Correspondence

Supplemental Data: Cormorants keep their power: visual resolution in a pursuit-diving bird under amphibious and turbid conditions

Experimental procedures

The birds

The five great cormorants (1 female, 4 males) were obtained from the Ramat-Gan Safari Park, under license from the Israel Nature Authority, and hand-reared in a field experimental setup in the Hula Rift Valley, northern Israel. They were fed on live or defrosted fish (St. Peter's fish and carp) and tested when 3–5 years old. All experiments were performed under permission of the Ethics committees of the Haifa University and of the Technion, Israel Institute of Technology.

Experimental setup

The setup for testing grating resolution in clear water comprised a pre-test pool and a test pool, inter-connected by an underwater trapdoor with circulating, filtered freshwater and an opaque cover. A y-maze tunnel of rigid mesh (50 × 50 cm in cross-section) was placed on the pool's floor (depth: 1–1.5 m), with its entrance at the trapdoor and with each y-arm opening to a stimulus box.

The stimuli were square-wave, high contrast (0.89 ± 0.03; n = 20), black and white gratings, printed on white paper (20.5 × 20.5 cm) and sealed between two Perspex plates. Contrast was calculated as C = (IW-IB)/(IW+IB); (I: illuminance, B: black, W: white). A single grating plate was attached to the vertically sliding front door of each stimulus box. Stripe width varied between 2 and 7 mm at 1 mm increments. Resolution was calculated based on the subtending angle of a single stripe as viewed from the distance of a given y-junction to the stimulus plate. In any test, stripes on opposite boxes were similar in width yet perpendicular to each other, and with vertically orientated stripes serving as the positive stimulus.

Video recordings of the head on approach of the bird were taken with a Sony TR440e camera in an underwater housing, positioned between the stimulus boxes, and supplemented by an overhead view through a 45° mirror. The camera projected to an above-water VCR and monitor.

In testing underwater, a bird swam into the y-maze, was required to make a choice while in motion toward the y-junction, continue through the respective maze arm to the stimulus and subsequently return underwater to the pre-test pool. In all tests, the choice of the positive stimulus resulted in opening of the front pane of the box and rewarding the bird with a fish impaled within. The left-right position of the positive stimulus on a given test was pre-determined by a pseudo-random order, but not more than two consecutive presentations with the same side as positive was allowed.

Resolution in clear water

Visual resolution in clear water was tested in five birds, at three distances of the y-junction to the stimuli (0.8 m, 1.3 m and 1.8 m) and a subsequent control series (at 1.3 m distance) two months later. Water turbidity was kept at 0.1-0.3 NTU (nephlometric turbidity units; nephlometry is the relative measurement of light scattering through a restricted range of angles to the incident light beam). Each cormorant was trained and tested individually. An experiment comprised 5 consecutive test days, with 13 trials per bird per day for each y-junction distance. The order of presenting the stimuli on left-right was pre-determined on the basis of ten random orders for each bird. Visual resolution was determined from the proportion of correct choices. The visual resolution values attained by testing at the three y-junction distances were not statistically different (Friedman's two-way ANOVA, p = 0.07).

In over 80% of the trials, the approaching cormorant performed a distinct head-turning toward one of the targets, before reaching the y-junction. This head turning led to the alignment of the head axis with the target subsequently chosen, and was regarded as the 'point of decision'. Determination of the distance of the point of head turning to the y-junction was made by through video analyses of between 33 and 42 trials per bird. Pre-junction distances ranged from 67 ± 3 cm (mean ± s.e.) to 95 ± 3 cm (mean ± s.e.). The mean distance of points of decision from the stimuli in correct choices did not differ from those of incorrect choices (paired t-test; $p > 0.05$).

Resolution in air

To determine grating resolution in air, we tested the cormorants in a setup allowing the birds to dive through the y-junction yet view the targets only after surfacing. The test-pool was divided by one vertical mesh partition, parallel to the stimuli boxes and ~3 m away and with an opening and a perch above water level, and one partition perpendicular to it. The bases of the stimulus boxes were at water level, so the tested bird had to surface at the opening in order to simultaneously view both stimuli from a distance and swim

Table S1. Grating resolution (min of arc) for individual cormorants in air and water.

Individual	I	II	III	IV	V
Water	6.49, 8.91	5.84, 7.66	5.66, 8.43	5.95, 8.66	7.61, 10.43
Air	3.51, 4.29	3.02, 3.69	2.72, 3.33	-	-

Values provided were calculated for the distance of decision making (head turning, left values) and for the distance of the y-junction (right values).

