal modulation of spatial contrast vision in pigeons (*Columba livia*). *Vision Research*, *43*, 761-767.

Hughes, A. (1977). The topography of vision in mammals of contrasting life style: comparative optics and retinal organization. In F. Crescitelli. (Ed.), *The visual system in vertebrates* (series title: *Handbook of sensory physiology*, vol. VII/5) (pp. 613-656). Berlin: Springer-Verlag.

Jacobs, G.H. (1977). Visual capacities of the owl monkey (*Aotus trivirgatus*): II. Spatial contrast sensitivity. *Vision Research*, *17*, 821-825.

Jacobs, G.H., Birch, D.G., & Blakeslee, B. (1982). Visual acuity and spatial contrast sensitivity in tree squirrels. *Behavioural Processes*, *7*, 367-375.

Jacobs, G.H., Blakeslee, B., McCourt, M.E., & Tootell, R.B.H. (1980). Visual sensitivity of ground squirrels to spatial and temporal luminance variations. *Journal of Comparative Physiology*, *136*, 291-299.

Jacobson, S.G., Franklin, K.B.J., & McDonald, W.I. (1976). Visual acuity of the cat. *Vision Research*, *16*, 1141-1143.

Jarvis, J.R., Abeyesinghe, S.M., McMahon, C.E., & Wathes, C.M. (2009). Measuring and modelling the spatial contrast sensitivity of the chicken (*Gallus g. domesticus*). *Vision Research*, *49*, 1448-1454.

Johnson, H.M. (1914). Visual pattern-discrimination in the vertebrates: II. Comparative visual acuity in dog, the monkey and the chick. *Journal of Animal Behavior*, *4*, 339-361.

Kay, R.F., & Kirk, E.C. (2000). Osteological evidence for the evolution of activity pattern and visual acuity in primates. *American Journal of Physical Anthropology*, *113*, 235-262.

Keller, J., Strasburger, H., Cerutti, D.T., & Sabel, B.A. (2000). Assessing spatial vision: automated measurement of the contrast-sensitivity function in the hooded rat. *Journal of Neuroscience Methods*, *97*, 103-110.

Kiltie, R.A. (2000). Scaling of visual acuity with body size in mammals and birds. *Functional Ecology*, *14*, 226-234.

King-Smith, P.E., & Kulikowski, J.J. (1973a). Lateral interaction in the detection of composite spatial patterns. *Journal of Physiology (London)*, *234*, 5P-6P.

King-Smith, P.E., & Kulikowski, J.J. (1973b). Spatial arrangement of the flicker and pattern detectors for a fine line. *Journal of Physiology (London)*, *234*, 33P-35P.

King-Smith, P.E., & Kulikowski, J.J. (1975). Pattern and flicker detection analysed by subthreshold summation. *Journal of Physiology (London)*, *249*, 519-548.

Kirk, E.C., & Kay, R.F. (2004). The evolution of high visual acuity in the Anthropoidea. In C. Ross & R.F. Kay (Eds.), *Anthropoid origins: new visions* (pp. 539-602). New York: Kluwer Academic/ Plenum.

Krauskopf, J. (1962). Light distribution in human retinal images. *Journal of the Optical Society of America*, *52*, 1046-1050.

Kulikowski, J.J. (1971a). Effect of eye movements on the contrast sensitivity of spatio-temporal patterns. *Vision Research*, *11*, 261-273.

Kulikowski, J.J. (1971b). Some stimulus parameters affecting spatial and temporal resolution of human vision. *Vision Research*, *11*, 83-93.

Kulikowski, J.J. (1978). Pattern and movement detection in man and rabbit: separation and comparison of occipital potentials. *Vision Research*, *18*, 183-189.

Kulikowski, J.J., Abadi, R., & King-Smith, P.E. (1973). Orientational selectivity of grating and line detectors in human vision. *Vision Research*, *13*, 1479-1486.

Kulikowski, J.J., & Campbell, F.W. (1971). Effect of varying the presentation time on the potential evoked by grating patterns.

Vision Research, *11*, 1202.

Kulikowski, J.J., & King-Smith, P.E. (1973). Spatial arrangement of line, edge and grating detectors revealed by subthreshold summation. *Vision Research*, *13*, 1455-1478.

Kulikowski, J.J., & Tolhurst, D.J. (1973). Psychophysical evidence for sustained and transient detectors in human vision. *Journal of Physiology (London)*, *232*, 149-162.

