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# Stimulus luminance and the spatial acuity of domestic fowl (Gallus g. domesticus)

## Nick Gover\*, John R. Jarvis, Siobhan M. Abeyesinghe, Christopher M. Wathes

The Royal Veterinary College, University of London, Hawkshead Lane, North Mymms, Hatfield, Hertfordshire AL9 7TA, UK

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## ABSTRACT

The luminance dependence of spatial acuity in domestic fowl was measured directly over stimulus luminances ranging from 0.06 to 57.35 cd m<sup>-2</sup>. At the highest luminance, acuity was around 6.5 c deg<sup>-1</sup>, in agreement with previous studies in this species. As stimulus luminance decreased, acuity fell with increasing rate to 3.2 c deg<sup>-1</sup> at 0.06 cd m<sup>-2</sup>, following the same shape as acuity functions for other mammalian and avian species. These findings suggest that the rod–cone transition for domestic fowl is between 0.45 and 1.79 cd m<sup>-2</sup>. Over the photopic range from 1.79 to 57.35 cd m<sup>-2</sup> the change of acuity for fowl was 1%, compared with 32% for humans. For domestic fowl, the Rovamo–Barten MTF model of contrast sensitivity accounted for the behaviour of acuity as a function of luminance down to mesopic levels.

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## 1. Introduction

Domestic fowl (*Gallus gallus domesticus*) are used as an animal model in biomedical research as well as being an important food source worldwide. Most fowl are reared indoors where the luminance, spectral composition and flicker characteristics of the light environment differ greatly from the natural environment in which their ancestors evolved (Prescott, Jarvis, & Wathes, 2004; Prescott & Wathes, 1999a; Prescott, Wathes, & Jarvis, 2003). Vision is considered the dominant sense in most avian species (Appleby, Mench, & Hughes, 2004) and the unnatural light environment of commercial farming can affect social and other behaviours – and hence the welfare – of domestic fowl.

All three basic visual processes (spectral, temporal and spatial) have previously been quantified for domestic fowl. The spectral sensitivity of domestic fowl has been measured using a psychophysical method, and its consequences for the calculation of luminous flux have been determined (Prescott & Wathes, 1999b; Saunders, Jarvis, & Wathes, 2008). Opponent mechanisms underlying colour vision have also been proposed (Osorio, Vorobyev, & Jones, 1999). The flicker sensitivity of domestic fowl has also been measured psychophysically and a mechanistic model of temporal vision has been formulated using these data (Jarvis, Taylor, Prescott, Meeks, & Wathes, 2002). Within the spatial domain of vision, the minimum separable acuity of domestic fowl has been measured by various methods; a psychophysical Y-maze method yielded an acuity of 1.5 c deg<sup>-1</sup> in chicks, aged from 1 to 25 days old (Over & Moore, 1981), a psychophysical operant task with hens

(age unspecified) provided a value of  $4-6 \text{ c deg}^{-1}$  (DeMello, Foster, & Temple, 1992) and an optokinetic nystagmus paradigm (head tracking movements indicating that a stimulus rotating around the bird is perceived) with 8 day-old chicks yielded 7.7–8.6 c deg $^{-1}$ (Schmid & Wildsoet, 1998). These values were all measured under photopic conditions but provide a wide range of estimates of acuity, possibly due to different experimental conditions and techniques, as well as the range in age of the birds used. The contrast sensitivity function (CSF) has recently been quantified for adult laying hens using an operant task (Jarvis, Abeyesinghe, McMahon, & Wathes, 2009); this method describes the spatial visual abilities more fully than allowed by measurements of acuity. The CSF was shown to be much lower than that of humans at all spatial frequencies, with the peak of the function at approximately 1 c deg $^{-1}$ and an acuity of about 7 c deg<sup>-1</sup> under photopic conditions (at a stimulus luminance of 16 cd m<sup>-2</sup>). In mammalian, fish and some avian species, spatial contrast sensitivity and acuity are known to decrease as stimulus luminance decreases, but the responses of most avian, and indeed mammalian and fish, species are not known. To provide a preliminary estimate of the response to stimulus luminance in domestic fowl, the CSF was also measured at 0.1 cd m<sup>-2</sup>, which, when extrapolated to high contrast stimuli, provided an acuity measurement of about  $5 c deg^{-1}$  (Jarvis et al., 2009). However, the luminance-dependence of spatial vision in domestic fowl has not been investigated comprehensively.