Table S2. List of species and resolution values for Figure 1C based on [S2,S4–S23]

Species	Visual resolution (min of arc)
Birds — air	
Alauda arvensis	1.30
Alauda arvensis	1.33
Alauda arvensis	1.94
Alauda arvensis	2.00
Aquila audax	0.21
Aquila audax	0.22
Bubo virginianus	4.48
Bubo virginianus	4.00
Columba livia	1.70
Corvus frugilegus	1.00
Corvus macrorhynchos	3.57
Corvus monedula	0.94
Coturnix coturnix	4.30
Coturnix coturnix	4.41
Curvus (Japanese)	3.30
Dryotriorchus spectabilis	0.25
Emberiza achoeniclus	3.10
Emberiza citrinella	2.83
Emberiza citrinella	3.13
Emberiza schoeniclus	3.19
Emberiza schoeniclus	3.85
Erithracus rubecula	2.63
Erithracus rubeculus	2.33
Falco berigora	0.39
Falco berigora	0.41
Falco sparverius	0.72
Falco sparverius	1.15
Fringilla coelebs	1.32
Fringilla coelebs	1.61
Fringilla montifingilla	2.73
Gallus domesticus	3.49
Garrulus glandarius	1.00
Garrulus glandarius	1.40
Bubo virginianus	4.00
Parus atricapillus	2.21
Phlacrocorax carbo	2.70
Pica pica	0.94
Pyrrhula pyrrhula	1.86
Strix aluco	3.00
Strix aluco	3.75
Struthio camelus	1.55
Turdus merula	1.33
Turdus merula	1.65
Turdus musicus	1.79
Turdus pilaris	1.17
Turdus pilaris	1.33
Tyto alba	3.75
Birds- water	
Phlacrocorax carbo	3.80
Mammals - air	
Amblonyx cineria	14.00
Zalphus californianus	5.00
Mammals - water	
Amblonyx cineria	15.00
Eumetopias jubata	6.50
Lagenorynchus obliuquidenus	6.10
Orcinus orca	5.50
Phoca vitulina	8.30
Zalphus californianus	4.80
Fishes — water	
Aequidens portalegrensis	5.80
Astronotus ocellatus	5.30
Carassius auratus	4.40
Cichlasoma meeki	8.90
Epinephalus sp.	4.30
Euthynnus affinis	7.70
Hemichromis bimaculatus	7.00
Katsuwonus pelamis	5.60
Lebistes reticulatus	9.00
Lepomis macrochirus	14.20
Microcanthus strigatus	5.00
Phoxiunus laevis	10.80
Pleuronectes platessa	11.00
Salmo gairdneri	14.00
Scopthalmus maximus	11.00
Thunnus albacares	3.70

to either. The choice had to be performed by the perch's edge, after which the bird could swim on one side of the perpendicular partition only. Aerial resolution was tested in 3 birds only, at perch distances of 2.2 m and 2.7 m from the stimuli. The cormorants made their choice as they rapidly approached the targets, and video analysis indicated that the birds' direction to the target was determined at the entrance window, i.e. at the greatest distance possible from the stimuli.

Resolution in turbid water

We tested visual resolution in the cormorants (n = 5) under controlled levels of low levels of turbidity of between 0.6 and 3.0 NTU in the underwater y-maze in the setup described for clear water above. Turbidity was controlled by adding fine-grained soil ca. 20 hr before a test and was measured 3 times/day with a portable Hach 2100P turbidimeter (range: 0–10 NTU, resolution: 0.01 NTU). Tests were conducted at one y-junction distance (1.3 m) with grating widths of 4, 5, 6 and 7 mm. Each bird was tested on a single day only (13 trials) as it was impossible to retain a constant level of turbidity over two or more consecutive test days.

Light intensity

All tests were conducted under natural, diffuse, high level illumination. Down-welling underwater illumination was measured at the y-junction using a Li-Core L-189 photometer with a quantum sensor providing readings given in μEin/m^2/sec units. As the cormorants' spectral sensitivity is not known, these readings were converted to human photopic lx units based on the manufacturer's conversion table. Illumination levels ranged mostly between 1100 and 1770 Lux in air, down-welling illumination was (1380-2330 Lux in air, 770 and 2200 Lux in tests of turbidity). Both underwater and in air, these light levels are above those known to affect visual resolution in other birds [S1,S2].

Analysis

In each test, the proportion of correct choices was determined for each subtending angle. The critical value for correct choices, based on binomial distribution [S3], was 0.75 for n = 26 trials in clear water and in air and 0.77 for the tests in turbid water (n = 13 trials). This procedure and the use of a critical value of 0.75 are common in psychophysical tests of visual resolution [S2,S4,S5].

The results presented for clear water and air are from the first two consecutive days (26 trials) during which the bird reached the critical value of at least 0.75 correct choices. If not achieved - the results of days 4 and 5 were taken. The results for turbid water are for a single test day (13 trials per day). Maximal resolution was determined from the intersection of the slope with the predetermined critical value line.

