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 photorefraction—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 verner 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 Natural 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. I*. New York: John Wiley & Sons.

Wilhelm, H., Schaeffel, F., & Wilhelm, B. (1993). Die Altersabhängigkeit der Pupillennahreaktion. *Klinischu Monatsblatter fur 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.