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Visual discrimination learning and critical spatial acuity in sheep

Sumita Sugnaseelan^{a,b†*}, Neville B. Prescott^b, Donald M. Broom^a, Christopher M. Wathes^{b†} and Clive J. C. Phillips^{a§}

^a*Centre for Animal Welfare and Anthrozoology, Department of Veterinary Medicine, University of Cambridge, Madingley Road, Cambridge CB3 0ES, United Kingdom*

^b*Silsoe Research Institute, Wrest Park, Silsoe MK45 4HS, UK*

‡Present address: Department of Animal Science, Faculty of Agriculture, Universiti Putra Malaysia, 43400 UPM Serdang, Selangor, Malaysia

†Present address: Centre for Animal Welfare, Department of Clinical Veterinary Sciences, The Royal Veterinary College, Hawkshead Lane, North Mymms, Hertfordshire, Hatfield AL9 7TA, UK

§Present address: Centre for Animal Welfare and Ethics, School of Veterinary Science, University of Queensland, Gatton, Queensland 4343, Australia

*Corresponding author: Sumita Sugnaseelan at: Department of Animal Science, Faculty of Agriculture, Universiti Putra Malaysia, 43400 UPM Serdang, Selangor, Malaysia. Tel.: +603 8947 4879; Fax: +603 8938 1024. E-mail address: sumi@agri.upm.edu.my

1 **Abstract**

2 Visual acuity is an important component of environmental recognition in sheep, yet knowl-
3 edge about it is limited in this or other herbivorous species. We tested the ability of British
4 Friesland × Texel female lambs to discriminate black and white square-wave grat- ings,
5 presented vertically or horizontally, from a grey stimulus. Animal and environmental
6 conditions were optimised for detection of visual acuity. Sheep could rapidly learn to dis-
7 criminate some gratings from a grey stimulus. There was no difference in the ability of sheep
8 to discriminate vertical or horizontal stimuli from a grey stimulus. Visual acuity, determined at
9 between 11.7 and 14.0 cycles/degree, was greater than that previously predicted from
10 anatomical measurements (7–10 cycles/degree), and considerably greater than that mea-
11 sured for sheep by the Landolt C ring technique (2.6–5.7 cycles/degree). It was also
12 greater than that measured previously in most research using ungulates and other
13 herbivores, with a variety of techniques. It is concluded that sheep visual acuity is potentially
14 greater than hitherto realised, but that standardisation of techniques is required to make
15 accurate comparisons with data gathered previously. Additionally, the ability to gauge an
16 animal’s awareness and its response(s) to various visual optotypes in its macro-environment
17 will enable us to design livestock housing, handling and transport facilities that promote
18 animal welfare.

19

20 Keywords: Discrimination learning, Sheep, Square-wave gratings, Visual acuity

21

22 **1. Introduction**

23

24 In ungulates, vision, in combination with the auditory, olfactory and gustatory senses, plays a
25 vital role in environmental perception (Baldwin, 1979), individual recognition (Lickliter and
26 Heron, 1984; Davis et al., 1998; Taylor and Davis, 1998; Hagen and Broom, 2003) and the
27 selection of ecological resources (Arnold, 1966; Bazely and Ensor, 1989) necessary for
28 survival and reproduction. While these senses are often used together, vision is believed to
29 be dominant in ungulates and in some other prey species and is of prime significance in the
30 sensation of the biological network (Fletcher and Lindsay, 1968; Lindsay and Fletcher, 1968;
31 Piggins and Phillips, 1996).

32 Ungulates have been reported to perform well in visual discrimination tasks. In studies
33 involving discrimination of shapes (Seitz, 1951; Schaeffer and Sikes, 1971; Baldwin, 1979;
34 Fiske and Potter, 1979; Baldwin, 1981; Blakeman and Friend, 1986; Entsu, 1989; Entsu et
35 al., 1992; Rehkämper and Görlach, 1997; Daniel and Mikulka, 1998; Rehkämper and
36 Görlach, 1998) and patterns (Rehkämper et al., 2000; Franz et al., 2002; Roitberg and
37 Franz, 2004), test animals were used in a two choice situation where they were required to
38 choose the visual cue on which they were trained. The task was made difficult by varying
39 either the size or complexity of the image, or by fixing the size of the image but varying the
40 distance of the visual stimulus from the animal.

