

Visual training improves underwater vision in children

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Received 26 October 2005; received in revised form 28 April 2006

Abstract

Children in a tribe of sea-gypsies from South-East Asia have been found to have superior underwater vision compared to European children. In this study, we show that the improved underwater vision of these Moken children is not due to better contrast sensitivity in general. We also show that European children can achieve the same underwater acuity as the Moken children. After 1 month of underwater training (11 sessions) followed by 4 months with no underwater activities, European children showed improved underwater vision and distinct bursts of pupil constriction. When tested 8 months after the last training session in an outdoor pool in bright sunlight—comparable to light environments in South-East Asia—the children had attained the same underwater acuity as the sea-gypsy children. The achieved performance can be explained by the combined effect of pupil constriction and strong accommodation.

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Keywords: Pupil; Accommodation; Acuity; Contrast sensitivity; Perceptual learning

1. Introduction

Seeing well underwater is not an easy task for a human being. Our eyes, being adapted to the terrestrial environment, lose more than two-thirds of their refractive power when immersed in water (Land, 1987). These two-thirds—or roughly 43 dioptres (D)—can be partly compensated for by accommodation, but never completely. High underwater acuity can only be achieved by using a diving mask that reintroduces the air-cornea interface.

In a recent study, sea-gypsy children in South-East Asia, the Moken, were found to see much better underwater than European children of the same age (Gislén et al., 2003). The Moken children's spatial resolution was more than twice as good (6.06 ± 0.59 c/deg compared to 2.95 ± 0.13 c/deg in the European children). It has been shown theoretically that such an improvement in underwater acuity may be achieved by the combined effect of maximum accommodation and pupil constriction, the latter increasing depth of field (Gislén & Gislén, 2004). These two

processes are also linked to each other as accommodation in all but extreme cases induces pupil constriction (Davson, 1990; Marg & Morgan, 1949). The mechanism triggering accommodation underwater, however, remains elusive. The underwater environment does not normally elicit reflex accommodation since it provides a retinal image that is far too blurry (Heath, 1956). One explanation for the surprisingly high underwater acuity of the Moken children could be that they have learned to accommodate when diving, thus explaining the pupil constriction observed by Gislén et al. (2003).

It is well established that human subjects can learn to accommodate voluntarily with practice (Cornsweet & Crane, 1973; Marg, 1951; McLin & Schor, 1988; Provine & Enoch, 1975; Roscoe & Couchman, 1987). However, the stimuli used in all of these studies were nowhere near as blurry as those that occur in an underwater environment. Provine and Enoch (1975) provided 9 D defocusing blur using contact lenses, and even from this comparatively weak blur the subjects reported side-effects including headaches, nausea, dizziness, and eye strain when trying to see the target more clearly. In all of the other studies accommodative demand was much smaller and in some cases

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there is no report on the strength of the accommodative stimuli at all. Moreover, children were not used in any of these studies. It is thus still unclear whether children might have the ability to use accommodation and concurrent pupil constriction as a means of improving underwater vision.

The improved underwater vision of the Moken children might partially be due to a general improvement in contrast sensitivity, which would reduce the accommodative effort needed. The contrast sensitivity function of a subject shifts upwards to higher sensitivities after practice using spatial gratings (De Valois, 1977), and Sowden et al. have recently shown that the ability to resolve low-contrast images is influenced by practice (Sowden, Davies, & Roling, 2000; Sowden, Rose, & Davies, 2002). Exposure to blur has also been shown to change both visual acuity and contrast sensitivity to some extent (Mon-Williams, Tresilian, Strang, Kochhar, & Wann, 1998; Rosenfield, Hong, & George, 2004; Webster, Georgeson, & Webster, 2002). As the brain and visual system are highly plastic (Gilbert, 1996; Karni & Bertini, 1997), the enhanced underwater acuity of the Moken children might thus be explained not only by learning to accommodate, but also by changes in the visual pathways of the nervous system.

To resolve this lack of clarity we measured contrast sensitivity on land in Moken and European children to determine whether improved general contrast sensitivity could account for the better underwater visual acuity of the Moken children. Since this was not the case, we trained European children in an underwater visual discrimination task to elucidate whether they could improve their visual acuity in this medium as a result of learning to control the optical apparatus of the eye.

If they could learn to do this we would observe pupil constriction and accommodation in trained children, but not in untrained ones. We thus measured pupil size during diving in both trained and untrained children and also attempted to measure accommodation in diving children. We then related the obtained results to the predictions of the previously published theoretical analysis, which suggested pupil constriction and maximum accommodation as the mechanisms explaining the improved underwater acuity (Gislén & Gislén, 2004).

2. Methods

2.1. Contrast sensitivity measurements

We used the Pelli–Robson chart at different distances to assess contrast sensitivity (Pelli & Farell, 1999; Pelli, Robson, & Wilkins, 1988). This method was used as there is no electricity where the Moken children live, the equipment had to be light and small for transport, and data collection time for each child was limited. In addition to Moken children (6 children, 4 girls and 2 boys age = 9–13), we performed measurements on European children in Thailand who were on holiday with their families (5 children, 3 girls and 2 boys, age = 9–11). Children from a school in Lund, Sweden, were used as a reference group (20 children, 15 girls and 5 boys,

age = 9–10). These children were tested in Sweden. None of the subjects wore correction glasses or had any known visual defect. All Pelli–Robson tests were done on land with the eyes in air.