Acknowledgments

R.A. Kiltie, M.L. Brooke, W. Hodos and J. Vogel generously provided us with their data and H.C. Howland, G.R. Martin and D. Weihs and two anonymous referees provided constructive comments. We thank R. Almon, D. Amar, E. Yona, A. Levy, Y. Harari and the fish-farmers of Kibbutz Baram for their assistance. This work was funded by a grant from the Israel Ministry of Arts and Sciences.

References

S1. Hodos, W., Leibowitz, R.W., and Bonbright, J.C. (1976). Near-field visual acuity of pigeons: effects of head position and stimulus luminance. J. Exp. Anal. Behav. *25*, 129–141.

S2. Reymond, L. (1987). Spatial visual acuity of the falcon, *Falco berigora*.

A behavioral, optical and anatomical investigation. Vision Res. *27*, 1859–1874.

S3. Zar, J.H. (1984). Biostatistical Analysis (New Jersey: Prentice-Hall).

S4. Hodos, W. (1994). The visual capabilities of birds. In Perception and Motor Control in Birds: an Ecological Approach, M.N.O. Davies, P.R. Green, eds. (Berlin: Springer Verlag), pp. 63–76.

S5. Martin, G.R., and Gordon, I.E. (1974). Visual acuity in the tawny owl (*Strix aluco*). Vision Res. *14*, 1393–1397.

S6. Douglas, R.H., and Hawryshyn, C.W. (1990). Behavioural studies of fish vision: An analysis of visual capabilities. In The Visual System of Fish, R.H. Douglas, M.B.A. Djamgoz, eds. (London: Chapman and Hall), pp. 373–442.

S7. Fite, K.V. (1973). Anatomical and behavioral correlates of visual acuity in the great horned owl. Vision Res. *13*, 219–230.

S8. Fite, K.V., Stone, R.J., and Conley, M. (1975). Visual acuity in the northern blue jay: Behavioral and anatomical correlates. Neurosci. Abs. *1*, 82.

S9. Fox, R., Lemkuhle, S., and Westendorf, D.H. (1976). Falcon visual acuity. Science *192*, 263–265.

S10. Hodos, W., Bessette, B.B., Macko, K.A., and Weiss, S.R.B. (1985). Normative data for pigeon vision. Vision Res. *25*, 1525–1527.

S11. Rahman, H. Die Sehschärfe bei Wirbeltieren. (1967). Naturw. Rdsch. *20*, 8–14.

S12. Reymond, L. (1985). Spatial acuity of the eagle *Aquila aud*ex. Behavioral, optical and anatomical investigation. Vision Res. *25*, 1477–1491.

S13. Schusterman, R.J., and Balliet, R.F. (1970). Conditioned vocalization as a technique for determining visual acuity thresholds in sea lions. Science *169*, 498–501.

S14. Schusterman, R.J., and Balliet, R.F. (1970). Visual acuity of the Harbour Seal and the Steller Sea Lion under water. Nature *226*, 563–564.

S15. Schusterman, R.J., and Barret, B. (1973). Amphibious nature of visual acuity in the Asian 'clawless' otter. Nature *244*, 518–519.

S16. Sinclair, W., Dunstone, N., and Poole, T.B. (1974). Aerial and underwater visual acuity in the Mink *Mustela vison* Schreber. Anim. Behav. *22*, 965–974.

S17. Spong, P., and White, D. (1971). Visual acuity and discrimination learning in the dolphin (*Lagenorynchus oblicuidens*). Exp. Neurol. *31*, 431–436.

S18. White, D., Cameron, N., Spong, P., and Bradford, J. (1971). Visual acuity of the killer whale (*Orcinus orca*). Exp. Neurol. *22*, 230–236.

S19. Kiltie, R.A. (2000). Scaling of visual acuity with body size in mammals and birds. Funct. Ecol. *14*, 226–234.

S20. Brooke, M., Hanley, S., and Laughlin, S.B. (1999). The scaling of eye size with body mass in birds. Proc. R. Soc. Lond. B. Biol. Sci. *266*, 405–412.

S21. Kirschfeld, K. (1976). The resolution of lens and compound eyes. In Neural Principles in Vision, F. Zettler, R. Weiler, eds. (Berlin: Springer Verlag), pp. 354–370.

S22. Douglas, R.H., and Hawryshyn, C.W. (1990). Behavioural studies of fish vision: An analysis of visual capabilities. In The Visual System of Fish, R.H. Douglas, M.B.A. Djamoz, eds. (London: Chapman and Hall), pp. 373–442.

S23. Schusterman, R.J. (1981). Behavioral capabilities of seals and sea lions: a review of their hearing, visual learning and diving skills. Psychol. Rec. *31*, 125–143.