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.

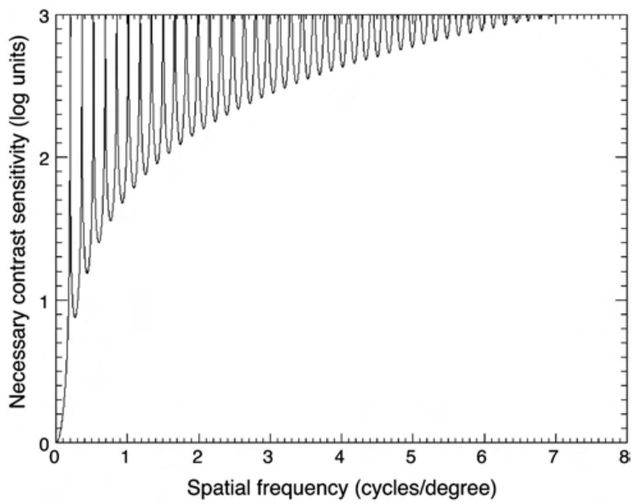

Fig. 1. Necessary contrast sensitivity as a function of spatial frequency, with a set pupil diameter of 2.50 mm and a defocus of 43 D. Notice how the minimum values of contrast sensitivity required to detect a spatial pattern increase only slowly.

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).

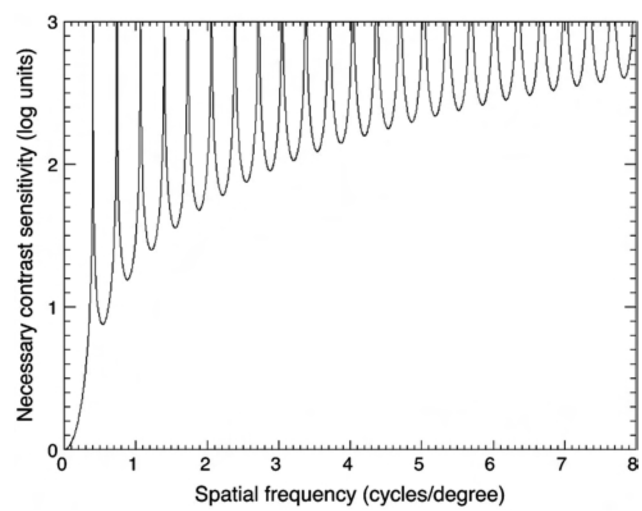

Fig. 2. Necessary contrast sensitivity as a function of spatial frequency for Moken children in an underwater environment. Accommodation of 16 D results in a defocus of 27 D; measured pupil size was 1.96 mm. This curve should be compared with that in Fig. 1, which corresponds to the pupil size and defocus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

Corresponding author Anna Gislén may be reached by e-mail at anna.gislen@cob.lu.se.

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