The Pelli–Robson chart consists of eight lines of letters with each letter subtending 3° at 1 m distance. Each line contains two groups of three letters, each group having a different contrast. At the top left corner the contrast is 100%, and the contrast in each consecutive group decreases by $1/\sqrt{2}$ to 0.6% at the lower right corner. Threshold detection of letters at the top left corner then corresponds to a contrast sensitivity of 0.00 log-units, and this increases by 0.15 log-units for each consecutive group. Threshold detection for the letter group in the lower right corner then corresponds to a contrast sensitivity of 2.25 log-units. The chart has two sides with different groups of letters and all letters are Sloan letters C, D, H, K, N, O, R, S, V, and Z in random order.

The Swedish children in the reference group were tested outdoors in Sweden to mimic the conditions found in remote areas far from civilization. On all occasions the test was performed in the shade where light levels were 300 cd/m^2 as measured with a Spotmeter V (Pentax) using a Kodak 18% grey card (light level should exceed 85 cd/m^2 for the Pelli–Robson test). The distances between the chart and the child were 3, 6, 9, and 12 m, with tests always starting at the shorter distance. As the chart has two sides with different letters, we switched sides when changing the distance and randomized the starting side. The child was asked to identify the letters starting from the top left corner. In the testing procedure, the subject was allowed to make one mistake in each triplet and the letters O and C are interchangeable. When the subject made two or three mistakes in a triplet the contrast of the previous triplet was used to determine the contrast sensitivity limit. The children were encouraged to take their time looking at the low contrast letters.

Contrast sensitivities of European children in Thailand were measured in the same way, the test being set up in the shade where light levels were 350 cd/m^2 . The Moken children were studied at Ko Surin, Thailand. As the Moken children were not familiar with letters (they have their own language although some of them speak some Thai) we had a representation of the letters on a board on which they could point out the correct letter. The children grasped the concept quickly and had no trouble following our instructions.

2.2. Underwater visual training of European children

Four young females (one 13-year-old, three 9 year-old) were used as subjects, from now on called A, B, C, and D. The training experiments were performed in an indoor swimming pool (Högevallsbadet, Lund, Sweden). All training and tests were conducted between 2 and 4 pm, and light intensity at the surface of the pool during these hours was 8 cd/m^2 as measured with a Spotmeter V (Pentax) using a Kodak 18% grey card.

Training was conducted 11 times during 33 days. Four months after the last training session we did a follow-up study where each child's underwater acuity and contrast threshold were measured again. The same tests were conducted once more 8 months after the last training session, this time in an outdoor pool in bright sunshine (light levels 4500 cd/m^2) in the Swedish summer.

On Day 1 (before the first training session) and Day 33 (after the last training session), we measured pupil diameter on land and underwater as well as underwater acuity and contrast threshold. Sinusoidal gratings were used as stimuli, presented either vertically or horizontally at random. For determining spatial resolution, 100% contrast gratings of 1.75, 2.18, 2.49, 2.91, 3.49, 4.36, and 5.82 c/deg were used. Each child dived down and put the forehead on the stationary headrest viewing the pattern at a distance of 50 cm. When the child surfaced, he or she was asked to indicate the orientation of the pattern. Each grating was presented five times and five correct answers were interpreted as evidence that the child could resolve the grating (the probability of the child correctly guessing five times in a row is less than 5%). Any other result was interpreted as an inability to resolve the pattern. Finer and finer gratings were then presented until the child could no longer correctly determine which way the gratings were oriented. The finest grating the child could resolve was taken as the resolution limit. For underwater contrast sensitivity measurements, a grating

of 0.44 c/deg was used with various contrasts [0.19, 0.24, 0.30, 0.40, 0.48, 0.56, 0.65, and 0.76 (log-values)]. Contrast sensitivity, defined as the reciprocal of threshold contrast, was determined by the same threshold criterion of five correct answers.

During training, the subjects practiced to correctly detect the orientations of particular gratings, one at threshold acuity and one at threshold contrast. To each subject, the patterns were presented 10 times at random orientations and the child was instructed to try really hard to determine which way the presented pattern was oriented. After a training session was terminated, a testing session was conducted to determine whether the child's ability to see underwater had improved or not. If performance had improved, a new resolution limit and/or contrast threshold was noted and used in subsequent training sessions.

2.3. Measurements of pupil diameters

Equivalent measurements had earlier been performed on Moken and European children in Thailand (Gislén et al., 2003). We took measurements on the children trained in Sweden. An infrared-sensitive video camera (Sony) in a watertight housing was used to record pupil diameters, both on land and underwater. The lens of the camera was covered with an infrared transmitting filter that blocked visible light (Schott RG 9). Iris diameter of each child was first measured on land to obtain a reference for underwater measurements of pupil diameter. Each child was asked to put the forehead against a stationary headrest with the camera positioned 50 cm in front of the headrest. On the headrest, facing the camera, a metric scale was placed for calibration of measurements. During recording, the child was asked to keep the head as steady as possible.

The experimental setup was then submerged. Forty-eight light-emitting diodes, positioned on a circle around the camera lens and powered by a 21 V DC source, were used as an infrared light source. The diodes could be turned on and off by a reed switch, controlled by a magnet outside the watertight housing. The child was asked to dive down, put the forehead on the headrest, and look in the direction of the stimulus (a sinusoidal grating of 2.91 c/deg, subtending 22.6° of the visual field) during the entire dive. The stimulus was centered in front of the camera with a hole in the middle for the camera to record through. The response of the pupil underwater was filmed throughout the dive (typically 6–8 s) and the first 0.5 s of each recording were excluded from the analysis to avoid bias by onset fluctuations. As the child's head for safety reasons could not be completely stabilized underwater, the measured iris diameter on land was used to calibrate underwater measurements of pupil diameter.

