

THE FUNCTIONAL SIGNIFICANCE OF THE AVIAN PECTEN: A REVIEW

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The pecten oculi of the avian eye is an intriguing structure which, despite intensive study, has defied conclusive functional analysis for over 300 years. The reviews of O'Rahilly and Meyer (1961) and Wingstrand and Munk (1965) summarized research done on the pecten up to 1965. Both of these reviews confirmed the observation of Walls (1942) that although anatomical studies and purely speculative accounts of the function of the pecten abound in the literature, the number of experimental investigations has been small.

In his classic study of the vertebrate eye, Walls (1942) marshalled considerable anatomical and circumstantial evidence for the hypothesis that the pecten, which is the only vascular structure within the posterior chamber of the avian eye, serves as a replacement for the direct vascularization of the retina found in most other vertebrates. In recent years, the ablation experiments of Wingstrand and Munk (1965) have been taken by most ornithologists and physiologists (e.g., Jasinki 1973, Sillman 1973) as positive proof of this hypothesis. However, my recent investigations of the physiology of the pecten (Brach 1975a, b) have produced results which cast doubt on the trophic theory of pecten function. In this review, I summarize what is presently known about the structure and function of the pecten with the aim of providing a fresh look at the problems and partial answers which have arisen in studies of the pecten since 1965.

DESCRIPTION

The structure of the pecten has been described exhaustively on every level. The atlas of avian ophthalmoscopy by Wood (1917) is still the best survey of the gross appearance of the pectens and retinas of non-domestic species. The light and electron microscopy of the pecten have been described by many workers (Bacsich and Gellert 1935, Seaman and Storm 1963, Bacsich et al. 1966, Seaman 1966, Nguyen H. Anh et al. 1967, Raviola and Raviola 1967, Porte et al. 1968, Fielding 1972, Fischschweiger and O'Rahilly 1972, Welsch 1972, Dieterich et al. 1973, Jasinki 1973, Hanzely et al. 1976). Much of this work was performed on a small number of primarily domes-

tic species, especially the domestic chicken (*Gallus domesticus*) and the domestic pigeon (*Columba livia*).

Embryologically, the pecten arises as an ectodermal (glial) process from the edges of the optic fissure (Mann 1922). The ectodermal elements are largely replaced later in development by an extensive invasion of mesodermal vascular tissue. In most birds, the pecten is largely complete at hatching, although in some species full pigmentation may be delayed for some time (Hailman 1964).

The gross appearance of the typical pecten is suggestive of a steam radiator. Wood's atlas (1917) demonstrates the remarkable variability of a number of external pecten features such as color, length, thickness, and number of pleats. Early anatomical investigations (Rabl 1900, quoted in Walls 1942, Bacsich and Gellert 1935) showed that the gross morphology of the pecten was highly variable even among related genera, but tended toward three distinct patterns: the "pleated fan," the commonest type, found in most neognathous birds; the "pleated cone" of some ratites, which has a radiate appearance due to the circular cross-section of the optic nerve head; and the bridgeless, often greatly reduced pectens of kiwis, owls, and the caprimulgi-forms. Except for the degenerate pectens of kiwis, the pectens of all birds are folded or pleated. The purpose of these pleats is apparently to increase the surface area of the pecten rather than to produce rigidity as proposed by Tucker (1975), because the pecten is supported entirely by the vitreous body and collapses limply against the retina when the vitreous body is excised.

The histological features of the pectens of all birds are remarkably similar. The pecten consists of a thin, pleated plexus of rather large capillaries held together by a sparse matrix of pigmented stroma cells (Fig. 1). In most birds, the pecten apex is held together by a densely-pigmented, fibrous "bridge" of tissue which has a reduced vascularization with respect to the pecten pleats. The pecten is attached basally to the optic nerve head and distally to the vitreous body by fine strands of vitreous tissue which interdigitate with processes of the bridge cells.