41 Similar techniques have been employed to determine the ability of ruminants to distinguish
42 brightness (Wenzel et al., 1964; Bazely and Ensor, 1989; Phillips and Weiguo, 1991),
43 conspecifics (Arnold et al., 1975; Alexander, 1977; Alexander and Shillito, 1977a,b, 1978;
44 Alexander and Shillito Walser, 1978; Kendrick et al., 1995, 2001; Hagen and Broom, 2003;
45 Ferreira et al., 2004) and individuals of other species (Kendrick and Baldwin, 1989; Kendrick,
46 1991; Kendrick et al., 1995; de Passillé et al., 1996; Boivin et al., 1997; Davis et al., 1998).

47 Data obtained from these behavioural learning studies have improved our under-
48 standing of how an animal perceives its environment and indirectly address issues related to
49 improvements in the husbandry, management, and design of housing and transport facilities.
50 The importance of different sensory modalities in sheep is illustrated by the strong part that
51 vision plays in recognition for dam-young relationships and in conspecific recognition and
52 discrimination (Arnold et al., 1975; Alexander, 1977; Alexander and Shillito, 1977a,b, 1978;
53 Alexander and Shillito Walser, 1978; Alexander and Stevens, 1981). The capacity of its
54 visual system to resolve spatial detail, i.e. visual acuity, and motion detection are not well
55 understood.

56

57 Visual acuity has been well studied in humans using various techniques, some of which
58 have been adapted to study visual acuity in ungulates and other herbivores (Table 1). In
59 non-human animals and young children, sine- or square-wave gratings and the Landolt 'C'
60 ring, are commonly used optotypes, but need to be standardised for a number of
61 environmental factors, namely illuminance, wavelength, light frequency and viewing
62 distance. Discrimination learning experiments normally precede visual acuity studies in
63 animals that have been trained either by classical or operant condi-
64 tioning to a two-choice situation, before inferences can be made.

65

66 Test subjects, regardless of their species, are easily distracted (Fletcher and Lindsay, 1968;
67 Kendrick, 1994; Porter et al., 1997; Porter and Bouissou, 1999), agitated (Daniel, 1994;
68 Daniel and Mikulka, 1998) or lose interest in a visual task after a few trials (Jacobson et al.,
69 1976; Rehkämper and Görlach, 1997; Tanaka et al., 1998). As well as experimental design
70 and the skill of the experimenter, the number of opportunities provided to the subjects may
71 influence conclusions about performance of a visual task (Manske and Schmidt, 1976;
72 Daniel and Mikulka, 1998).

73

74 As these variables have become better understood in recent years, an operant test was
75 conducted to determine visual acuity in sheep, by investigating their ability to discriminate
76 between horizontal and vertical, black and white square-wave gratings, compared with a
77 blank grey stimulus.

78

79 **2. Materials and methods**

80

81 *2.1. Test subjects*

82 Fourteen, 5-week-old, hand-raised British Friesland x Texel ewe lambs were used in this
83 study. They were randomly allocated to two treatment groups of seven and were housed
84 indoors in two adjacent ventilated rooms. Each room was divided into two pens, measuring
85 1.7 m x 3.2 m, and bedded with straw and wood shavings. In order to reduce potential bias
86 due to variation in the housing environment, each pen contained three or four animals from
87 each group.

88

89 The lambs were maintained on a diet of hay and water *ad libitum*, supplemented with lamb
90 creep pellets offered at 0.1 kg/kg body weight daily. The concentrates were delivered in a
91 stainless steel bowl that was subsequently used during the experiment to contain the food
92 reward. Concentrates were withheld prior to experimentation and subsequently used as part
93 of the food reward. All lambs were fitted with a body harness to facilitate safe handling. They
94 were pronounced healthy following a physical examination by a veterinarian, which included
95 examination of the eyes to ensure that they were free from abnormalities that might affect
96 vision.