Frames were extracted using Adobe Premiere 6.0 software. Pupil diameters were measured in Adobe Photoshop 7.0, where the edges of the pupil were detected by a threshold criterion of pixel contrast.

2.4. Measurements of accommodation under water

The subjects were two females (11 and 13 years) and two males (13 and 48 years), from now on called E, F, G, and H, respectively. The children had no known refractive errors; the adult was 1.5 dioptres hyperopic in both eyes. An infrared photoretinoscope (Schaeffel, Farkas, & Howland, 1987; Schaeffel, Wilhelm, & Zrenner, 1993) was assembled from an infrared-sensitive video camera (Sony) and six tightly packed infrared light-emitting diodes (ir-LEDs) as light source. The eccentricity of the light source below the optical axis was 50 mm and the lower half of the camera objective was covered with a black occluder. The apparatus was used from a distance of 50 cm. Light intensity was 4 cd/m². The subject looked through a glass window while diving and was confronted with a grating target. The eyes of the diving subject were videotaped with the ir-LEDs switched on. Frames were later exported for analysis using Adobe Premiere 6.0 software. The analysis was done with Scion Image Beta 4.0.2 and Microsoft Excel 2002 SP3 software. Refractive state of the eye was calculated according to (Bobier & Braddick, 1985) and (Howland, 1985) as

$$RS = e/(d * df * p) \quad (1)$$

where e is the eccentricity of the light source, d the distance between the eye and the light source (and camera), and p pupil diameter. The optical reduction of the eccentricity of the light source by the water–air interface was calculated as

$$e = E/(n_w * af) \quad (2)$$

where E is the actual eccentricity (50 mm), n_w the refractive index of water (1.333), and af the fraction in air of the distance between the eye and the camera (0.94). The optical effect of the glass window was neglected.

Tests were performed on untrained European children who were instructed to try hard to solve a visual task and to occasionally cross their eyes to induce accommodation. For comparison, measurements were taken under the same conditions on a 48-year-old adult who had an accommodative range of 3 dioptres at maximum. Underwater visual acuity was not quantified in detail in the children participating in these tests since the number of dives was kept to a minimum in order to minimize training effects.

2.5. Informed consent

Following the tenets of the Declaration of Helsinki, all subjects were fully informed on the nature of the tests and for the minors written consent was obtained from the parents before the experiments.

3. Results

3.1. Contrast sensitivity

We did not find any significant difference between the European children tested in Thailand or Sweden (t -test: $p > 0.05$ at all distances) and therefore pooled the results from these two groups (Fig. 1). The lack of a difference is

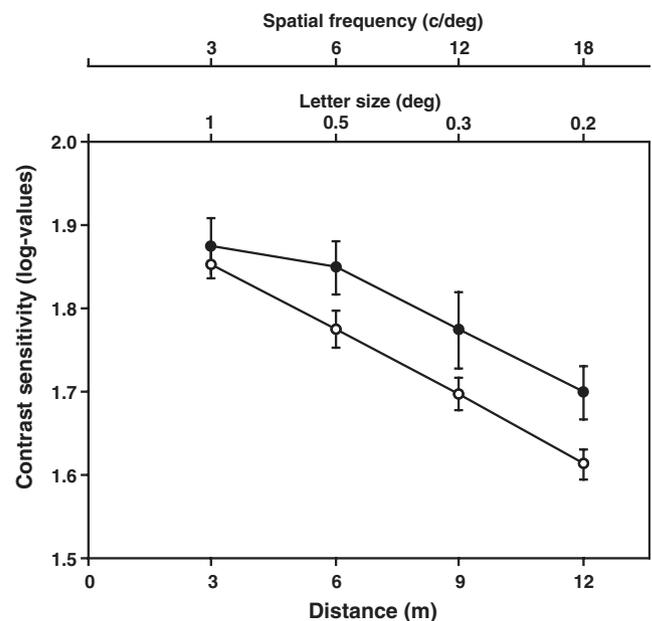


Fig. 1. Contrast sensitivity as measured with a Pelli–Robson test at different distances. Black circles, Moken children, white circles, European children. Error bars represent SE. The Moken children have slightly better contrast sensitivity at all distances, significantly so at 9 and 12 m distance. (t -test: $p < 0.05$). Equivalent spatial frequencies for letters are calculated from the fact that observers use the same channel to detect a grating with a spatial frequency of 3-deg and 1-deg letter (Solomon & Pelli, 1994; Pelli and Farell, 1999).

not surprising considering that the Pelli–Robson test has been found to be quite robust under a variety of light environments (Zhang, Pelli, & Robson, 1989), a necessary property for us since light levels could not be strictly controlled in remote areas of Thailand.

The Moken children had, on average, slightly better sensitivities at all distances, although not significantly so at 3 and 6 m (t -test: $p = 0.29$ and 0.069 , respectively). Only at distances of 9 and 12 m had the Moken children significantly higher contrast sensitivities (t -test: $p = 0.047$ and 0.020 , respectively).

3.2. Training experiments

All four children improved their performances during the training period, in terms of both underwater acuity and contrast sensitivity. On Day 1, before training had commenced, the mean acuity for all four children was 2.63 ± 0.18 c/deg (mean \pm SEM). On the last day, underwater acuity had improved by 27% to 3.35 ± 0.14 c/deg (Fig. 2). Contrast sensitivity improved from 0.26 ± 0.03 to 0.56 ± 0.09 , an improvement of 0.30 log-units (Fig. 3).

