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Measuring and modelling the spatial contrast sensitivity of the chicken (*Gallus g. domesticus*)

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ABSTRACT

The spatial contrast sensitivity (CSF) of the chicken has been measured using a behavioural technique. The results obtained show that spatial vision in this species is relatively poor compared with the human observer. For a visual stimulus luminance of 16 cd m^{-2}, the upper frequency limit of spatial vision in the chicken (acuity) was found to be about 7.0 c deg^{-1}, with peak spatial vision occurring at around 1.0 c deg^{-1}. Under equivalent stimulus conditions, the acuity of the human is around 50 c deg^{-1} with a peak in spatial vision at about 3.0 c deg^{-1}. Peak spatial contrast sensitivity in the chicken was also found to be only about 2% that for the human. At a lower stimulus luminance of 0.1 cd m^{-2}, the chicken CSF reduced in overall magnitude and indicated an acuity level of about 5.0 c deg^{-1}. These experimental results were successfully modelled using modulation transfer (MTF) theory. This theoretical treatment enabled important neural mechanisms underlying spatial vision in the chicken to be revealed. The role played by spatial vision in the chicken's ability to recognise detailed shapes in its visual environment was also examined by deploying the CSF as a visual weighting function with the Fourier series of a chicken comb.

1. Introduction

Chicken vision has been the subject of a number of detailed studies due to the importance of this species as an animal model in biomedical research. From an animal welfare perspective, a basic knowledge of visual sensing capabilities is of interest in the understanding of how an animal will react to conspecifics when reared intensively and under artificial lighting schemes (Prescott, Jarvis, & Wathes, 2004; Prescott, Wathes, & Jarvis, 2003).

Of the three basic characteristics of the visual system (spectral, spatial and temporal sensitivity), spectral sensitivity and its impact on the calculation of luminous flux has now been well quantified in the chicken (Prescott & Wathes, 1999; Saunders, Jarvis, & Wathes, 2008; Wortel, Rugenbrink, & Nuboer, 1987). Associated retinal mechanisms subserving colour vision have also been identified (Osorio, Vorobyev, & Jones, 1999). Optical performance particularly with respect to the formation of aberrations during chicken eye growth, has also been studied (Garcia de la Cera, Rodriguez de Castro, Merayo, & Marcos, 2007; Garcia de la Cera, Rodriguez, & Marcos, 2006; Kisilak, Campbell, Hunter, Irving, & Huang, 2006). In the chicken, pupil size varies with level of ambient illumination (Li & Howland, 1999; Schaeffel, Howland, & Farkas, 1986) leading to changes in both retinal illuminance and optical quality of the retinal image (Coletta, Marcos, Wildsoet, & Troilo, 2003). A variation in pupil size with stimulus luminance is well documented in human observers (see for example, Le Grand, 1968) and is primarily mediated by midbrain pathways (Erichsen, Hodos, & Evinger, 2000). In both chickens and humans, pupil responses can also be induced by changes in stimulus features such as spatial structure and colour (Barbur, Prescott, Douglas, Jarvis, & Wathes, 2002). Temporal vision in the chicken has been examined using a psychophysical technique for the determination of temporal contrast sensitivity and the formulation of a mechanistic model of underlying neural mechanisms (Jarvis, Prescott, & Wathes, 2003; Jarvis, Taylor, Prescott, Meeks, & Wathes, 2002). Spatial vision as quantified by visual acuity, has been the subject of a number of studies, but these have produced conflicting results. Values of acuity for the chicken have been cited as 1.5 c deg^{-1} (Over & Moore, 1981), 4–6 c deg^{-1} (DeMello, Foster, & Temple, 1992) and 7 c deg^{-1} calculated by DeMello et al. (1992) from Johnsen (1914).

As a metric, acuity provides only partial information since it reveals just the upper limit or resolving power in spatial vision. To understand more fully sensitivity to a structured visual scene, the spatial contrast sensitivity function (CSF) should be measured. This function, as determined from the threshold detection of spatial sine-wave gratings, has now become a common indicator of the ability of the vertebrate system to process spatial frequency information (De Valois & De Valois, 1990; Jarvis & Wathes, 2007, 2008; Regan, 1991). Moreover it can provide information on the

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relative sensitivity to shape, form and detail in a real scene if this is described in Fourier space (Topfer & Jacobson, 1993).

In human vision, there have been many experimental determinations of the CSF, covering a wide range of stimulus sizes, angular orientations and luminance levels. Barten (1999) has provided a useful review of the majority of these studies. CSF has also been measured in non-human subjects using both electrophysiological and behavioural techniques. Species examined are far ranging, including cat (Pasternak & Merigan, 1981), rat (Birch & Jacobs, 1979), macaque (De Valois, Morgan, & Snodderley, 1974), goldfish (Bilotta & Powers, 1991) and a range of avian species (Ghim & Hodos, 2006; Hodos, 1993). Reviews of the majority of these animal studies are available (Ghim & Hodos, 2006; Jarvis & Wathes, 2008; Uhlrich, Essock, & Lehmkuhle, 1981).

To-date, the CSF has not been fully quantified for the chicken, although some measurements have been determined using a nystagmus paradigm (Diether, Gekeler, & Schaeffel, 2001; Diether & Schaeffel, 1999; Schmid & Wildsoet, 1998). The amount of data is, however, limited to only a few spatial frequencies and no firm conclusions can be drawn regarding the shape or magnitude of the CSF.