97

98 *2.2. Visual stimuli and lighting*

99 The primary visual stimuli were evenly spaced black and white square-wave gratings with a
100 spatial frequency of 0.125 cycles cm⁻¹, generated by Adobe® Illustrator® 9. The computer-
101 generated images were printed on A3-sized white paper (Premium Glossy Photo, Epson,
102 Long Beach, California, USA), using a HP® DeskJet 1220C (Palo Alto, California, USA). The
103 visual angle of the square-wave grating was 0.44 cycles/degree when viewed at a distance
104 of 2 m. Grey-background paper (Cloud Grey 23, Colorama™ Photodisplay, Coalville,
105 Leicestershire, United Kingdom) was used as the blank (negative) visual stimulus. This was
106 visually matched against the highest spatial frequency gratings (4 cycles/cm), so that both
107 stimuli appeared similar in colour intensity. The visual stimuli were trimmed to 28 cm x 28
108 cm, mounted on card, placed in 350 [µm](#) encapsulator wallets and laminated. The gratings

109 could be orientated either horizontally or vertically and were placed in a translucent pocket
110 (Bayer Polymer, Plexiglas, Makrolon[®], PSP Ltd, Auckland, New Zealand) at the mean eye
111 height of the test animals (66 cm).

112

113 A ceiling-mounted, single, 1.8 m fluorescent light fitting with a single tube (Luxline Plus
114 Daylight Deluxe F70W, Sylvania[™], Erlangen, Germany), was used as the light source in
115 both the indoor pens and in a Y-maze discrimination chamber (Figure 1). The luminance of
116 the gratings in the translucent pocket was measured with a luminance meter (LS-110,
117 Minolta[™], Tokyo, Japan), at nine locations (centre, corners and sides) for each visual
118 stimulus. The visual stimuli were placed in each arm of the Y-maze. The mean (\pm SE)
119 luminance of the stimuli was 9.4 ± 0.1 cd/m²; the Michelson contrast for the square-wave
120 grating was 0.88.

121

122 Illuminance was measured at the average eye height of the sheep (corresponding to the
123 centre point of the translucent pocket holding the visual stimuli) using a light (lux) meter (545
124 Testo[™], Lenzkirch, Germany), at nine locations. The mean illuminance in the indoor pens
125 and the Y-maze was 200 lux.

126

127 *2.3. Experimental procedure*

128 The lambs, which were aged 12 weeks by the start of the discrimination training, were
129 exposed to the Y-maze (Figure 1) for two h per day (one h in the morning and one h in the
130 afternoon) for one week prior to experimentation in order to familiarise them with the novel
131 environment of the test chamber. A stainless steel food bucket contained the feed reward,
132 comprising a mixed ration of 80% lamb creep pellets, 9% rolled oats, 9% rolled barley and
133 2% seedless raisins, and was placed behind each screen. The bucket behind the negative
134 stimulus was covered with a wire mesh in order to prevent access. This eliminated the
135 possibility of subjects making a choice of stimulus based on olfactory rather than visual

136 stimuli. Once the subjects were familiar with the routine, they were brought into the test room
137 individually to start the discrimination task.

138

139 The subjects were trained to differentiate either a horizontally or vertically orientated grating,
140 with a visual angle of 0.44 cycles/degree, from the blank cloud-grey stimulus. The fourteen
141 subjects were randomly allocated to be trained with a vertical ($n = 7$) or horizontal ($n = 7$)
142 grating, these comprising the positive stimuli for which they were rewarded. The blank grey
143 stimulus was the negative stimulus for which they were not rewarded. Four of the test
144 animals from the vertical group were tested alongside three individuals from the horizontal
145 group, each alternate day, and *vice versa*. This ensured that subjects from both treatment
146 groups were tested each day. The order of training the subjects followed a randomised block
147 design, therefore each animal had the opportunity to learn the task at different times of the
148 day.

149

150 An experimental session was conducted once the subjects had been conditioned for a
151 minimum of 20 min (Piggins, 1992) at 200 lux, ensuring that the effect of illuminance on
152 visual acuity and the discrimination task was standardised. Illuminance was checked daily in
153 both experimental rooms and the light conditioning pen before the start of each light
154 treatment, to ensure that the light output from the fluorescent light source was as specified.