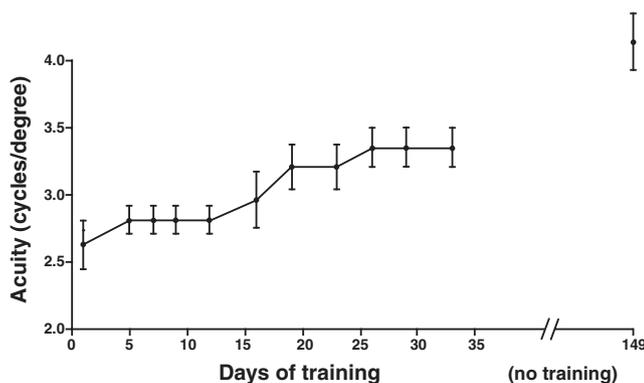


Fig. 2. Underwater acuity improved during training. The curve shows the mean of four subjects (age 9–13 years) with error bars representing standard error of the mean (SEM). Training took place 11 times during 33 days, and a follow-up study was performed on Day 149.

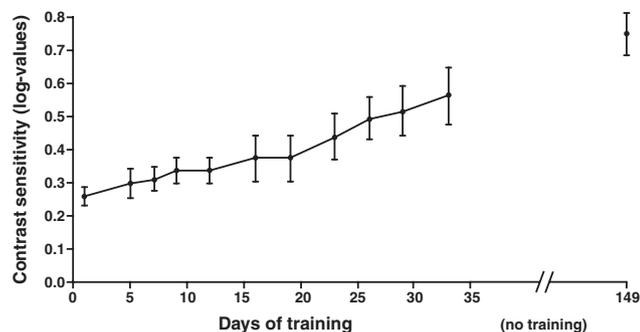


Fig. 3. Underwater contrast sensitivity for a sinusoidal grating pattern of 0.44 c/deg improved during training. The curve shows the mean of four subjects (age 9–13 years) with error bars representing SEM. Training took place 11 times during 33 days, and a follow-up study was performed on Day 149.

For one subject (D), however, acuity did not improve by more than 17% and contrast sensitivity only improved by 0.12 log-units.

Measurements of pupil diameters showed that there was a dramatic change in the temporal pattern of pupil constriction in all children except for subject D (Fig. 4). Before training, no constriction took place upon diving and pupil diameter showed only small fluctuations underwater. On the last day of training, three of the subjects exhibited bursts of pupil constriction while submersed (Fig. 4A–C) and the mean pupil diameters in these three subjects now differed significantly from the mean pupil diameters on Day 1 (Day 1: 5.79 ± 0.02 mm, 5.87 ± 0.01 mm, 6.34 ± 0.02 mm; Day 33: 4.97 ± 0.05 mm, 4.72 ± 0.05 mm, 5.68 ± 0.04 mm, respectively; t -test $p < 0.0001$ in all cases; values are mean \pm SEM). Subject D (Fig. 4D), however, showed no change in the amount of pupil constriction (Day 1: 6.92 ± 0.02 mm; Day 33: 6.86 ± 0.03 mm; t -test $p = 0.1319$). Excessive convergence was not observed in any of the children.

In the first follow-up study performed 4 months later, underwater acuities and contrast sensitivities had further increased, even though the subjects had not participated in any underwater activities after the initial 11 training sessions. Mean acuity was now 4.14 ± 0.22 c/deg and mean contrast sensitivity 0.76 ± 0.06 , an improvement of 57% and 0.5 log-units, respectively. Subject D had improved the most, almost to the level of the other subjects. All subjects now exhibited pupil constriction when diving and the response seemed to be even more pronounced than before (Day 149: mean pupil diameters in subject A to D when diving were 4.78 ± 0.06 mm, 4.56 ± 0.07 mm, 5.31 ± 0.06 mm, 6.00 ± 0.10 mm; the constriction pattern of subject D is shown in Fig. 4D).

The above tests were conducted under rather low light conditions due to the demands of the season. To be able to compare the level of improvement of the European children to the performances of the Moken children, a second follow-up study was conducted during the summer in bright sunshine at Källbybadet (Lund, Sweden), using the same experimental procedure as before. The experiments took place between 10 am and 2 pm and light levels were 4500 cd/m², equivalent to measured light levels in Thailand (4600 cd/m² in the sun). The four children now showed much improved acuity underwater with a mean value of 8.01 ± 0.72 c/deg, compared to the 2.95 ± 0.13 c/deg under the same lighting conditions in earlier experiments (Gislén et al., 2003). Initial pupil diameters were small on land due to the bright light, but all children exhibited pupil constriction when diving (mean pupil diameters: on land 2.21 ± 0.01 mm, underwater 1.90 ± 0.01 mm). Such pupil constriction during diving is absent in untrained European children but similar to that found in Moken children (Gislén et al., 2003). The underwater acuity of the trained European children now equaled or surpassed that of the Moken children, the two groups not differing significantly (European children 8.01 ± 0.72 c/deg, Moken children 6.06 ± 0.59 c/deg; Mann–Whitney test: $p > 0.05$).

