

Saccadic oscillations facilitate ocular perfusion from the avian pecten

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THE evolution of the eye is constrained by two conflicting requirements—good vascular perfusion of the retina, and an optical path through the retina that is unobstructed by blood vessels. Birds are interesting in that they have higher metabolic rates and thicker retinas than mammals, but have no retinal blood vessels. Nutrients and oxygen must thus reach the neurons of the inner retina either from the choroid through 300 μm of metabolically very active retina, or from the pecten, a pleated vascular structure protruding from the head of the optic nerve into the vitreous chamber, and more than a centimetre away from some retinal neurons. Despite the diffusional distance involved, several lines of evidence indicate that the pecten is the primary source of nutrients for the inner retina: the presence of an oxygen gradient from pecten to retina¹, the large surface area produced by macroscopic folds^{2,3} and by microscopic infoldings of the luminal and external surfaces of the capillary endothelium^{4–6}, extrusion of circulating fluorescein⁷, high content of carbonic anhydrase and alkaline phosphatase^{8,9}, and retinal impairments after pecten ablation¹. Another peculiarity of birds, their saccadic oscillations, occur with a large cyclotorsional component during every saccadic eye movement¹¹. In different species, saccades, which occur at intervals of 0.5–40 s, have up to 13 oscillations with frequencies of 15–30 Hz and amplitudes of about 10° (ref. 12). Therefore, as much as 12% of some birds' total viewing time may be subject to the image instability caused by the oscillations¹³. Using fluorescein angiography, we show here that during every saccade, the pecten acts as an agitator

which propels perfusate towards the central retina much more effectively than is observed during intersaccadic intervals.

Five species of birds were examined with indirect ophthalmoscopy after an injection of fluorescein into a wing vein: domestic chicken (*Gallus gallus*); tawny frogmouth, (*Podargus strigoides*); boobook owl (*Ninox novaeseelandiae*); bush thick-knee (*Burhinus grallarius*); and the laughing kookabura (*Dacelo gigas*). In all the birds examined, the fluorescent dye filled the pecten (Fig. 1a) within 4–10 s of injection and then leaked more slowly from the pecten into the vitreous chamber, thus confirming earlier reports^{7,14}. Our observations concern the effects of saccadic oscillations (Fig. 1b) on the outward movement of the dye from the pecten. A single saccade (Fig. 1b) propelled the dye, in a plume or series of wavelets, to distances that were an order of magnitude further from the pecten than had occurred in the entire previous intersaccadic interval. This was most easily seen in the thick-knee and the frogmouth, neither of which tended to blink during a saccade.

An experiment on a frogmouth is illustrated in Fig. 2. Six seconds after intravenous injection as a bolus, fluorescein filled the pecten—a visually dramatic event as the previously black pecten turned bright green and its folds became evident. Subsequently, the dye seemed to leak from the pecten into the vitreous chamber to form a slowly intensifying halo at the base of the pecten close to the retina. Leakage of dye from the pecten became noticeable at 40 s. More than 1 min after leakage was first observed, the outer edge of the dye had moved less than 0.5 mm from the margins of the pecten. A saccade at this point dispersed the halo and caused a plume of dye to be propelled in a superior and nasalward direction (Fig. 2). During the saccade, the pecten was observed to oscillate orthogonally to its long axis as might be expected if, as in chickens, oscillations are mainly cyclotorsional¹⁰. At the end of the saccade, the plume of dye extended more than 3 mm (the length of the pecten) and the edge of the dye at the lateral margins of the pecten had also moved outwards by 1–2 mm. Each subsequent saccade was accompanied by plumes and by stepwise extensions of the outermost edge of the dye. Similar plumes have been observed during fluorescein angiography of pigeon and rhea, but no association with eye movements was made¹⁴.

