Correspondence

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

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Cormorants (Aves; Phalacrocoracidae) are active fliers, yet they forage by pursuit diving and capture of fish with the bill. In air, the cormorant's cornea provides most of the total refractive power of the eye [1]. Underwater, however, corneal power is lost, as the cornea is now bathed in liquids of similar refractive index. The retention of a sharp image, while performing precise visual tasks underwater, requires that the cormorant's optical system compensates for the loss of refractive power of the cornea. In addition, the underwater photic environment differs markedly from the aerial one, with the image quality undergoing a rapid deterioration through scatter and absorption [2,3]. Upon submergence, cormorants compensate for the loss of corneal power (>55 dioptres, D) and rapidly (>1000 D/sec) attain a state of emmetropia, i.e. they are well focussed [4], by marked changes in the shape of their very flexible lens [1,5]. However, the visual capacities of pursuit-diving birds under the optical demands imposed by moving from one medium to another and the respective differences in the photic environments have not been determined to date.

We tested the aerial and underwater visual resolution of the great cormorant (*Phalacrocorax carbo sinensis*) for high contrast, square wave gratings. Stimuli were presented in a forced choice situation (y-maze) under high levels of natural illumination. Visual resolution was calculated from gratings of given bar widths at given distances from the y-junction to the stimuli. In clear water, the cormorants' resolution was 8.9′ ± 0.5′ (minutes of arc, mean ± s.e, $n = 5$, range 10.4′ – 7.8′; Figure 1A), while in air it was 3.8′ ± 0.3′ ($n = 3$, range 4.3′ – 3.3′; Figure 1B). The birds' choice underwater was performed while they swam at ~1.7 m/sec so that the testing of resolution replicated the naturally occurring dynamic discrimination of underwater events. The position at which an actual choice was made could be determined from the abrupt change in the orientation of the head toward the stimulus. In all tests, the choice was made between ~60 and 90 cm before the y-junction. Calculating underwater visual resolution for the positions of choice provided a value of 6.3′ ± 0.4′ ($n = 5$) underwater and 3.1′ ± 0.3′ ($n = 3$) in air.

While vision is regarded as the major modality used in the detection and capture of prey by pursuit-diving birds, this is the first quantitative estimate of the amphibious visual capacity in any bird. Compared with other bird species, the cormorants' resolution in air (Supplemental Table 1) was relatively low in both absolute terms (Figure 1C) and when body mass [6,7] or eye height above the ground [8] were considered. The cormorants' resolution underwater was comparable with the higher values reported for fishes [9], Pinnipeds (e.g., seals, sea lions) [10] and Cetaceans (e.g., killer whales, dolphins) [11] (Figure 1C). Because visual resolution in single chambered eyes tends to increase with eye size [6,7], it was expected that cormorants, with corneo-scleral diameters of ~18–19 mm will have a lower resolution than aquatic mammals having eye diameters of ~20 mm (dolphins) and ~50 mm (baleen whales). The requirements to perform precise visuo-motor tasks in two optically different media, and the uniqueness of the lenticular system of these birds [1,5] make the vision of pursuit-diving birds a model of vertebrate capacities at the extreme.

Performing visual tasks underwater is hindered by the rapid degradation of image brightness and contrast due to scatter and absorption of light by water molecules and by suspended particles (turbidity) [2]. We tested the visual resolution of cormorants ($n = 5$) under controlled, low levels of water turbidity (< 3 nephlometric turbidity units; NTU). The minimal resolvable stripe width was linearly correlated with turbidity ($y = 3.71x + 7.6$; $R^2 = 0.98$; $p < 0.001$), hence, resolution declined with increasing turbidity within the tested range. The results obtained for clear water (~0.2 NTU) fitted the regression line well. Experimental results on the effects of turbidity on visually guided behavior of aquatic vertebrates are uncommon and, in fishes, are confined mostly to turbidity levels higher than 3 NTU and to the use of reactive distance as a behavioral measure [12]. Our results show that turbidity levels lower than 1 NTU have a clear effect on image formation underwater and consequently on the underwater visual environment in general. Low turbidity levels are commonly encountered in natural water bodies and thus are of crucial importance in our understanding of the evolution, sensory ecology, and micro-habitat selection in aquatic organisms [13–15].