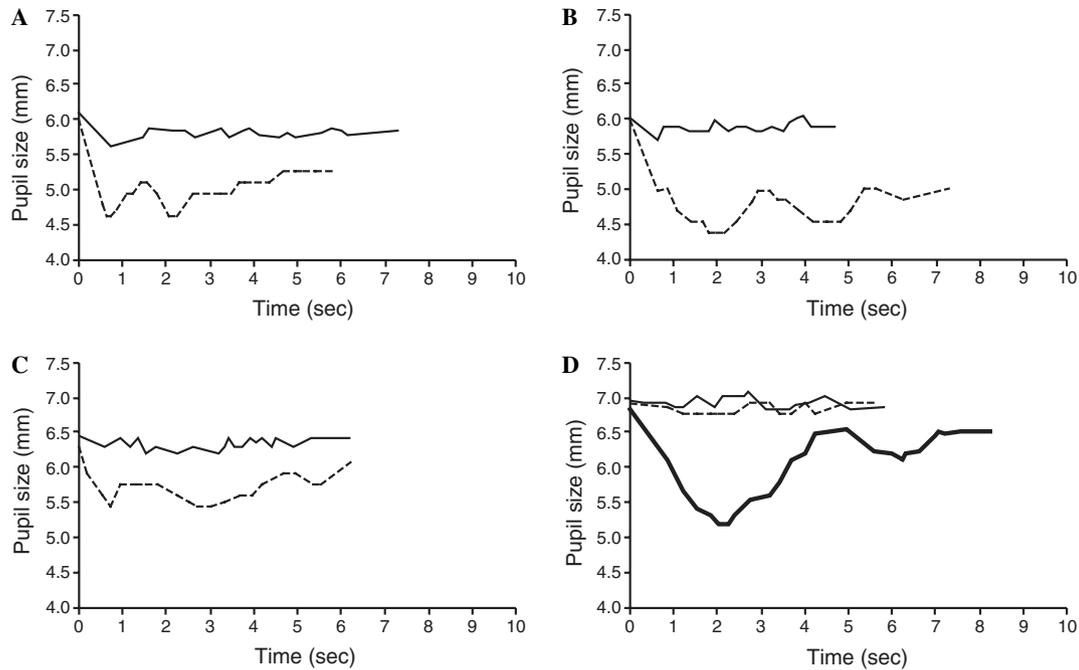


Fig. 4. Changes in pupil diameter during diving for four different subjects (A–D), aged 9–13 years. Thin solid line, typical pupil diameter changes before underwater acuity training. Dashed line, typical pupil diameter changes after 33 days of training. Error bars represent SEM. All children except subject D showed constriction in bursts after training. Even subject D did exhibit pupil constriction when diving 149 days after training had been initiated (thick solid line).

3.3. Measurements of accommodation

Voluntary crossing of the eyes by the diving children was correlated with constriction of the pupils and an upward movement of the retinoscopic reflex (Fig. 5A and B). Subject G was not able to voluntarily cross his eyes. This subject showed repeated bursts of pupil constriction, little or no convergence, and an upward movement of the retinoscopic reflex when confronted with a grating that could be resolved. When the target could not be resolved, such a reaction occurred only in the beginning of the dive. All children showed some improvement of underwater acuity during the experiments that required five diving sessions. Subject E quickly learned to keep one eye directed on the grating while crossing her eyes (Fig. 5B). When she did so, she considerably outperformed the about equally experienced subjects F and G.

Underwater refractive states of the children calculated with Eq. (1) were 30.1 ± 4.3 dioptres in the relaxed state (large pupil) and 26.4 ± 1.6 dioptres when accommodation was induced (small pupil) by voluntary convergence (subjects E and F) or a grating that could just be resolved (subject G). Refractive state calculated for subject H (48 years) was 32.3 ± 2.8 dioptres.

4. Discussion

All European children in the training experiments improved both their spatial acuities and specific contrast sensitivities underwater. From our results we can rule out that the enhanced underwater contrast sensitivities of the

Moken and trained European children is due to better contrast sensitivity per se as the difference in general contrast sensitivity in Moken children and untrained European children is small or non-existent at the low spatial frequencies of the patterns used in the underwater experiments. Other possible factors such as differences in resting refractive state, accommodative range, and corneal curvature had been ruled out in the first study on Moken children (Gislén et al., 2003).

A theoretical analysis published earlier (Gislén & Gislén, 2004) has revealed that the superior underwater visual capabilities of Moken children, when compared with untrained European children, may be explained by maximum accommodation (16 D) and the observed difference in underwater pupil diameter (1.96 vs. 2.50 mm, Moken vs. untrained European children, respectively). No difference in general contrast sensitivity had to be postulated (2.42 log-units in both groups; Gislén & Gislén, 2004). Our current results show that the contrast sensitivities of Moken and untrained European children indeed are similar at the low spatial frequencies used in underwater experiments.