Although the infrequent pulsatile dispersion of fluorescein in the frogmouth makes the saccadic facilitation of perfusion dra-

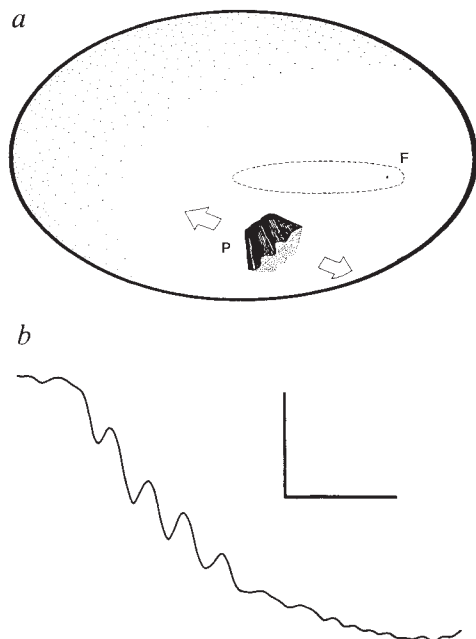


FIG. 1 a, Pecten oculi and relations in the left eye of the tawny frogmouth. The pecten is the folded pigmented structure (P) that projects into the eye from the optic nerve head. Its base is ~3 mm long and it is 3 mm high. In the frogmouth, there is a single binocular fovea in temporal retina (F). The fovea is located within a region of high ganglion cell density which extends towards the nasal retina (dotted ellipse). The arrows indicate the transverse movements of the pecten produced by the torsional component of the saccadic oscillations. The boobook owl had an arrangement very similar to that shown here, except that the pecten had an extra fold on its inferior limb. Other birds may have longer pectens with more folds and a second (monocular) fovea located in the central retina near the nasal end of the zone of high density. The thick-knee had a pecten with 11 folds, but the superior limb had the same position as shown here for the frogmouth pecten, which has three folds (that is, the extra eight folds are added to the inferior limb of the pecten to maintain a comparable relationship between the superior tip of the pecten and the retinal horizon). The thick-knee had a monocular fovea in a position corresponding to the nasal end of the ellipse of high ganglion cell density shown. The kookabura had an extra 17 pecten folds added to the inferior limb, and two foveas, a binocular fovea in the same relative position as the frogmouth's, and a monocular fovea like the thick-knee, with a position corresponding to the nasal end of the dotted region of increased density. b, An oscillatory saccade from the tawny frogmouth. Recording obtained with a sub-conjunctival search coil as described by Wallman and Pettigrew¹². Only the horizontal component is shown. The actual amplitude of the oscillations would be larger if the coil had been orthogonal to the cyclotorsional plane in which the oscillations occurred. Down is motion to the right. Horizontal scale, 250 ms; vertical scale, uncalibrated, ~5°. In frogmouths, the number of oscillations in a given saccade varies from five to ten and the mean intersaccadic interval is 40 s.