Langston, A., Casagrande, V.A., & Fox, R. (1986). Spatial resolution of the Galago. *Vision Research*, *26*, 791-796.

Lashley, K.S. (1930). The mechanism of vision: III. The comparative visual acuity of pigmented and albino rats. *Journal of Genetic Psychology*, *37*, 481-484.

Lashley, K.S. (1938). The mechanism of vision: XV. Preliminary studies of the rat's capacity for detail vision. *Journal of Comparative Psychology*, *18*, 123-193.

Lee, J.Y., Holden, L.A., & Djamgoz, M.B.A. (1997). Effects of ageing on spatial aspects of the pattern electroretinogram in male and female quail. *Vision Research*, *37*, 505-514.

Legg, C.R. (1984). Contrast sensitivity at low spatial frequencies in the hooded rat. *Vision Research*, *24*, 159-161.

Lettvin, J.Y., Maturana, H.R., McCulloch, W.S., & Pitts, W.H. (1959). What the frog's eye tells the frog's brain. *Proceedings of the Institute of Radio Engineers*, *47*, 1940-1951.

Linden, R., Cowey, A., & Perry, V.H. (1983). Tectal ablation at different ages in developing rats has different effects on retinal ganglion cell density but not on visual acuity. *Experimental Brain Research*, *51*, 368-376.

Maffei, L., & Campbell, F.W. (1970). Neurophysiological localization of the vertical and horizontal visual coordinates in man. *Science*, *167*, 386-387.

Maffei, L., Fiorentini, A., & Bisti, S. (1990). The visual acuity of the Lynx. *Vision Research*, 30, 527-528.

Manske, U., & Schmidt, U. (1976). Untersuchungen zur optischen usterunterscheidung bei der Vampirfledermaus, *Desmodus rotundus*. *Zeitschrift für Tierpsychologie*, *49*, 120.

Manteuffel, G., & Himstedt, W. (1978). The aerial and aquatic visual acuity of the optomotor response in the crested newt (*Triturus cristatus*). *Journal of Comparative Physiology A*, *128*, 359-365.

Martin, G.R., & Gordon, I.E. (1974). Visual acuity in the tawny owl (*Strix aluco*). *Vision Research*, *14*, 1393-1397.

Martin, R.D. (1990). *Primate origins and evolution: a phylogenetic reconstruction*. London: Chapman and Hall.

Merigan, W.H. (1976). The contrast sensitivity of the squirrel monkey (*Saimiri sciureus*). *Vision Research*, *16*, 375-379.

Merigan, W.H., Pasternak, T., & Zehl, D. (1981). Spatial and temporal vision of macaques after central retinal lesions. *Investigative Ophthalmology and Visual Science*, 21, 17-26.

Monroy, J.A., & Nishikawa, K. (2011). Prey capture in frogs: alternative strategies, biomechanical trade-offs, and hierarchical decision making. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*, *315A*, 61-71.

Moran, G., Timney, B., Sorensen, L., & Desrochers, B. (1983). Bionocular depth perception in the meerkat (*Suricatta Suricatta*). *Vision Research*, *23*, 965-969.

Mueller, K.P., & Neuhauss, C.F. (2010). Quantitative measurements of the optokinetic response in adult fish. *Journal of Neuroscience Methods*, *186*, 29-34.

Mullen, K.T. (1985). The contrast sensitivity of human colour vision to red-green and blue-yellow chromatic gratings. *Journal of Physiology (London)*, *359*, 381-400.

Navarro, R., Artal, P., & Williams, D.R. (1993). Modulation transfer of the human eye as a function of retinal eccentricity. *Journal of the Optical Society of America*, *10*, 201-212.

Neuringer, M., Kosobud, A., & Cochrane, G. (1981). Visual acuity of *Lemur catta*, a diurnal prosimian. *Investigative Ophthalmology and Visual Science*, *20*, 49.

Northmore, D.P.M., & Dvorak, C.A. (1979). Contrast sensitivity and acuity of the goldfish. *Vision Research*, *19*, 255-261.

Northmore, D.P., & Granda, A.M. (1991). Refractive state, contrast sensitivity, and resolution in the freshwater turtle, *Pseudemys scripta elegans*, determined by tectal visual-evoked potentials. *Visual Neuroscience*, *7*, 619-625.

