On the optical theory of underwater vision in humans

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Defocus changes the visual contrast sensitivity function, thereby creating a complex curve with local dips and peaks. Since underwater vision in humans is severely defocused, we used optical theory and the phenomenon of spurious resolution to predict how well humans can see in this environment. The values obtained correspond well with experimental measurements of underwater human acuity from earlier studies and even point to an opportunity for humans with exceptional contrast sensitivity to see better underwater than the children in those studies. The same theory could be useful when discussing the visual acuity of amphibious animals, as they may use pupil constriction as a means of improving underwater vision. © 2004 Optical Society of America

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1. INTRODUCTION

Contrast sensitivity declines quite rapidly with even small amounts of defocus. Parameters such as pupil diameter and spatial frequency will affect the contrast sensitivity function during defocus in a way predicted by optical theory,[1] showing that the resulting complex curve is not smooth but contains several local dips and peaks. Some studies have theoretically and experimentally shown how contrast sensitivity can change in humans with only a few diopters of defocus.[2,3] However, there is one situation in which humans experience a considerable amount of defocus and that has never been considered, namely, unaided underwater vision. Without the help of goggles, our vision is severely blurred when we dive. Because of the similar refractive index of water and the aqueous humour behind the cornea, we lose ≈43 diopters (D) of refractive power when our eyes are immersed in water, and this loss generally makes vision underwater quite difficult.

However, in a recent study, Moken children from a tribe of sea nomads in Southeast Asia have been found to have an underwater visual acuity that is more than twice as high as that of European children.[4] It has been shown that this ability comes from a trained response to control accommodation that is followed by pupil constriction: After practice, European children learn to control their accommodation and show the same visual acuity underwater as the Moken children.[5] Pupil constriction and substantial accommodation (up to 16 D) endows these children with enhanced underwater acuity.

The main purpose of this study is to use optical theory to predict how well humans can see during conditions of extreme defocus such as those experienced underwater.

2. THEORY AND RESULTS

We first calculate the contrast sensitivity required for detecting the defocused image of a sinusoidal pattern on the retina. As we are studying cases with very large defocus (≈43 D), we can safely ignore diffraction effects. Light levels are high in tropical countries, and the light flux on the retina can be assumed to be constant, irrespective of small changes in pupil size.

The geometric modulation transfer function S of a sinusoidal wave modulation is given by[1]

$$S = \frac{2J_1(z)}{z}, \tag{1}$$

where J_1 is the first-order Bessel function and z the dimensionless parameter

$$z = \pi B f_S, \tag{2}$$

where B is the diameter of the blur circle produced by defocusing and f_S the spatial frequency of the sinusoidal wave pattern in cycles per meter. For our purpose it is more convenient to use the equivalent parameterization

$$z = 0.180 f_a P \Delta D, \tag{3}$$

where f_a is the angular spatial frequency of the wave pattern in cycles per degree, P the pupil diameter in millimeters, and ΔD the defocus in diopters. All these quantities can easily be measured. At the higher spatial frequencies that we consider in this paper, we can use the function

$$C = -\log(|S|) \tag{4}$$

as the contrast sensitivity necessary to detect a sinusoidal pattern. The z positions of the minima of the function C

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Table 1. Contrast Sensitivity as a Function of z for the First 24 Values Only

z	CS[a]	z	CS[a]	z	CS[a]
5.14	0.88	30.57	2.03	55.73	2.42
8.42	1.19	33.72	2.09	58.87	2.45
11.62	1.40	36.86	2.15	62.02	2.49
14.80	1.55	40.01	2.20	65.16	2.52
17.96	1.68	43.15	2.25	68.30	2.55
21.12	1.78	46.30	2.30	71.45	2.58
24.27	1.88	49.44	2.34	74.59	2.61
27.42	1.95	52.59	2.38	77.73	2.63

[a] CS is contrast sensitivity in log units.