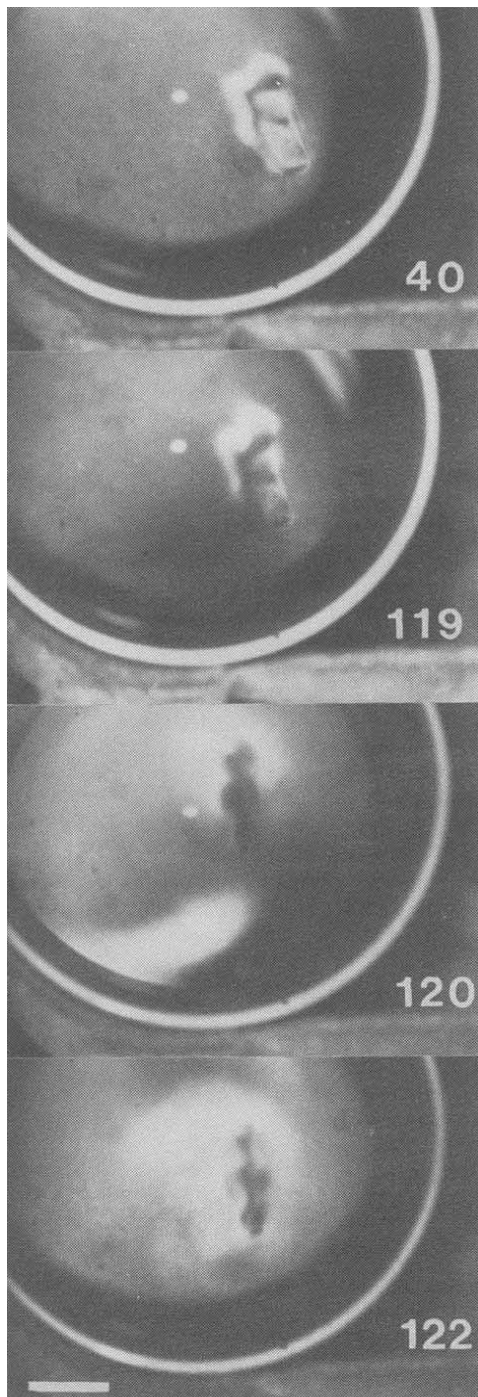


FIG. 2 Fundus of tawny frogmouth: sequence at various times (indicated in seconds) after intravenous injection of fluorescein. In the fundus at 40 s the pecten stands out as brightly fluorescent with a small amount of leaked dye accumulating as a halo around the pecten. Dye leakage is restricted to within 0.5 mm of the pecten. At 119 s just before the first saccade, the dye is still restricted to within 0.5 mm of the pecten. At 120 s, during the first saccade following the injection, a plume of dye has been propelled upward and nasally from the superior limb of the pecten. At 122 s, immediately after the saccade, the dye has been propelled 2–3 mm from the pecten. Note that the intersaccadic interval of the frogmouth was particularly long in this experimental situation, thus providing a clear view of perfusion in both situations, when saccades were either present or absent. In other situations and other birds, intersaccadic intervals were shorter, but the same phenomena were also observed. Mean intersaccadic intervals for the species were: chicken, 1.3 s; kookaburra, 8.8 s; tawny frogmouth, 40 s; boobook owl, 34 s; bush thick-knee, 16 s. Scale bar, 2 mm.

METHODS. Pupils were dilated by application, at least 1 h before examination, of proxymetacaine drops (Ophthalmic Allergan); followed by 1 drop min^{-1} of vecuronium bromide (4 mg ml^{-1} , Organon Teknika B.V.) for 20 min (as well as providing local anaesthesia, the proxymetacaine drops improved penetration of the curariform drugs). The procedure was effective in producing wide pupillary dilation for all species except the kookaburra and thick-knee, whose pupils were dilated with an injection of $50 \mu\text{l}$ of the vecuronium solution directly into the anterior chamber. The fundus in the region of the pecten was visualized by focusing an operating microscope (Wild Leitz M-650) on the inverted aerial image produced by a 30 D aspheric field lens clamped just in front of the eye. General anaesthetic agents were avoided because of their inhibitory effects on eye movements, particularly the saccadic oscillations. Local anaesthetic (4% lignocaine) was sprayed on the venipuncture site over the brachial vein. Sodium fluorescein (50 mg as a 100 mg ml^{-1} solution, Fluorescite Alcon) was injected as a bolus. Efflux of fluorescein from the pecten was monitored using a Wratten 47A excitation filter placed in the path of the illuminator of the operating microscope. Two beam splitters on the operating microscope enabled the sequence of changes in the fundus to be recorded on video tape and on 35 mm film.

rotation during the saccadic oscillations passes about a millimetre beyond the superior limb of the pecten (J. C. Letelier, personal communication).

The diverse shapes and dispositions of avian pectens have excited much unresolved speculation about their function^{15–18}. In the light of the present observations, the fan-shape and folds of most pectens take on new significance as potential propulsive surfaces, the arrangement of which must be coupled with the pattern of saccadic oscillations to produce the fluid motion we have observed. We propose that saccadic oscillations have co-evolved with pecten shape to optimize retinal perfusion. As a result, birds may have been able to exploit a range of ocular designs unavailable to mammals, such as the thicker, more complex avian retina and the achievement of panoramically high optical quality and visual acuity¹⁹. □

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matic to observe, the fluctuations in gas exchange might not be so large because oxygen and carbon dioxide are smaller molecules than fluorescein and, because in most birds the pecten is larger, the eye smaller and the saccades more frequent. The advantage of using the frogmouth and thick-knee was that their large eyes and small pectens permitted visualization of the entire pecten and the surrounding retina in one field of view. We were therefore able to observe that dye movement created by oscillations was always directed upwards, roughly parallel to the long axis of the pecten and outward from its less-folded sweeping upper limb, a pattern we subsequently confirmed in the chicken. In other words, the combined action of pecten and oscillations is to direct the flow against gravity and towards the high-density regions of the retina. Consistent with this observation, quantitative studies of chickens show that the instantaneous axis of