Neural adaptation to visual blur has been shown to improve both contrast sensitivity and visual acuity. However, it has most likely not influenced our contrast sensitivity measurements, as Mon-Williams et al. (1998) found no effect of habituation to blur on contrast sensitivity at frequencies below 5 c/deg. It may, however, have slightly influenced visual acuity: Rosenberg et al. (2004) noticed an improvement in visual acuity in myopic subjects after only 3 h of exposure to blur. If this kind of adaptation took

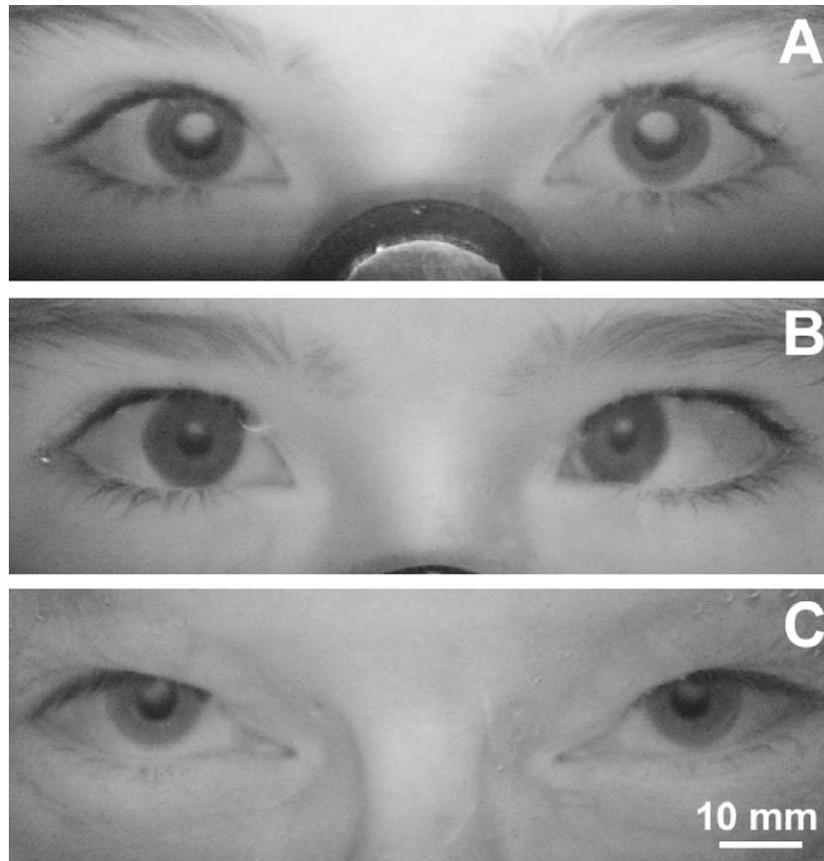


Fig. 5. Infrared photoretinoscopic images of an untrained female child 11 years of age (A,B; subject E) and a 48-year-old male adult (C; subject H). The subjects were diving and through a glass window looking at a grating held close to the camera in air. The round structure central in (A), barely visible also in (B), is a suction cup that was used as an orientation aid for correct positioning of the head. The large pupils in (A) suggest that the child had relaxed accommodation. In (B) the child had crossed her eyes, keeping the right eye directed toward the visual stimulus and camera. Voluntary convergence usually induces strong accommodation, which is consistent with the reduction of pupil sizes (compare A and B). Images of this kind were used in an attempt to determine refractive states in diving subjects.

place in our subjects, the effect would have been rather immediate and cannot explain the improvement later on. Blur adaptation may nevertheless to some extent have reduced the need for accommodation, though only by roughly one dioptre.

The attempt to measure accommodation underwater using photoretinoscopy returned inconsistent results. Refractive states of about 26 dioptres of hyperopia as indicated when the children made an effort to see better underwater (constricted pupils) would be an expected result if the children accommodated about 17 D. The relaxed human eye is defocused by about 43 dioptres underwater (Land, 1987) and children between 11 and 13 years of age are able to accommodate up to about 15 dioptres (Westheimer, 1986). However, refractive states of about 30 dioptres of hyperopia in relaxed children (open pupils) would mean that the subjects accommodated more than 10 dioptres upon diving without concurrent pupil constriction. This is a quite unlikely result that persisted despite various adjustments to the setup. Also, the results obtained from a 48-year-old adult—whose accommodative range was limited to three

dioptres—seem to indicate that even a near-presbyopic adult accommodated by about 10 dioptres upon diving. It is thus clear that photoretinoscopy in the form we used it does not to return reliable results in diving humans.

If the experienced diving children accommodated, concurrent pupil constriction is an expected effect. Before training had commenced, no child in the training experiment showed any sign of pupil constriction during diving, which suggests that no compensation for defocus took place. After 11 sessions of training, three subjects showed significantly smaller pupil diameters during diving (Fig. 4) while the remaining child showed similar reduction in pupil diameter first in the follow-up study 4 months after the last training session (Fig. 4D). The pattern of pupil constriction suggests that accommodation came in bursts. Possible reasons for this are that it may have been too strenuous for the children to strongly accommodate for longer periods of time or that the trained European children had not (yet) acquired the same amount of control over their eyes as the much more experienced Moken children.

Excessive convergence was not seen in neither in the trained European children nor the Moken children. In order to see well underwater, these children seem to have learned to uncouple accommodation from convergence while diving. Uncoupling convergence from accommodation can be achieved by most subjects after some training—a requirement for viewing certain types of three-dimensional images (Rushton & Ridell, 1999; Schowengerdt & Seibel, 2004).

Amongst the European children under training, there was sometimes a clear improvement from 1 day to the other, and when asked they could not explain how they did it, just that they “could see it much better now”. This indicates that the children unconsciously compensated for underwater defocus. The results of the second follow-up study in a bright outdoors environment also show that the children’s ability to compensate became so good that they achieved at least the same ability to solve the underwater visual tasks as the Moken children. The superior performance of trained European children (8.01 vs. 6.06 c/deg in the Moken children) may to some extent have been due to their extensive experience in looking at highly defocused gratings. They may have learned to make better use of spurious resolution, which certainly is a factor in this type of experiment (Gislén & Gislén, 2004). It is, however, also clear from the theoretical analysis (Gislén & Gislén, 2004) that the achieved performance can only be explained if the children accommodated strongly, which is in agreement with the observed pupil constrictions.