155

156 The subjects were initially placed in the start box (Figure 1) for one min to acclimatise them
157 to the experimental environment and separation from their pen-mates. Side doors were
158 available for emergency evacuation of the subject, if necessary. The opaque partition that
159 separated the start chamber and the Y-maze was then raised to allow the subject to observe
160 the visual stimuli through an extruded polycarbonate translucent door (Plexiglas 3.22 mm
161 thick; Bayer Polymer, Makrolon[®], PSP Ltd, Auckland, New Zealand) for 5 s. The door was
162 then lifted to allow the subject access into the Y-maze. Selection of the positive visual stimuli
163 in preference to the negative stimuli in each trial earned the subject a small food reward (12

164 g of mixed ration described above). Each time the subject made an incorrect choice, it was
165 left in the erroneous arm of the Y-maze for a period of 10 s, before it was taken back to the
166 start box to commence the next trial. Each subject was subjected to 20 consecutive trials per
167 session, each alternate day.

168

169 A subject was deemed to have made a choice as soon as it completely exited the start box.
170 Both the opaque partition and the translucent doors were then lowered to prevent it from
171 retreating. Left and right positions of the visual stimuli were alternated in a Gellerman series
172 (Gellerman, 1933) to prevent habituation of orientation. A stimulus did not occur in a given
173 position more than twice consecutively.

174

175 For the first ten trials of the conditioning session the feed bowls were placed in front of the
176 visual panels, directly below the translucent pocket on the visual screen, to encourage the
177 subjects to make an initial positive association between the visual stimuli and food reward.
178 Conditioning data were not included in subsequent analysis.

179

180 Having fulfilled the learning criterion, subjects were exposed to the visual acuity test in
181 artificial daylight at an illuminance of 200 lux. Success in discriminating the gratings from the
182 grey stimulus was deemed to have been achieved when a subject attained 15 or more (\geq
183 75%) correct choices in a session comprising 20 trials (for justification see statistical analysis
184 below). If the subject maintained its score of 75% or more for three consecutive sessions or
185 in three out of five sessions, it was subsequently tested on a grating one half width narrower
186 than used previously. If it was unable to achieve the criterion, the width of the grating was
187 increased by 50% of the previously undistinguishable grating stimulus. Upon finding that
188 sheep failed the >75 % correct choices test, they were re-presented with the last grating to
189 confirm their ability to discriminate.

190

191 *2.4. Statistical analysis*

192 Chi-square determination of significance for choice experiments is widely employed in
193 operant conditioning studies (e.g., Child, 1946; Grant, 1946; 1947; Entsu et al., 1992;
194 Tanaka et al., 1995; Rehkämper and Görlach, 1998; Rehkämper et al., 2000). The null
195 hypothesis (H_0), that a subject cannot discriminate between visual stimuli, assumes an equal
196 probability of choosing a positive or negative stimulus.

197

198 From the χ^2 formula with one degree of freedom, a threshold value of 15 correct choices out
199 of 20 trials for significance at $P \leq 0.05$ was obtained. Therefore, a learning criterion was set
200 that required the subject to make 15 or more ($\geq 75\%$) correct choices out of 20 consecutive
201 trials, for four successive sessions, in order for it to be categorised as having learnt to
202 discriminate between positive and negative visual stimuli.

203

204 Data were analysed using SPSS[®]18 for Windows[®]. Their normality was determined from a
205 Kolmogorov-Smirnov test for goodness of fit. Untransformed percentage values were used
206 to plot graphs. When percentage values were used for statistical analysis, the data were arc
207 sine-transformed.

208

209 An independent samples t -test was used to compare means within and between groups, as
210 the number of sessions to attain the learning criterion per subject per group was normally
211 distributed. Levene's test ($P > 0.05$) provided evidence that the variance within and between
212 the groups was equal. The learning rate, i.e. the total number of sessions taken and the
213 percentage of qualified sessions throughout the discrimination learning study, within the two
214 different image groups was also examined for individual subjects. Since the visual acuity
215 data were not normally distributed, a ranked Fisher's exact test was utilised.

216

217

218 **3. Results**

219 Individual sheep varied in their rate of learning the visual discrimination collectively, at a
220 grating visual angle of 0.44 cycles/degree and illuminance of 200 lux, the learning criterion
221 was achieved between 4 and 12 sessions, corresponding to 80 and 240 trials, respectively
222 (Figure 2). The mean (\pm SE) number of sessions over which the sheep in the horizontal and
223 vertical group took to qualify was 6.7 ± 0.6 and 8.7 ± 1.1 sessions, respectively. Six sheep
224 (out of 7) in the horizontal group achieved the learning criterion by the end of the eighth
225 session, whereas in the vertical group only four attained the criterion by this time. Two sheep
226 in the vertical group required 13 sessions to qualify for the acuity experiment. However,
227 there was no significant difference in the number of sessions taken to satisfy the learning
228 constraint between the two groups ($P > 0.05$).