Ultrastructural investigations of the pecten

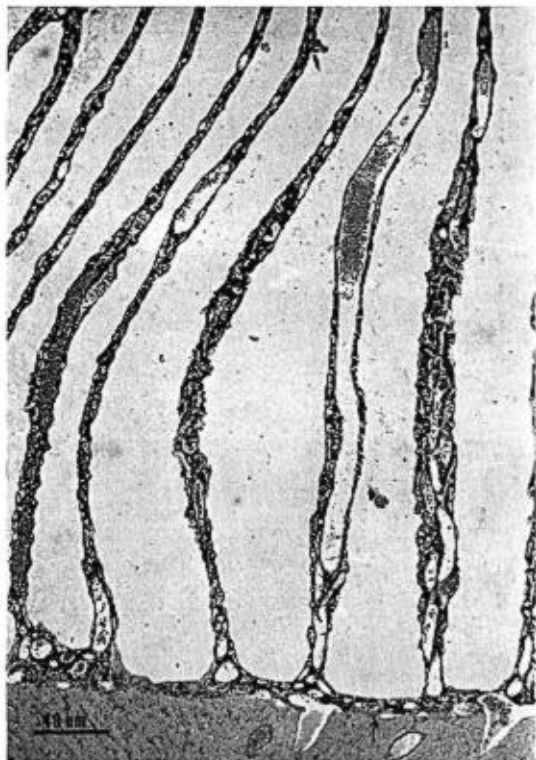


FIGURE 1. 10 μ m vertical section of the pecten and optic nerve head of the Burrowing Owl, *Athene cucularia*. Note the extensive vascularization of the pecten-optic nerve junction (arrow) as well as the pecten pleats. In this species, the bridge of the pecten is lacking. (125 \times).

reveal one of its most unusual features, the extensively reduplicated apical and basal plasmalemma of the capillary endothelium (Fig. 2). This condition has no known parallel in the animal kingdom except in the capillaries of the lizard conus papillaris, which exhibits a remarkable histological similarity to the pecten (Brach 1976). The nature of this infolding is that of microfolds rather than microvilli (Dieterich et al. 1973). The basal folds are oriented perpendicular to the apical folds, the latter being pointed in the direction of the blood flow. Wingstrand and Munk (1965) found that capillaries having an endothelium of this type are restricted to the folds of the pecten. Surrounding each capillary is a multi-layered lamina of fibrous material with a distinct outer boundary which has been shown histochemically to be composed of polysaccharide or mucopolysaccharide material (O'Rahilly and Meyer 1961). Except for the pigment-containing stroma cells, a few spindle-shaped cells within the fibrous laminae (fibroblasts or pericytes), and an occasional mast cell, no other cell types have been reported from the pecten folds and bridge.

However, Dieterich et al. (1976) reported the presence of some primitive smooth muscle cells in the walls of the pre-fold vessels in *Passer domesticus*. The absence of nervous tissue is especially significant as it renders unlikely the numerous sense-organ theories of pecten function.

A scanning electron microscope study by Dieterich et al. (1973) showed that the pecten capillaries form an extensively anastomosed network, but neither this study nor that of Tucker (1975) disclosed any regular arrangement of vessels which might suggest the presence of a rete system.

The pecten also shows a number of interesting biochemical features. Several enzymes, including carbonic anhydrase (Leiner 1951, Kauth and Sommer 1953, Welsch 1972), alkaline and acid phosphatases (Seaman and Storm 1963, Bawa and YashRoy 1972), and aminopeptidase (Welsch 1972) have been found in large amounts in the pecten. The relatively large amount of carbonic anhydrase prompted the study of Seaman and Himelfarb (1963), in which the carbonic anhydrase inhibitor acetazolamide was administered to chickens in large doses and the effect on the ultrastructures of the pecten and ciliary body explored. The principle finding of this study was that the amount of infolding of the apical and basal plasmalemma of the capillary endothelium in both the pecten and the ciliary body increased greatly after administration of acetazolamide. However, because the quantity of acetazolamide administered was greatly in excess of the recommended therapeutic dose, these results easily could have been caused by nonspecific tissue damage and must be viewed with caution. Bawa and YashRoy (1972) found that the alkaline phosphatase activity of pecten tissue changes markedly upon dark adaptation, about which more will be said below.

HYPOTHESIZED FUNCTIONS

The intriguing shape of the pecten has provoked more than 30 ingenious hypotheses of pecten function, many of which directly link the pecten with the proverbial acuity of avian vision. Most of these proposed functions are either physical (usually in reference to optics) or metabolic. Walls (1942) and Wingstrand and Munk (1965) discussed many of these extensively.