Interestingly, the subject whose learning process took the longest was the child with the largest pupil diameter, and this may have affected her chances of controlling pupil closure. Children naturally have larger pupils than adults (Kadlecova, Peleska, & Vasko, 1958; Winn, Whitaker, Elliott, & Phillips, 1994) and this may affect the pupillary near response. In some studies where initial pupil diameter has been large, the authors reported only minor pupil constrictions when children accommodated (Schaeffel et al., 1993; Wilhelm, Schaeffel, & Wilhelm, 1993). In another study, where the initial pupil diameter of young subjects was slightly smaller due to higher ambient illumination, the pupillary response from accommodation was pronounced (Schäfer & Weale, 1970). Thus, children seem to be affected more than adults by the conflict between the regulation of light levels on the retina and pupil constriction induced by accommodation. Schäfer and Weale (1970) also observed that if subjects of different ages start with the same pupil diameter, accommodation induces a greater constriction response in the older subjects. The reflex to constrict the pupil when accommodating may still be under development in young people, or the connection may not always be functional when light levels are low.

The larger pupil of subject D may thus have been a problem when she tried to accommodate—she may have suffered more than the other subjects from what is known as “night presbyopia” (Alpern & Larson, 1960). However, although her learning was slower, her underwater visual abilities

eventually improved (after 4 months) almost to the levels in the other subjects. This means that there are individual differences in the learning process. Such variability between subjects in learning rate is common when training perceptual tasks (Fahle & Edelman, 1993). Learning to control accommodation seems to be no exception. From the results of the follow-up studies we also conclude that the ability to learn to accommodate in response to underwater defocus is subject to what is commonly known as consolidation, or reminiscence (Mollon & Danilova, 1996)—that is, the effect of training is not manifested until after a certain period of time has elapsed, with training-induced neural processes continuing to develop even after practice has ceased. This effect has been shown in several studies concerning visual performance (Gilbert, Sigman, & Crist, 2001; Karni, Tanne, Rubenstein, Askenasy, & Sagi, 1994; Sagi & Tanne, 1994), memory processes (Gaffan, 1996), and motor skills (Brashers-Krug, Shadmehr, & Bizzi, 1996; Karni & Sagi, 1993).

5. Conclusion

It is clear from this study that Moken children, which are highly experienced in underwater visual tasks, do not have significantly higher general contrast sensitivities in the critical range than untrained European children. Other neuronal changes in the visual pathways can only explain a fraction of the observed ability to see better underwater. Accommodation and pupil constriction, however, can together improve underwater vision to the observed degree.

The most likely explanation for the superior underwater performances of Moken and trained European children is therefore that they have learned to control their accommodation—which would result in the observed constrictions of the pupil—and to decouple accommodation from convergence. In this paper, we have thus provided an explanation for how the ability to see better underwater has developed in the Moken people of South-East Asia who depend on superior underwater acuity for their survival.

Acknowledgments

We thank the children who participated in these experiments, Maths Abrahamson for providing us with invaluable help with the design of the ophthalmological tests, and Howard Howland and Frank Schaeffel for advice on photoretinoscopic measurements. We like to thank our guide in Thailand, Aroon Thaewchatturat. Financial support came from the Swedish research council (EW: 621-2002-348, RK: 621-2001-1574).

References

- Alpern, M., & Larson, B. F. (1960). Vergence and accommodation. *American Journal of Optometry*, 49, 1140–1149.
- Bobier, W. R., & Braddick, O. J. (1985). Eccentric photorefractive optical analysis and empirical measures. *American Journal of Optometry Physiological Optics*, 62(9), 614–620.