Supplemental data

Supplemental data containing experimental procedures are available at http://www.current-biology.com/cgi/content/full/14/10/R376/DC1/

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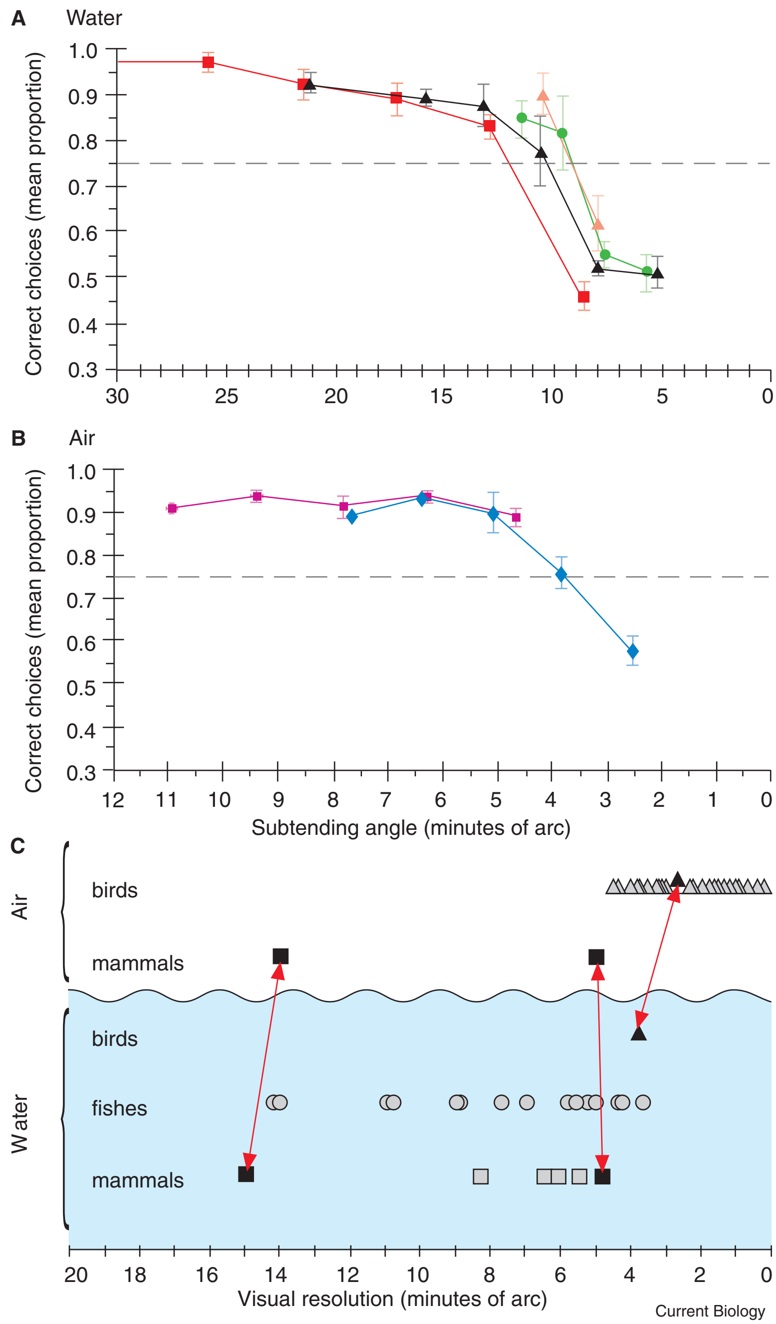

Figure 1.
Grating resolution (in minutes of arc) of the great cormorant in clear water (A) and in air (B). Correct choices are given as proportions (means ± s.e.). Broken horizontal lines show the critical values of significance for the binomial distribution. $n = 5$ birds in water, $n = 3$ birds in air. Y-junction distances to stimuli boxes in water were 0.8 m (red squares), 1.3 m (black triangles), 1.8 m (green circles), and a subsequent control at 1.3 m (orange triangles). Y-junction distances in air were 2.2 m (purple squares) and 2.7 m (blue diamonds). (C) Visual resolution of the great cormorant compared with fishes, aquatic mammals and birds (Supplemental Table 2). Each symbol represents the maximal resolution reported for a given species in a given reference. Amphibious diving mammals (solid squares) suffer little or no loss of resolution upon submergence. Cormorant's (solid triangles) visual resolution in air is in the lower range reported for birds, while underwater it is within the higher range reported for fishes (circles) and higher than that of diving mammals. Most current reports on avian visual resolution are for chicken (*Gallus domesticus*), pigeon (*Columba livia*), raptors (Accipitriformes) and passerines. No comparable data are available for water birds (e.g., Anseriformes, Charadriiformes, Procellariiformes).

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