Northmore, D.P.M., Oh, D.J., & Celenza, M.A. (2007). Acuity and contrast sensitivity of the bluegill sunfish and how they change during optic nerve degeneration. *Visual Neuroscience*, *24*, 319-331.

Nye, P.W. (1968). The binocular acuity of the pigeon measured in terms of the modulation transfer function. *Vision Research*, *8*, 1041-1053.

Odom, J.V., Bromberg, N.M., & Dawson, W.W. (1983). Canine visual acuity: retinal and cortical field potentials evoked by pattern stimulation. *American Journal of Physiology*, *245*, R637-R641.

Oswaldo-Cruz, E., Hokoç, J.N., & Sousa, A.P.B. (1979). A schematic eye for the opossum. *Vision Research*, *19*, 263-278.

Oswaldo-Cruz, E., Picanço-Diniz, C.W., & Silveira, L.C.L. (1982). Optical and neural factors involved in spatial resolution by the visual system of the opossum *Didelphis marsupialis*. *Proceedings of the Third Japan-Brazil Symposium on Science and Technology* (pp. 147-161). Tokyo.

Over, R., & Moore, D. (1981). Spatial acuity of the chicken. *Brain Research*, *211*, 424-426.

Owsley, C. (2003). Contrast sensitivity. *Ophthalmology Clinics of North America*, *16*, 171-177.

Pak, M.A. (1984). Ocular refraction and visual contrast sensitivity of the rabbit, determined by the VECP. *Vision Research*, *24*, 341-345.

Pasternak, T., & Merigan, W.H. (1981). The luminance dependence of spatial vision in the cat. *Vision Research*, *21*, 1333-1339.

Patel, A.S. (1966). Spatial resolution by the human visual system: the effect of mean retinal illuminance. *Journal of the Optical Society of America*, *56*, 689-694.

Pepper, R.L., & Simmons, J.V., Jr. (1973). In-air visual acuity of the bottlenose dolphin. *Experimental Neurology*, *41*, 271-276.

Petry, H.M., Fox, R., & Casagrande, V.A. (1984). Spatial contrast sensitivity of the tree shrew. *Vision Research*, *24*, 1037-1042.

Picanço-Diniz, C.W., Silveira, L.C.L., & Oswaldo-Cruz, E. (1983). Electrophysiological determination of the refractive state of the eye of the opossum. *Vision Research*, *23*, 867-872.

Pickett-Seltner, R.L., Sivak, J.G., & Pasternak, J.J. (1988). Experimentally induced myopia in chicks: morphometric and biochemical analysis during the first 14 days after hatching. *Vision Research*, *28*, 323-328.

Porciatti, V., Fontanesi, G., & Bagnoli, P. (1989). The electroretinogram of the little owl (*Athene noctua*). *Vision Research*, *29*, 1693-1698.

Porciatti, V., Fontanesi, G., Raffaelli, A., & Bagnoli, P. (1990). Binocularity in the little owl, *Athene noctua*: II. Properties of visually evoked potentials from the Wulst in response to monocular and binocular stimulation with sine wave gratings. *Brain, Behavior and Evolution*, *35*, 40-48.

Porciatti, V., Hodos, W., Signorini, G., & Bramanti, F.(1991) Electroretinographic changes in aged pigeons. *Visual Research,* 31 , 661-668.

Prusky, G.T., West, P.W.R., & Douglas, R.M. (2000). Behavioral assessment of visual acuity in mice and rats. *Vision Research*, *40*, 2201-2209.

Rahmann, H., Rahman, M., & King, J.A. (1968). Comparative visual acuity (minimum separable) in five species and subspecies of deermice (Peromyscus). *Physiological Zoology*, *41*, 298-313.

Regan, D. (2000). *Human perception of objects: early visual processing of spatial form defined by luminance, color, texture, motion, and binocular disparity*. Sunderland, MA: Sinauer Associates.

Rehkämper, G., Perrey, A., Werner, C.W., Opfermann-Rüngeler, C., & Görlach, A. (2000). Visual perception and stimulus orientation in cattle. *Vision Research*, *40*, 2489-2497.

Reymond, L. (1985). Spatial visual acuity of the eagle *Aquila audax*: a behavioural, optical and anatomical investigation. *Vision Research*, *25*, 1477-1491.