- Brashers-Krug, T., Shadmehr, R., & Bizzi, E. (1996). Consolidation of human motor memory. *Nature*, *382*, 352–355.
- Cornsweet, T. N., & Crane, H. D. (1973). Training the visual accommodation system. *Vision Research*, *13*, 713–715.
- Davson, H. (1990). *Physiology of the eye*. London: The MacMillan Press Ltd, p. 830.
- De Valois, K. K. (1977). Spatial frequency adaptation can enhance contrast sensitivity. *Vision Research*, *17*, 1057–1065.
- Fahle, M., & Edelman, S. (1993). Long-term learning in vernier acuity: effects of stimulus orientation, range and of feedback. *Vision Research*, *33*(3), 397–412.
- Gaffan, D. (1996). Associative and perceptual learning and the concept of memory systems. *Cognitive Brain Research*, *5*, 69–80.
- Gilbert, C. D. (1996). Learning and receptive field plasticity. *Proceedings of the National Academy Sciences of the United States of America*, *93*, 10546–10547.
- Gilbert, C. D., Sigman, M., & Crist, R. E. (2001). The neural basis of perceptual learning. *Neuron*, *31*, 681–697.
- Gislén, A., Dacke, M., Kröger, R. H. H., Abrahamson, M., Nilsson, D.-E., & Warrant, E. J. (2003). Superior underwater vision in a human population of sea-gypsies. *Current Biology*, *13*(10), 833–836.
- Gislén, A., & Gislén, L. (2004). On the optical theory of underwater vision in humans. *Journal of Optical Society A*, *21*(11), 2061–2064.
- Heath, G. G. (1956). The influence of visual acuity on accommodative responses of the eye. *American Journal of Optometry*, *33*, 513–524.
- Howland, H. C. (1985). Optics of photoretinoscopy—results from ray tracing. *American Journal of Optometry Physiological Optics*, *62*(9), 621–625.
- Kadlecova, V., Peleska, M., & Vasko, A. (1958). Dependence on age of diameter of the pupil in the dark. *Nature*, *182*, 1520–1521.
- Karni, A., & Bertini, G. (1997). Learning perceptual skills: behavioural probes into adult cortical plasticity. *Current Biology*, *7*, 530–535.
- Karni, A., & Sagi, D. (1993). The time course of learning a visual skill. *Nature*, *365*, 250–252.
- Karni, A., Tanne, D., Rubenstein, B. S., Askenasy, J. J. M., & Sagi, D. (1994). Dependence on REM sleep of overnight improvement of a perceptual skill. *Science*, *265*, 679–682.
- Land, M. F. (1987). Vision in air and water. In P. Dejours, L. Bolis, C. R. Taylor, & E. R. Weibel (Eds.), *Comparative physiology: Life in water and on land* (pp. 289–302). Padova: IX-Liviana Press.
- Marg, E. (1951). An investigation of voluntary as distinguished from reflex accommodation. *American Journal of Optometry*, *28*, 347–356.
- Marg, E., & Morgan, M. W. (1949). The pupillary near reflex. *American Journal of Optometry*, *26*(5), 183–198.
- McLin, L. N., & Schor, C. M. (1988). Voluntary effort as a stimulus to accommodation and vergence. *IOVS*, *29*(11), 1739–1746.
- Mollon, J. D., & Danilova, M. V. (1996). Three remarks on perceptual learning. *Spatial Vision*, *10*(1), 51–58.
- Mon-Williams, M., Tresilian, J. R., Strang, N. C., Kochhar, P., & Wann, J. P. (1998). Improving vision: neural compensation for optical defocus. *Proceedings of the Royal Society of London B*, *265*, 71–77.
- Pelli, D. G., & Farell, B. (1999). Why use noise? *Journal of the Optical Society of America A*, *16*(3), 647–653.
- Pelli, D. G., Robson, J. G., & Wilkins, A. J. (1988). The design of a new letter chart for measuring contrast sensitivity. *Clinical Vision Science*, *2*(3), 187–199.
- Provine, R. R., & Enoch, J. M. (1975). On voluntary ocular accommodation. *Perception & Psychophysics*, *17*(2), 209–212.
- Roscoe, S. N., & Couchman, D. H. (1987). Improving visual performance through volitional focus control. *Human Factors*, *29*(3), 311–325.
- Rosenfield, M., Hong, S. E., & George, S. (2004). Blur adaptation in myopes. *Optometry and Vision Science*, *81*(9), 657–662.
- Rushton, S. K., & Ridell, P. M. (1999). Developing visual systems and exposure to virtual reality and stereo displays: some concerns and speculations about the demands on accommodation and vergence. *Applied Ergonomics*, *30*, 69–78.
- Sagi, D., & Tanne, D. (1994). Perceptual learning: learning to see. *Current Opinion in Neurobiology*, *4*, 195–199.
- Schaeffel, F., Farkas, L., & Howland, H. C. (1987). Infrared photoretinoscope. *Applied Optics*, *26*, 1505–1509.
- Schaeffel, F., Wilhelm, H., & Zrenner, E. (1993). Inter-individual variability in the dynamics of natural accommodation in humans: relation to age and refractive errors. *Journal of Physiology*, *461*, 301–320.
- Schowengerdt, B. T., & Seibel, E. J. (2004). True three-dimensional displays that allow viewers to dynamically shift accommodation, bringing objects displayed at different viewing distances into and out of focus. *Cyberpsychology & Behavior*, *7*(6), 610–620.
- Schäfer, W. D., & Weale, R. A. (1970). The influence of age and retinal illumination on the pupillary near reflex. *Vision Research*, *10*, 179–191.
- Sowden, P. T., Davies, I. R. L., & Roling, P. (2000). Perceptual learning of the detection of features in X-ray images: a functional role for improvement in adults' visual sensitivity? *Journal of Experimental Psychology: Human perception and performance*, *26*(1), 379–390.
- Sowden, P. T., Rose, D., & Davies, I. R. L. (2002). Perceptual learning of luminance contrast detection: specific for spatial frequency and retinal location but not orientation. *Vision Research*, *42*(10), 1249–1258.
- Webster, M. A., Georgeson, M. A., & Webster, S. M. (2002). Neural adjustments to image blur. *Nature Neuroscience*, *5*(9), 839–840.
- Westheimer, G. (1986). The eye as an optical instrument. In K. R. Boff, L. Kaufman, & J. P. Thomas (Eds.), *Handbook of perception and human performance*, Vol. 1. New York: John Wiley & Sons.
- Wilhelm, H., Schaeffel, F., & Wilhelm, B. (1993). Die Altersabhängigkeit der Pupillennahreaktion. *Klinische Monatsblätter für Augenheilkunde*, *203*, 110–116.
- Winn, B., Whitaker, D., Elliott, D. B., & Phillips, N. J. (1994). Factors affecting light-adapted pupil size in normal human subjects. *IOVS*, *35*(3), 1132–1137.
- Zhang, L., Pelli, D. G., & Robson, J. G. (1989). The effect of luminance, distance and defocus on contrast sensitivity as measured with the Pelli–Robson chart. *IOVS*, *30*(Suppl.), 406.