Understanding of the luminance-dependence of spatial vision in domestic fowl provides essential information on how the visual system of this – and potentially other avian – species functions under scotopic, mesopic and photopic conditions. This has direct relevance to animal welfare, as in poultry farming illuminance is commonly reduced to 5 lux or less (Prescott et al., 2003) to control





<sup>\*</sup> Corresponding author. Fax: +44 (0) 1707 666298. E-mail address: ngover@rvc.ac.uk (N. Gover).

outbreaks and prevent the recurrence of injurious feather pecking and cannibalism. Five lux corresponds to mesopic viewing conditions in the human, but it is unknown what viewing conditions it corresponds to in domestic fowl. This husbandry practice may impede the ability of domestic fowl to discriminate between one another, thereby inhibiting the maintenance of peck-orders that can be well defined and are thought to be important in their social behaviour (Rushen, 1982; Williams & McGibbon, 1956). Measurements of the CSF at a low luminance by Jarvis et al. (2009), equivalent to an illuminance at the pecking key of 0.02 lux, inform us of the visual ability of domestic fowl, but not over a range of illuminance including scotopic, mesopic and photopic conditions.

In humans, the transition from cone- to rod-dominated vision causes a marked change in acuity. This rod-cone transition has been well demonstrated in mice with rod-only phenotype and cone-only phenotype populations compared against a wild-type strain (Umino, Solessio, & Barlow, 2008), although the transition was not derived from acuity but peak contrast sensitivity. In pigeons, the transition between cone- and rod- dominated vision occurs after about 20 min of dark adaptation (Blough, 1955, 1956). The luminance level identifying this break in pigeons is about 1 cd m<sup>-2</sup> (Ghim, 1997; Hodos & Leibowitz, 1977; Hodos, Leibowitz, & Bonbright, 1976), however has not been identified in any other diurnal avian species. Pigeons showed a 60% decrease in acuity as retinal illuminance decreased from approximately 2400-46 Trolands, Td (Ghim, 1997). As spatial vision of pigeons and domestic fowl is based on analogous physiological and anatomical mechanisms (Jarvis & Wathes, 2007), a similar reduction in acuity should be expected in domestic fowl. Pigeon acuity appeared to decrease at a steady rate as luminance decreased, not demonstrating the expected increase in gradient of the acuity-luminance function with the rod-cone transition (Ghim, 1997). The lack of apparent rodcone transition in these data may be due to an inadequate luminance range; a plateau in the acuity-luminance function whereby acuity is at a maximum that is not apparent at higher luminances and the lower luminances may not have provided conditions where vision is rod-dominated in pigeons.

It is now known that the vertebrate CSF can be simulated accurately with a modulation transfer function (MTF) model (Jarvis & Wathes, 2007, 2008). This model is based on that outlined for human vision by Barten (1999), Rovamo, Kankaanpaa, and Kukkonen (1999), Rovamo, Luntinen, and Nasanen (1993), Rovamo, Mustonen, and Nasanen (1994) and is given by:

$$CSF(u,I) = K \cdot O(u) \cdot H(u) \cdot A(u) \cdot [N(u,I)]^{-0.5}$$
(1)

where *u* and *I* represent spatial frequency in c deg<sup>-1</sup> and retinal illuminance in Td, respectively. Functions *O*, *H* and *A* are MTFs associated with different parts of the visual system. Function *O* is associated with the optics of the eye and receptor sampling, function *H* represents lateral inhibition in the retina and *A* represents spatial integration. Function *N* represents the combination of neural and photon noise in the visual system. The term *K* is a cortical detection factor. This model, including full mathematical descriptions of *O*, *H*, *A*, *N* and *K*, together with the methods used to evaluate numerical values for their parameters are given elsewhere (Jarvis & Wathes, 2007, 2008). This model has been applied to spatial vision of domestic fowl and shown to adequately predict the CSF (Jarvis et al., 2009), thereby providing a tool that can be used to predict spatial visual abilities of domestic fowl under photopic conditions.