Reymond, L. (1987). Spatial visual acuity of the falcon, *Falco berigora*: a behavioural, optical and anatomical investigation. *Vision Research*, *27*, 1859-1874.

Reymond, L., & Wolfe, J. (1981). Behavioural determination of the contrast sensitivity function of the eagle *Aquila audax*. *Vision Research*, *21*, 263-271.

Rinner, O., Rick, J.M., & Neuhauss, C.F. (2005). Contrast sensitivity, spatial and temporal tuning of the larval zebrafish optokinetic response. *Investigative Ophthalmology and Visual Science*, *46*, 137-142.

Robson, J.G. (1966). Spatial and temporal contrast-sensitivity functions of the visual system. *Journal of the Optical Society of America*, *56*, 1141-1142.

Röhler, R. (1962). Die abbildungseigenschaften der augenmediern. *Vision Research*, *2*, 391-429.

Ross, C.F. (2000). Into the light: the origin of Anthropoidea. *Annual Review of Anthropology*, *29*, 147-194.

Rydell, J., & Eklöf, J. (2003). Vision complements echolocation in an aerial-hawking bat. *Naturwissenschaften*, *90*, 481-483.

Schade, O.H. (1956). Optical and photoelectric analog of the eye. *Journal of Optical Society of America*, *46*, 721-738.

Schmid, K.L., & Wildsoet, C.F. (1998). Assessment of visual acuity and contrast sensitivity in the chick using an optokinetic nystagmus paradigm. *Vision Research*, *38*, 2629-2634.

Schultz, A.H. (1940). The size of the orbit and the eye in primates. *American Journal of Physical Anthropology*, *26*, 389-408.

Schusterman, R.J., & Balliet, R.F. (1970a). Visual acuity of the harbour seal and Steller sea lion under water. *Nature*, *226*, 563-564.

Schusterman, R.J., & Balliet, R.F. (1970b). Conditioned vocalization as a technique for determining visual acuity thresholds in sea lions. *Nature*, *169*, 498-501.

Silveira, L.C.L. (1980) *Estudo eletrofisiológico da acuidade visual do Didelphis marsupialis aurita* (Dissertação de Mestre em Ciências). Programa de Pós-graduação em Ciências Biológicas, Instituto de Biofísica, Universidade Federal do Rio de Janeiro.

Silveira, L.C.L., Heywood, C.A., & Cowey, A. (1987). Contrast sensitivity and visual acuity of the pigmented rat determined electrophysiologically. *Vision Research*, *27*, 1719-1731.

Silveira, L.C.L., Picanço-Diniz, C.W., & Oswaldo-Cruz, E. (1982). Contrast sensitivity function and visual acuity of the opossum. *Vision Research*, *22*, 1371-1377.

Sinclair, W., & Dunstone, N., & Poole, T.B. (1974). Aerial and underwater visual acuity in the mink *mustela vison* schereber. *Animal Behaviour*, *22*, 965-974.

Sinex, D.G., Burdette, L.J., & Pearlman, A.L. (1979). A psychophysical investigation of spatial vision in the normal and reeler mutant mouse. *Vision Research*, *19*, 853-857.

Smith, K.U. (1936). Visual discrimination in the cat: IV. The visual acuity of the cat in relation to stimulus distance. *Journal of Genetic Psychology*, *49*, 297-313.

Spence, K.W. (1934). Visual acuity and its relation to brightness in chimpanzee and man. *Journal of Comparative Psychology*, *18*, 333-361.

Spong, P., & White, D. (1971). Visual acuity and discrimination learning in the dolphin (*Lagenorrrynchus obliquidens*). *Experimental Neurology*, *31*, 431-436.

Suthers, R.A. (1966). Optomotor responses by echolocating bats. *Science*, *152*, 1102-1104.

Tejada, P.H., & Tedó, C.M. (1998). Contrast sensitivity function of the albino rat determined electrophysiologically. *Spanish Journal of Psychology*, *1*, 11-17.

Timney, B., & Keil, K. (1992). Visual acuity in the horse. *Vision Research*, *32*, 2289-2293.

Tisdale, V., & Fernández-Juricic, E. (2009). Vigilance and predator detection vary between avian species with different visual acuity and coverage. *Behavioral Ecology*, *20*, 936-945.