A number of the hypotheses for pecten function in both the physical and the metabolic categories seem speculative and highly unlikely. For example, the pecten has been

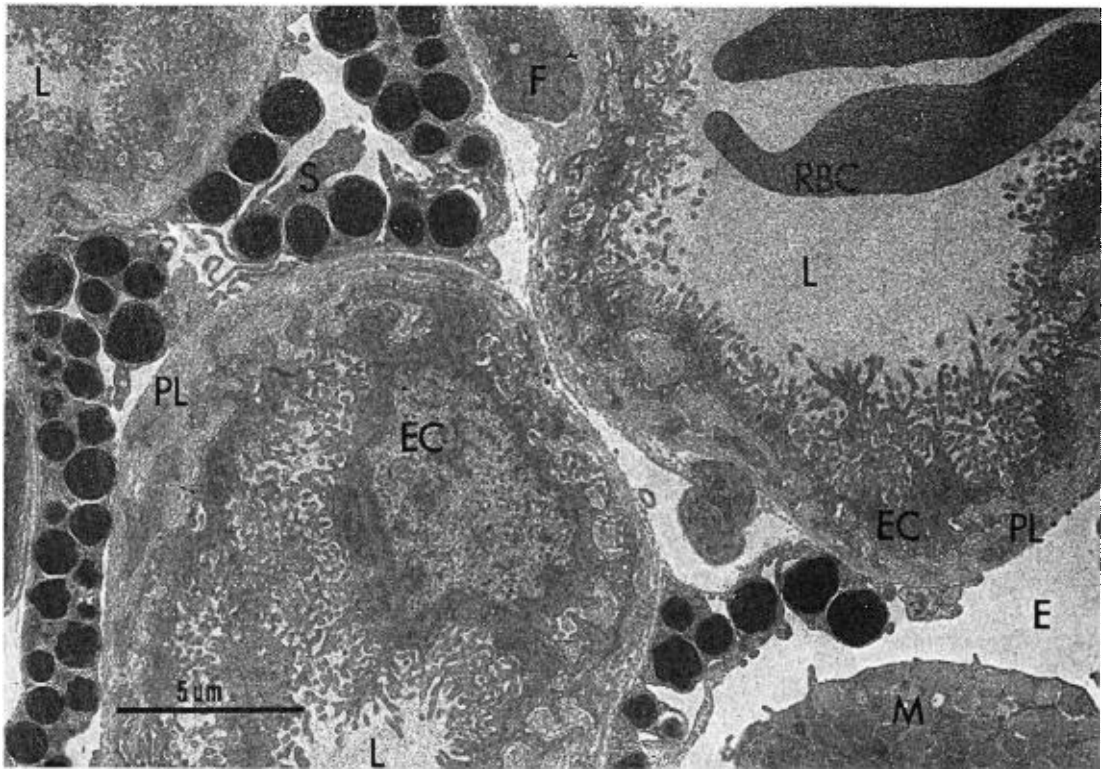


FIGURE 2. Electron micrograph of glutaraldehyde-osmium fixed pecten tissue from the domestic chicken. E = extravascular space, EC = endothelial cell, F = fibroblast, L = vessel lumen, M = mast cell, PL = perivascular lamina, RBC = red blood cell, S = stroma. Note the extensively reduplicated endothelial cell plasmalemma.

implicated as the seat of an avian magnetic "sense" by at least one group (Danilov et al. 1970). As the pecten is devoid of nervous tissue (Ehinger 1967), it is improbable that the pecten is the seat of any sort of sensory system, although the possibility remains that photic environmental cues could be transduced through humoral rather than neurological routes, should the pecten be directly photosensitive with respect to its function.

"Optical" hypotheses of pecten function tend to ignore the histological and ultrastructural features of the pecten and concentrate instead on its form, position, or color. The most ingenious of these hypotheses is that of Menner (1938). With the aid of models, Menner argued that a grid-like pattern of shadows was cast upon the retina by the pecten, increasing the sensitivity of the retina to small moving objects by causing their images to flicker. This theory was developed further by Crozier and Wolff (1943a, b) who were able to increase the flicker response contour of the human eye to a level comparable to that of the House Sparrow (*Passer domesticus*) by throwing a grid-like shadow onto the retina. However, this hypothesis requires that the

pecten cast a sharp, grid-like shadow on the retina, which in fact is not the case. My own observations confirm those of Wingstrand and Munk (1965) that the pecten is so situated in the eye as to cast a minimal, rather un-grid-like shadow on the retina, which in any case falls almost exclusively on the photoreceptor-free optic nerve head. This suggests that birds may not actually perceive the presence of their pectens. The dark pigmentation and somewhat velvety texture of the pecten surface, especially on the bridge, indicate that the pecten absorbs light. This led Barlow and Ostwald (1972) to suggest that light absorption might actually be the pecten's function, making it analogous to the light baffles found in many cameras. However, because "grid," "baffle," and other purely optical hypotheses of pecten function account for only the external shape and coloration of the pecten and ignore its unique histological and physiological features, they are incomplete.