The aims of this study were to investigate the visual acuity of domestic fowl as a function of luminance down to scotopic conditions and to compare the results with human acuity measured under similar conditions. A key hypothesis to be tested was that the gradient of the acuity-luminance function of domestic fowl would reveal a luminance level similar to that found in pigeons of about 1 cd  $m^{-2}$  for the rod-cone transition in vision.

### 2. Materials and methods

#### 2.1. Subjects

Sixteen domestic fowl of a commercial laying strain (obtained at point-of-lay, age 16 weeks Hyline Brown; Noble Foods Ltd., UK) were housed under natural light in an outdoor paddock with access to shelter. Prior to acquisition, the fowl were reared from day-old on litter under commercial conditions. The fowl had *ad libitum* access to water, grit and commercial layer pellets. Six human volunteers, two emmetropic, and the others wearing corrective lenses to compensate for any myopia, were selected from volunteers with a mean  $\pm$  standard error age of  $24.2 \pm 1.14$  years for the human comparison. Only one subject had prior experience as a psychophysical subject.

### 2.2. Operant apparatus, stimulus presentation and control

The apparatus consisted of an instrumented cage controlled by a PC. On one side of the cage were two transparent, pecking keys (Perspex, each 125 by 110 mm, positioned 340 mm from the floor of the cage and separated by 130 mm). The keys were hinged at the top and movement of the key was registered as a peck response by a linked PC via a circuit break. A small food trough was located between the keys and 270 mm from the floor of the cage. Blue bottle maggots, bought from a local angling shop, then frozen for storage and boiled when required were delivered to this trough by a motorised conveyor belt that could be controlled either manually or by the PC.

The stimuli were presented on two monitors (AL1511; Acer, Taiwan), placed 400 mm behind the pecking keys, viewed through them and controlled by the same PC system that controlled the instrumented cage. The output of each monitor was balanced to provide the same luminance using a calibrated luminance meter (LS-110; Minolta Camera Co., Osaka, Japan). Achromatic, vertical sine wave gratings of between 20 and 210 cycles across the width of the monitor with Michelson contrasts of 0.94 were generated and presented on either of the monitors with bespoke software. Plain grey images of the mean luminance of the sine wave grating stimuli could also be generated and were presented simultaneously with the corresponding grating stimuli. Neutral density filters (combinations of 0.3, 0.6, 0.9 and 1.2 ND, product numbers 209, 210, 211 and 299, respectively, Lee Filters, Andover, UK) were placed immediately behind the pecking keys in order to reduce the luminance of the stimuli. For the human comparison, only one monitor was used at a viewing distance of 5400 mm in order to present stimuli of high enough frequency to cover the expected range of human acuity  $(50-60 \text{ c deg}^{-1})$ . Human subjects wore blacked-out, safety goggles fitted with neutral density filters to reduce the light flux reaching the eye.

Acuity was measured at eight mean stimuli luminances, ranging between 0.06 and 57.35 cd m<sup>-2</sup>. A lux meter (Testo 545, Testo Ltd., Germany) was used to measure illuminance from the point domestic fowl viewed the stimuli, illuminance ranged from less than 1–52 lux. Using measurements of the pupil size (Barbur, Prescott, Douglas, Jarvis, & Wathes, 2002) and posterior nodal distance (PND; Jarvis, Prescott, & Wathes, 2003) of domestic fowl, retinal illuminance was estimated to be between 8.84 and 5060 Td. For the human study, six luminances (0.01, 0.05, 0.11, 3.47, 13.87 and 62.00 cd m<sup>-2</sup>) were chosen, ranging from photopic to the upper limit of scotopic viewing conditions; these were similar to a subset of those used in the fowl study. The equivalent retinal

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