229

230 All sheep in the vertical group had the same visual acuity threshold of 13.12 cycles/degree
231 (Figure 3). No variability was detected among these vertical selectors. However for the
232 horizontal group, 3 out of 7 sheep had a visual acuity of 11.71 cycles/degree while the other
233 four had a visual acuity of 13.12 cycles/degree. This produced a mean (\pm SE) visual acuity of
234 12.56 ± 0.28 cycles/degree for the horizontal selectors. Upon finding that sheep failed the
235 75% correct choice threshold, discrimination at the previous visual stimulus was confirmed in
236 all cases.

237

238 There was no significant difference in the visual acuity between the test animals in the
239 horizontal and vertical groups ($P > 0.05$). No sheep were able to discriminate the grating with
240 a spatial frequency of 4 cycles/cm. Therefore, the collective visual acuity of the sheep in this
241 study was between 11.71 and 13.96 cycles/degree, with the critical value lying within this
242 range.

243

244 **4. Discussion**

245 *4.1. Grating discrimination*

246 Various factors may influence the ability of an animal to learn a visual task. These include
247 animal factors (e.g., species, age, health and temperament), environmental factors (e.g.,
248 illuminance and ambient temperature), and aspects of experimental design such as the
249 training regime. Consequently, any study aiming to address the ability of a species to learn a
250 visual task must take these factors into consideration when designing a discrimination
251 experiment, in order to make a reasonable inference on the animal's learning capabilities.
252 Standardisation of variables, such as visual stimuli, lighting, learning criterion and training
253 protocol, is important to facilitate meaningful, quantitative inter- and intra-species
254 comparisons.

255

256 The young (12 week) subjects may have increased their success rate in the discrimination
257 task. In a similar discrimination experiment that involved different age groups (Kovalèik and
258 Kovalèik, 1986; Tanaka et al., 1995), young (15 months) heifers made fewer errors than
259 adult cows during learning. Similarly learning operant tasks, including visual discrimination,
260 is faster in calves than adult cattle (Rehkämper and Görlach (1997) Kovalèik and Kovalèik
261 (1986), probably because young animals are more inquisitive, and have increased interest in
262 learning tasks (Murphey et al., 1981; Phillips, 2002).

263

264 Temperament directly influences the ability of an animal to cooperate during training. The
265 ease of training the lambs in the present study, and their ability to achieve the learning
266 criterion at a relatively early stage of experimentation may be because this breed of dairy
267 sheep is docile and easily adapted to human handling. The animals were hand-raised from
268 an early age and were accustomed to the experimenter and experimental setting, facilitating
269 their training. The provision of a quiet facility may have helped our subjects to learn their
270 task, as disturbances easily create a distraction and reduce learning rates (Daniel and
271 Mikulka (1997)).

272

273 The alternate day testing regime employed did not appear to have any apparent deleterious
274 effects on the learning and memory of the ewe lambs. A good aptitude of animals to
275 remember a task following a lapse during training has also been demonstrated in other
276 ungulate visual discrimination and recognition studies. Rehkämper and Görlach (1997; 1998)
277 found when training adult dairy bulls once weekly in a repetitious visual task that they only
278 maintained interest for 1 h. Following this study the subjects successfully performed a visual
279 grating discrimination task after a lapse of several weeks (Sumita, 2006). Similar memory
280 retention in sheep has also been noted in research on animal handling, choice preference,
281 visual discrimination and recognition (Hutson, 1980; 1985; Kendrick, 1991; Kendrick et al.,
282 1996).