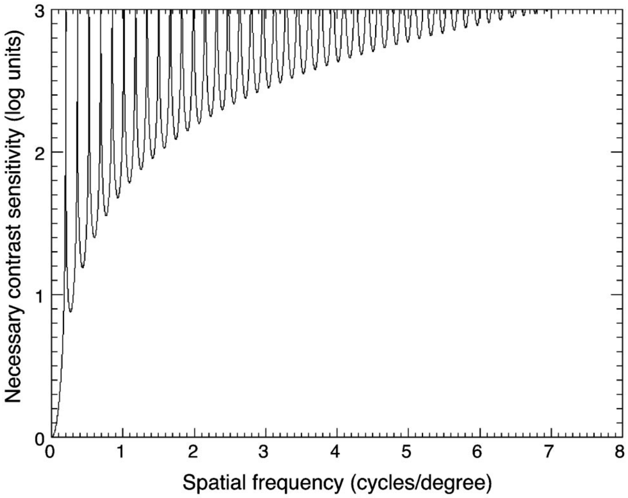

Fig. 1. Necessary contrast sensitivity as a function of spatial frequency, with a set pupil diameter of 2.50 mm and a defocus of 43 D. Notice how the minimum values of contrast sensitivity required to detect a spatial pattern increase only slowly.

Table 2. Values Used to Calculate Required Contrast Sensitivity[a]

Parameter	Untrained European Children	Moken Children	Trained European Children
f_a	2.95	6.06	8.01
ΔD	43	27	27
P	2.50	1.96	1.90
z	57.1	57.7	74.0
CS	2.42	2.42	2.58

[a] f_a is spatial acuity underwater (cycles per degree), ΔD is amount of defocus underwater (D), P is pupil diameter (mm). Values of ΔD are based on the assumption that the Moken children and the trained European children accommodate maximally (16 D) underwater and that the untrained European children do not accommodate at all. Pupil sizes and acuity values from earlier studies.[4,5] CS was obtained from Table 1 (lowest corresponding value) by using the values of z listed above.

can be shown to be the zeros of the second-order Bessel function $J_2(z)$. Table 1 shows the positions of these minima and the corresponding C value.

Figure 1 shows a plot of the contrast sensitivity needed to detect spatial frequencies with a pupil size of 2.5 mm and a defocus of 43 D. In the spiky peaks of the function the pattern will not be visible to a human subject. The interesting parts of this function are the regions around the minima where the least contrast sensitivity is required to detect the test pattern. These minimum values of necessary contrast sensitivity increase very slowly as the spatial frequencies become higher, which means it will be possible for humans to see spatial frequencies well beyond the first peak, or cutoff frequency. The dips and peaks of the modulation transfer function can be moved along the spatial-frequency axis by varying the amount of accommodation and–or changing the pupil size, and both can thus be used to optimize the contrast at a given spatial frequency.

The phase of the modulation transfer function will change by 180° for every minimum, which means that the wave pattern will then appear inverted (i.e., black stripes appearing where white stripes previously appeared). An additional means for the observer to obtain information about the pattern would be to change the defocus of the eye between two or more minima. To the observer this would produce an impression of movement or flip in the pattern, something indicated by some observers' comments concerning what they see underwater (unpublished observations). This movement could function as an additional cue when one is perceiving patterns in a severely defocused environment.

What does this theory tell us about the underwater visual performance of Moken and European children? The earlier studies[4,5] have provided us with values of pupil diameter P, underwater acuity f_a, and the amount of defocus ΔD for the Moken children and trained and untrained European children, values that we can use to calculate z [Eq. (3); see Table 2]. These z values provide us with a measure of how high the contrast sensitivity needs to be (see Table 1) for the underwater visual acuity shown in our earlier experiments[4,5] to be achieved (Fig. 2).

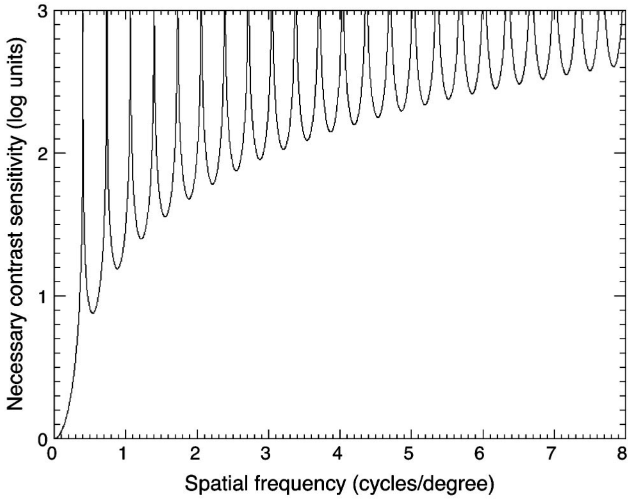

Fig. 2. Necessary contrast sensitivity as a function of spatial frequency for Moken children in an underwater environment. Accommodation of 16 D results in a defocus of 27 D; measured pupil size was 1.96 mm. This curve should be compared with that in Fig. 1, which corresponds to the pupil size and defocus of the untrained European children underwater.