This paper reports an investigation of the spatial contrast sensitivity of the chicken using a psychophysical operant method. Through use of the mechanistic modelling approach described elsewhere (Jarvis & Wathes, 2007, 2008), basic neural processing factors which determine contrast sensitivity and acuity are quantified and compared with those for the human. As an example of how the modelling can be used to indicate the perception of real scenes, the likely distance range that a chicken comb structure is visible to another bird is calculated. This is achieved by weighting the Fourier components of a triangular spatial waveform with the chicken CSF.

2. Materials and methods

2.1. Subjects

Seven, adult female domestic chickens (approximately 12 months old, Hy-Line strain) were used in the experiment. They were housed as a flock in a naturally ventilated barn, and natural daylight was supplemented by fluorescent lamps to produce an illuminance of approximately 200 lux on a 16 h (light): 8 h (dark) diurnal cycle. Birds were fed *ad libitum* on commercial layer pellets. Prior to experimentation, refractive error was measured by retinoscopy. After correction for both working distance and eye size (Glickstein & Millidot, 1970), the refraction of each animal was shown to be within 1D of emmetropia.

2.2. Operant apparatus, stimulus presentation and control

The apparatus, shown schematically in Fig. 1, consisted of an instrumented cage similar to that used previously in the determination of chicken temporal contrast sensitivity (Jarvis et al., 2002). On one side of the cage were two clear Perspex panels (13 × 10.5 cm) each 400 mm from the floor and separated by 140 mm. The panels were hinged at the top so that a chicken peck on them triggered a response key. Movement of the key was registered as a peck response by a linked PC via a circuit break. The Perspex was cleaned regularly between operating sessions and no significant pecking damage occurred during experimentation. A small feed trough was positioned centrally between the two pecking panels. Food (maggots) could be delivered to the feed trough via an enclosed and motorised conveyor that could be operated manually or controlled by computer software.

A computer monitor (SONY Trinitron Multiscan E100) was positioned at a distance of 40 cm behind each pecking panel. Each

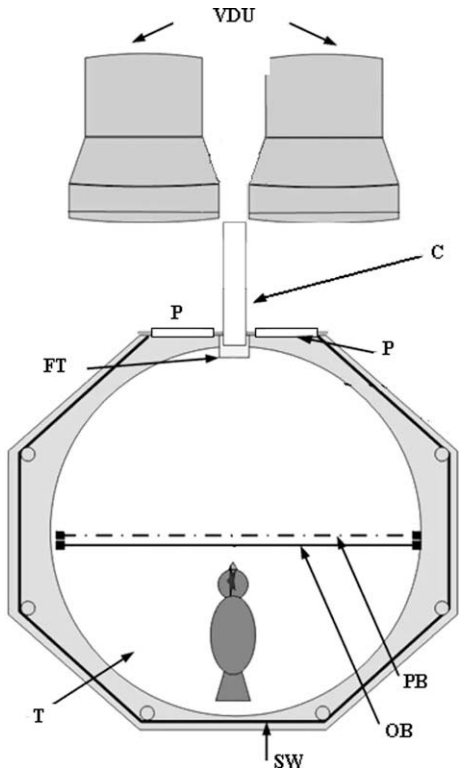

Fig. 1. Schematic diagram of the apparatus. Key; VDU = visual display monitors. C = conveyor feeder for reward food. P = Perspex pecking panels. FT = food trough. SW = cage black sheeting wall. T = turntable. OB = Opaque barrier. PB = clear Perspex barrier. Prior to stimulus presentation, the chicken is housed as shown behind OB and PB. When stimulus presentation is required OB and then PB are lifted to enable the chicken to view the VDUs. After a pecking response on P, both OB and PB are lowered and T rotated to return the chicken to the original position shown in the diagram. The stimulus presentation is then repeated as described in the text.

monitor screen was balanced to give the same luminance using a Minolta luminance meter. Vertical achromatic sine-wave gratings could be generated on each monitor using bespoke stimulus software provided by Silsoe Research Institute. Gratings of both variable spatial frequency and Michelson contrast[1] could be produced with this software package. The software also allowed the experimenter to select on which monitor the grating appeared. The other monitor would always contain a uniform field with a luminance equal to the mean grating level.

2.3. Experimental method

An operant conditioning paradigm was used to determine spatial contrast sensitivity. In this conditioning scheme, the chickens were initially trained to discriminate a grating of spatial frequency 1.0 c deg^{-1} and Michelson contrast of 90% from the uniform achromatic stimulus. These frequency and contrast levels were chosen because previous work had suggested they defined a stimulus near maximum grating sensitivity (Schmid & Wildsoet, 1998). During the discrimination procedure, grating and uniform stimuli swapped positions quasi-randomly such that they were presented an equal number of times, but not more than three consecutively on each side. Correct choice of the grating resulted in delivery of a small food reward to the feed trough. Any incorrect pecking responses resulted in a 'time-out' period of 5s with both monitors switched off. Each subject was tested in a daily session comprising

[1] Michelson contrast is defined as $(L_{max} - L_{min})/(L_{max} + L_{min})$, where L_{max} and L_{min} denote maximum and minimum luminance levels of the grating.