283 Behavioural evidence of active choice-making was often observed during this study, with
284 ewe lambs vacillating when viewing the visual stimuli behind the Plexiglas screen during the
285 initial 5 s time period before the Plexiglas door was raised. Rewarding the animal with food
286 when a correct choice was made provided a positive feedback in learning the task at hand.
287 The animals used in this study were not food deprived prior to experimentation. The test
288 animals were observed to be highly motivated and readily participated in the trials. Similar
289 levels of motivation have been observed in studies where the animals had been food
290 deprived (Van Hof, 1966; Schaeffer and Sikes, 1971), suggesting that food deprivation prior
291 to experimentation is not a requisite but however, choice of food reward may increase
292 motivation of the test animal to participate in the visual task.

293 A perusal of previous studies indicates that researchers sometimes neglect to standardise
294 various factors that may influence visual learning, e.g., randomisation and method of
295 optotype presentation (i.e., automated or manual), distance of the animal from the stimulus,
296 illuminance of the visual stimuli and test arena during the discrimination task, choice and
297 method of delivery of reward, consistency between the visual optotypes and learning
298 criterion. As a result, it is difficult to compare the training methods used here and those used
299 in previous studies (e.g., Baldwin, 1981; Baldwin and Start, 1981; Bazely and Ensor, 1989;

300 Tanaka et al., 1995).

301 The ability of sheep to learn to discriminate between a horizontal or vertical grating and a
302 uniform cloud-grey visual stimulus has been demonstrated for the first time in this study.
303 Previous operant studies on sheep have involved shape and pattern discrimination,
304 differentiating between shapes and letters of the Roman alphabet, of varying sizes, texture
305 and orientation (Seitz, 1951; Backhaus, 1959; Baldwin, 1981; Tanaka et al., 1995). Cattle
306 are able to discriminate between pairs of continuous or broken lines (Rehkämper et al.,
307 2000), but the viewing distance of the animal and illuminance was not mentioned even
308 though the study was a precursor for investigation of bovine vernier acuity.

309 Gratings and Landolt 'C' rings are common visual optotypes in studies of visual acuity in
310 animals and young children. Previous studies of ruminants showed that cattle took between
311 660 and 1200 trials to discriminate a Landolt 'C' ring from a closed circular ring of equal size
312 (Entsu *et al.*, 1992), while sheep required between 210 and 240 trials in a similar task
313 (Tanaka *et al.*, 1995). Operant conditioning studies with goats (Baldwin, 1979), dairy bulls
314 (Rehkämper and Görlach, 1997) and white rhinoceros (Daniel and Mikulka, 1998)
315 demonstrated an ability to discriminate different objects. Thus ungulates can learn to
316 discriminate objects visually.

317

318 *4.2. Ovine visual acuity*

319 This study is the first to determine the visual acuity of sheep using square-wave gratings.
320 The critical visual acuity was independent of orientation of the visual stimuli. In contrast,
321 Rehkämper *et al.* (2000) found that bulls had 60% less visual acuity for stimuli in the
322 horizontal rather than vertical plane, which they attributed to the horizontal elliptical pupil and
323 visual streak, which runs parallel to the pupillary cleft. However, our finding that orientation of
324 stimulus did not affect sheep acuity is supported by the absence of differences in
325 retinoscopic refraction of sheep in the vertical and horizontal meridians (Piggins and Phillips,
326 1996).

327

328 Hughes' (1977) 'terrain theory' suggests that the ungulate retina with its characteristic visual
329 streak is an adaptation to detect and avoid predators on the horizon. However, [Rehkämper](#)
330 [et al. \(2000\)](#) believed that the pupil and visual streak are only parallel with the horizon when
331 the animal's head is slightly elevated, and are slightly oblique (20–30%) to it during grazing.
332 They suggest that increased cattle vertical acuity could be of value in detecting vertical
333 objects on the horizon. Their origins in forest fringe environments, broad dental arcade, and
334 ability to cope with low quality feed suggest that cattle evolved as browsers, which would
335 require more vertical than horizontal acuity for middle distance selection. [Piggins and Phillips](#)
336 [\(1996\)](#) postulated that sheep, and presumably cattle, do not use their eyes to discriminate
337 near food items whilst grazing because they are obscured by their long muzzle, which is
338 supported by the absence of any effect of blindfolding sheep on food selection ([Arnold,](#)
339 [1966](#)). However, sheep can use their eyes for medium distance food selection, being able to
340 choose between dark and light herbage, tall and short ([Bazely and Ensor, 1989](#)).
341 Considering that sheep evolved in an open, undulating montane habitat, visual acuity for
342 both food selection and predator detection is likely to be required in both the horizontal and
343 vertical planes, in contrast to cattle which would require visual acuity mainly in the vertical
344 plane. There remains the possibility, as commented by [Rehkämper et al. \(2000\)](#), that
345 domesticated livestock have different visual acuity from their progenitors. If this is true, the
346 preponderance of domesticated cattle that were kept in grazing situations might be expected
347 to produce better vertical visual acuity, but this would be expected even more in sheep given
348 their greater susceptibility to predation.