3. DISCUSSION

Contrast sensitivity in humans varies according to age[6] and between individuals,[7] but by the age of 7–8 yr children have reached the adult level of contrast sensitivity.[8] The calculated necessary contrast sensitivities of the children in this study are all within the normal range of human vision [for example, at the underwater acuity noted for the Moken children (6 cycles/deg), normal contrast sensitivity lies between 2.2 and 2.6)[6,8,9]]. The trained European children seem to have acquired a better contrast sensitivity than the untrained children, but several studies have shown that contrast sensitivity can be enhanced by practice,[10–12] and an increase in contrast sensitivity clearly took place during the underwater training of the European children.[5]

An earlier study showed that Moken children have slightly better contrast sensitivity than European children.[13] It is thus a bit surprising that their calculated z value is so low. However, the z value is dependent on both the amount of defocus (i.e., the amount of accommodation and pupil constriction) and the contrast sensitivity. If the Moken children actually do not accommodate maximally, their contrast sensitivity needs to be higher to achieve the measured underwater acuity. Using Eq. (3) and assuming that they *do* have the same contrast sensitivity as the trained European children, we get a value for ΔD of 35 D; i.e., the Moken children would in this case need to accommodate only 8 D to achieve their measured underwater acuity. An indication that the trained European children actually did accommodate more than the Moken children can be observed in the size of their pupils—the pupils of the trained European children are slightly smaller than those of the Moken children. As accommodation and pupil constriction are highly coupled,[14,15] the more constricted pupils of the trained European children could be the result of differences in the amount of accommodation. Possibly this was due to enhanced motivation, as the European children were highly motivated to perform their task (unpublished observations).

Because of the experimental conditions, accommodation as such was not measured in the underwater studies. Another study has claimed that accommodation and pupil constriction are not coupled in children,[16] and the reason for the observed pupil constriction could thus be questioned—convergence instead of accommodation could be the cause. However, the experiments by Schaeffel *et al.*[16] were performed under very dim light conditions, and it is not clear whether the results would be the same if higher light intensities were used. Roth,[17] for example, claimed that dim light may limit the pupillary near reflex,[17] but the underwater experiments took place in bright light. Independent of the reason behind the pupil constriction, our paper shows that to explain the superior underwater vision of the Moken children and the trained European children, accommodation must have taken place. Pupil constriction and enhanced contrast sensitivity is simply not enough.

Since contrast sensitivity values also differ a great deal between individuals, one might suspect that some children could theoretically have even better underwater acuity than the children from our earlier studies.[4,5] The measured experimental values would thus not be extreme in any way but instead would lie within the normal range for children who have learned to control their accommodation.

Other animals may also benefit from using a smaller pupil size to improve acuity when moving from air to water. It has been suggested that seals[18] and dolphins[19,20] use a constricted pupil to improve depth of focus, and some species of semiaquatic snakes have been found to reduce pupil sizes by up to 60% when diving.[21,22] These snakes are agile predators underwater, and it is reasonable to assume that they rely on vision to catch their prey. As the optical theory used in this paper could be applied to any animal with camera eyes, knowledge of the pupil size and the amount of defocus underwater would allow calculation of the resolution limits in these snakes. Of course, the contrast sensitivity function is not known for these animals, so they possibly do not have sufficient contrast sensitivity to see beyond the first peak, or cutoff frequency, of the contrast sensitivity function (Fig. 1). However, since children underwater see spatial patterns at least ten times finer than at their cutoff frequency underwater, these semiaquatic snakes are also likely to see better underwater than this cutoff predicts.

In conclusion, pupil constriction may be a more common strategy than previously believed for animals that need to improve visual acuity when moving from air to water, or vice versa.

One last comment: The method of using gratings does not predict visual resolution when one is looking at natural scenes. Even though gratings are widely used for clinical and experimental studies, this paper shows that even with quite severe defocus it is possible to get enough information to perform much better with gratings than expected. Studies made on letters show that visual resolution drops faster under defocus if the stimuli contain complex patterns rather than one single frequency.[23] This paper explains the higher underwater visual resolution of trained European children and Moken children but also points out the limits of using gratings as visual stimuli. However, we stress that pupil constriction and accommodation will improve vision underwater no matter what is the nature of the stimuli.