The most thoroughly developed explanations of the pecten relate to the hypothesis that the pecten replaces the missing central retinal artery system in the avian eye. Walls (1942) and Wingstrand and Munk (1965)

presented the most thorough analyses of the various trophic hypotheses. Their conclusions, and the conclusions of almost all other workers to date, perhaps have been expressed most succinctly by Jasinki (1973:281): "The pecten oculi of birds is a nutritive organ supplying the inner layers of the retina with oxygen." Other investigators have suggested the possibility of glucose secretion (Kuwabara and Cogan 1961, Pedler 1963, Uga and Smelser 1973).

Wingstrand and Munk (1965) were the first to develop a controllable technique for the ablation of the pecten, which involved surgical cautery of the retrobulbar supplying arteries of the pecten in the domestic pigeon. This operation produced a rapid, irreversible degeneration of the inner retinal layers. These investigators also made a small number of intraocular measurements of vitreal oxygen tension before and after pecten ablation, which demonstrated that an oxygen gradient from the pecten to the retina had been destroyed. A relative anoxia in the vitreous humor following pecten ablation was advanced as the probable cause of retinal atrophy, even though the measured difference in oxygen tension at the retina was only 3–5 mm Hg in normal birds (three measurements) and 3 mm Hg in a single operated bird (one measurement). When the sensing electrode was pushed against or slightly into the retina, the oxygen tension recorded in both classes of bird was always three- to four-fold higher than at the vitreous-retina boundary. This suggests that the source of oxygen being measured at the vitreous-retina boundary may have been the richly vascular choriocapillaris behind the retina rather than the pecten. The retinal atrophy observed by these workers may actually have been caused by embarrassment of the circulation of the optic nerve head which appears to receive some supply from the arterioles at the pecten base (Fig. 1), rather than by a loss of pecten function. Hence, the explanations advanced by Wingstrand and Munk are questionable.

Recently, I devised a new technique for pecten ablation in the domestic chicken which involves intraocular electrocautery with specially-designed electric forceps (Brach 1975b). Essentially no change in retinal histology was produced from 13 total and 7 partial ablations of the pecten, and considerable visual capacity was retained. These results tend to confirm the less precise experiments of Kauth and Sommer (1953) and the preliminary report of François and Neetens (1974). Both of these studies reported the re-

tention of retinal and some visual integrity after varying degrees of pecten destruction in domestic pigeons, although neither study confirmed these findings by demonstration of histologically intact retina or total lesion of the pecten. However, all of these data suggest that the pecten does not perform any functions vital to the survival of the retina. Additional experiments, perhaps using different ablation techniques on non-domestic species, are needed before this can be considered proven.

Following the ablation of the pecten, I observed a small but significant ($P = .05$, paired t -test) reduction in the normal pH of the vitreous humor. The possibility that the pecten may have a role in the regulation of intraocular pH was first suggested by A. Hughes (in King-Smith 1971) and elaborated by Brach (1975b). This hypothesis would also explain why the pecten is so extraordinarily rich in carbonic anhydrase as this enzyme catalyzes the equilibration of the three species of carbonic acid. The need for a pH regulator within the avian eye may be linked to an unusual retinal metabolism. In the mammalian retina, although a substantial portion of the energy-generating metabolism is dependent upon aerobic glycolysis (Krebs 1927, 1972, Noell 1956, 1963), a vascular supply is still essential for retinal maintenance, and a significant portion of the retinal ATP is generated by oxidative phosphorylation. In the avascular avian retina, typical mitochondria inward to the photoreceptor layer (which abuts the vascular choriocapillaris) are reduced or possibly even absent (Hughes et al. 1972). If mitochondria are present in the avian inner retina, they are so deficient in oxidative enzyme capacity that these investigators were unable to demonstrate the presence of bound succinic acid dehydrogenase over much of the width of the retina in the domestic pigeon, even though the same techniques revealed abundant, typical mitochondria in the photoreceptor layer. If the avian retina employs glucose as a source of energy but lacks the capacity for oxidative phosphorylation, relatively large amounts of pyruvic and/or lactic acid would be generated in the glycolytic production of ATP, and some system serving the retina would be expected to be present to remove both excess hydrogen ions and the accumulation of lactate. Brach (1975b) speculated that vitreal lactate might be actively exchanged for blood bicarbonate across the pecten vessels, which would simultaneously eliminate both wastes.