349 The visual acuity of the lambs used in this study, between 11.71 and 13.96 cycles/degree at
350 a viewing distance of 2 m and illuminance of 200 lux, was greater than reported in most
351 previous investigations (Table 1). [Tanaka et al. \(1995\)](#) used a Landolt 'C' ring to assess the
352 visual acuity of three ewes, which they reported as ranging from 2.6 to 5.7 cycles/degree, at
353 an illuminance of more than 500 lux. [Clarke and Whitteridge \(1995\)](#) cited Hughes' estimation

354 of retinal ganglion cell density (500 cells/mm), which predicts a visual acuity of 7.5 to 10
355 cycles/degree. As the acuity range obtained from this study was closer to the anatomical
356 estimates of Hughes, square-wave gratings may be more appropriate than Landolt 'C' rings
357 visual acuity measurements.

358

359 The Landolt 'C' ring is insensitive to astigmatism (Baron and Westheimer, 1973)(Clarke and
360 Whitteridge, 1976), but Piggins and Phillips (1996) found no evidence of astigmatism in
361 sheep. Longer exposure to the stimulus may be necessary for the Landolt 'C' ring when the
362 gap is very small(Rubin, 1972), because it only presents a single gap, compared with the
363 repeated pattern in the grated visual stimuli. In our study, sheep were observed to oscillate
364 their head horizontally in the start box during the 5 s period before making their choice,
365 especially when presented with closer grating patterns. Thus the greater visual acuity
366 measured in our study may relate to the careful training and optimisation of animal and
367 environmental parameters.

368

369 Age may be another factor affecting the visual competence of animals (Warkentin and
370 Smith, 1937). Visual acuity of the lambs in this study was determined at 8 months of age,
371 whereas Tanaka *et al.* (1995) used 2 yearlings and a 4-year-old ewe. Deterioration of vision
372 in old animals could be due to the loss of retinal photoreceptor cells (Braekevelt, 1983) but it
373 is not known when visual ageing occurs in sheep.

374 **5. Conclusion**

375

376 Sheep learned rapidly to discriminate simple black and white interrupted patterns from a
377 similar sized blank grey stimulus. Their spatial acuity was more acute than that measured
378 previously. There was no difference between horizontal and vertical acuity, probably
379 because of a need for vigilance in both planes in this species.

380

381

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383

384

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386

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390

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392

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504 **Table and Figure captions (for version with Table and Figures, contact authors)**

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507 Table 1. A review of the spatial resolving capacity of the visual system in ungulates and
508 herbivorous mammals, assessed *via* either behavioural (method 1) or anatomical studies
509 (method 2), or a combination of techniques. In the behavioural method, visual cues utilised
510 were either square-wave (Sqw) or sine-wave (Snw) gratings, or the Landolt 'C' ring (Ldr).
511 Michelson contrast is expressed in parentheses. NA — Not available.

512

513 Figure 1. Y-maze test chamber used in this study, showing the positive (striped) and
514 negative (grey) visual cues in the left and right arm; the viewing distance was 2 m from the
515 Plexiglas screen of the start box.

516

517 Figure 2. Grating discrimination learning of British Friesland x Texel ewe lambs showing the
518 percentage of correct choices as a function of the number of training sessions for the
519 horizontal and vertical groups, respectively. Animals were conditioned to the experimental
520 protocol prior to data collection (C). Values are mean \pm SE, n = 7 unless indicated otherwise.

521

522 Figure 3. Visual acuity of British Friesland x Texel ewe lambs, showing the percentage
523 correct choices as a function of the spatial frequency for the horizontal and vertical group,
524 respectively. Values are mean \pm SE, n = 7 unless indicated otherwise above the value.