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REFERENCES

1. W. J. Smith, *Modern Optical Engineering* (McGraw-Hill, New York, 1966).
2. N. C. Strang, D. A. Atchinson, and R. L. Woods, “Effects of defocus and pupil size on human contrast sensitivity,” Ophthalmic Physiol. Opt. **19**, 415–426 (1999).
3. R. L. Woods, N. C. Strang, and D. A. Atchison, “Measuring contrast sensitivity with inappropriate optical correction,” Ophthalmic Physiol. Opt. **20**, 442–451 (2000).
4. A. Gislén, M. Dacke, R. H. H. Kröger, M. Abrahamson, D.-E. Nilsson, and E. J. Warrant, “Superior underwater vision in a human population of sea-gypsies,” Curr. Biol. **13**, 833–836 (2003).
5. A. Gislén, E. J. Warrant, and R. H. H. Kröger, “Voluntary accommodation improves underwater vision in humans,”

manuscript available from the authors (anna.gislen@cob.lu.se).

6. A. Bradley and R. D. Freeman, "Contrast sensitivity in children," Vision Res. **22**, 953–959 (1982).
7. L. A. Olzak and J. P. Thomas, "Seeing spatial patterns," in *Handbook of Perception and Human Performance*, K. R. Boff, L. Kaufman, and J. P. Thomas, eds. (Wiley, New York, 1986), Chap. 7.
8. J. Gwiazda, J. Bauer, F. Thorn, and R. Held, "Development of spatial contrast sensitivity from infancy to adulthood: psychophysical data," Optom. Vision Sci. **74**, 785–789 (1997).
9. F. W. Campbell and J. G. Robson, "The application of Fourier analysis to the visibility of gratings," J. Physiol. (London) **197**, 551–566 (1968).
10. K. K. De Valois, "Spatial frequency adaptation can enhance contrast sensitivity," Vision Res. **17**, 1057–1065 (1977).
11. P. T. Sowden, I. R. L. Davies, and P. Roling, "Perceptual learning of the detection of features in X-ray images: a functional role for improvement in adults' visual sensitivity?" J. Exp. Psychol. Hum. Percept. Perform. **26**, 379–390 (2000).
12. P. T. Sowden, D. Rose, and I. R. L. Davies, "Perceptual learning of luminance contrast detection: specific for spatial frequency and retinal location but not orientation," Vision Res. **42**, 1249–1258 (2002).
13. A. Gislén and M. Dacke, "A simple way to assess contrast sensitivity in children living in remote areas," manuscript available from the authors (anna.gislen@cob.lu.se).
14. H. Davson, *Physiology of the Eye*, 5th ed. (MacMillan, London, 1990), p. 830.
15. E. Marg and M. W. Morgan, "The pupillary near reflex," Am. J. Optom. Arch. Am. Acad. Optom. **26**, 183–198 (1949).
16. F. Schaeffel, H. Wilhelm, and E. Zrenner, "Inter-individual variability in the dynamics of natural accommodation in humans: relation to age and refractive errors," J. Physiol. (London) **461**, 301–320 (1993).
17. N. Roth, "Effect of reduced retinal illuminance on the pupillary near reflex," Vision Res. **9**, 1259–1266 (1969).
18. J. G. Sivak, "A survey of vertebrate strategies for vision in air and water," in *Sensory Ecology*, M. A. Ali, ed. (Plenum, New York, 1978), pp. 503–519.
19. L. Herman, M. F. Peacock, M. P. Yunker, and C. J. Madsen, "Bottlenose dolphin: double-slit pupil yields equivalent aerial and underwater diurnal activity," Science **189**, 650–652 (1975).
20. L. A. Rivamonte, "Eye model to account for comparable aerial and underwater acuities of the bottlenose dolphin," Neth. J. Sea Res. **10**, 491–498 (1976).
21. F. Schaeffel, "Underwater vision in semi-aquatic European snakes," Naturwissenschaften **78**, 373–375 (1991).
22. F. Schaeffel and A. De Queiroz, "Alternative mechanisms of enhanced underwater vision in the Garter snakes *Thamnopsis melanogaster* and *T. couchii*," Copeia **1**, 50–58 (1990).
23. F. Thorn and F. Schwartz, "Effects of dioptric blur on Snellen and grating acuity," Optom. Vision Sci. **67**, 3–7 (1990).