Tolhurst, D.J. (1972a). Adaptation to square-wave gratings: inhibition between spatial frequency channels in the human visual system. *Journal of Physiology (London)*, *226*, 231-248.

Tolhurst, D.J. (1972b). On the possible existence of edge detector neurones in the human visual system. *Vision Research*, *12*, 797-804.

Tolhurst, D.J. (1973). Separate channels for the analysis of the shape and the movement of moving visual stimulus. *Journal of Physiology (London)*, *231*, 385-402.

Tolhurst, D.J., & Hart, G. (1972). A psychophysical investigation of the effects of controlled eye movements on the movement detectors of the human visual system. *Vision Research*, *12*, 1441-1446.

Troilo, D., Howland, H.C., & Judge, S.J. (1993). Visual optics and retinal cone topography in the commom marmoset (*Callithrix jacchus*). *Vision Research*, *33*, 1301-1310.

Van Hof, M.W. (1967). Visual acuity in the rabbit. *Vision Research*, *7*, 749-751.

Van Nes, F.L., & Bouman, M.A. (1967). Spatial modulation transfer in the human eye. *Journal of the Optical Society of America*, *57*, 401-406.

Vaney, D.I. (1980). The grating acuity of the wild European rabbit. *Vision Research*, *20*, 87-89.

Veilleux, C.C., & Kirk, E.C. (2009). Visual acuity in the cathemeral strepsirrhine *Eulemur macaco flavifrons*. *American Journal of Primatology*, *71*, 345-352.

Wallman, J. (1975). A simple technique using an optomotor response for visual psychophysical measurements in animals. *Vision Research*, *15*, 3-8.

Weiffen, M., Möller, B., Mauck, B., & Dehnhardt, G. (2006). Effect of water turbidity on the visual acuity of harbor seals (*Phoca vitulina*). *Vision Research*, *46*, 1777-1783.

Weinstein, B., & Grether, W.F. (1940). A comparison of visual acuity in the rhesus monkey and man. *Comparative Psychology*, *30*, 187-195.

Westheimer, G. (1960). Modulation thresholds for sinusoidal light distributions on the retina. *Journal of Physiology*, *152*, 67-74.

Westheimer, G. (1963). Optical and motor factors in the formation of the retinal image. *Journal of the Optical Society of America*, *53*, 86-93.

Westheimer, G. (1978). Spatial phase sensitivity for sinusoidal grating targets. *Vision Research*, *18*, 1073-1074.

Westheimer, G., & Campbell, F.W. (1962). Light distribution in the image formed by living human eye. *Journal of the Optical Society of America*, *52*, 1040-1045.

White, D.O., Cameron, N., Spong, P., & Bradford, J. (1971). Visual acuity of the killer whale (*Orcinus orca*). *Experimental Neurology*, *32*, 230-236.

Wiesenfeld, Z., & Branchek, T. (1976). Refractive state and visual acuity in the hooded rat. *Vision Research*, 16, 823-827.

Wikler, K.C., & Rakic, P. (1990). Distribution of photoreceptor subtypes in the retina of diurnal and nocturnal primates. *Journal of Neuroscience*, *10*, 3390-3401.

Wood, I.C., & Kulikowski, J.J. (1978). Pattern and movement detection in patients with reduced visual acuity. *Vision Research*, *18*, 331-334.

Yamada, E.S., Marshak, D.W., Silveira, L.C.L., & Casagrande, V.A. (1998). Morphology of P and M retinal ganglion cells of the bush baby. *Vision Research*, *38*, 3345-3352.

Yamada, E.S., Silveira, L.C.L., Perry, V.H., & Franco, E.C.S. (2001). M and P retinal ganglion cells of the owl monkey: morphology, size and photoreceptor convergence. *Vision Research*, *41*, 119-131.

Yamamoto, K., Furuya, I., & Watanabe, S. (2001). Near-field acuity in Japanese jungle crows (*Corvus macrorynchos*). *Physiology and Behavior*, *72*, 283-286.

Yarczower, M., Wolbarsht, M.L., Galloway, W.D., Fligsten, K.E., & Malcolm, R. (1966). Visual acuity in stumptail macaque. *Science*, *152*, 1392-1393.

Zonderland, J.J., Cornelissen, L., Wolthuis-Fillerup, M., & Spoolder, H.A.M. (2008). Visual acuity of pigs at different light intensities. *Applied Animal Behaviour Science*, *111*, 28-37.