Since the classic fluorescein permeability ex-

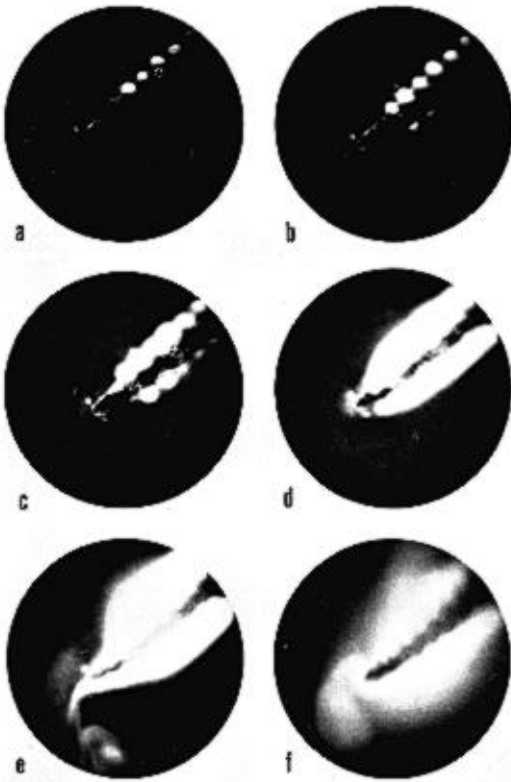


FIGURE 3. Representative stages from a typical fluorescein angiogram of the pecten and fundus of the domestic chicken after 0.5 ml of 5% sodium fluorescein was injected into the brachial vein. Times in sec from the start of the injection are: a) 1.0, b) 2.0, c) 4.0, d) 6.0, e) 10.0, f) 16.0. Note the dye plumes resulting from bulk flow within the vitreous in e and f. Some dye can also be seen in the choroidal circulation beneath the retina in c and d.

periments of Abelsdorff and Wessely (1909), it has been known that the pecten is grossly permeable to a variety of dyes (especially fluorescein) and some other substances, which suggests a high permeability to water (Seaman 1966, Fielding 1972, Bellhorn and Bellhorn 1975, Brach 1975b). Fluorescein injected into the heart or brachial vein in chickens begins to leak out of the pecten into the vitreous within 1.0 sec and appears to be caught up in a bulk flow or current, perhaps from the pecten itself (Fig. 3). Recently, R. W. Bellhorn and M. S. Bellhorn (pers. comm.) found that the pecten is essentially impermeable to fluorescein-labeled dextrans which suggests that the selective permeability of the pecten capillaries may be due to discrimination by molecular size, perhaps by pores. In this, the permeability characteristics of the pecten resemble those of the ciliary body more closely than those of mammalian retinal vessels. Sears (1960) demonstrated a carbonic

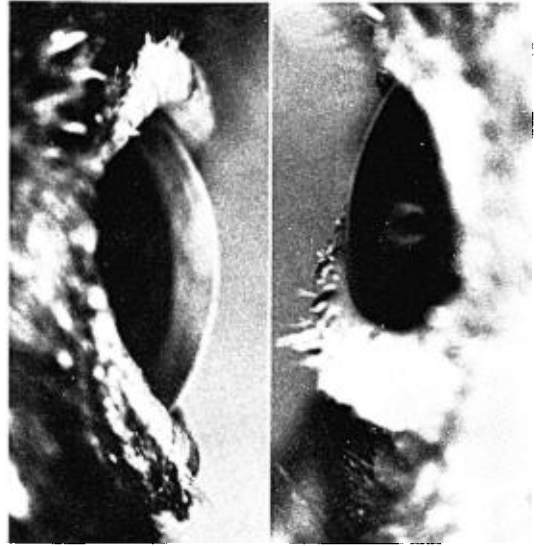


FIGURE 4. Head-on view of normal (left) and glaucomatous (right) chicken eyes in birds of equal ages. The bird on the right was reared in 24 h light for 14 weeks prior to this photograph. Note the reduction in the anterior chamber space.

anhydrase-independent source of fluid secretion within the avian eye although he did not mention the possibility that this might be the pecten. The extensively reduplicated pecten capillary endothelium is quite suggestive of a water-transport device, the most likely direction of movement being from the vessel lumen into the vitreous humor. Normally, the secretion of aqueous humor by vertebrate eyes is performed by the posterior portion of the ciliary body. The aqueous humor is therefore secreted into the posterior chamber of the eye; from there it flows around the lens through the pupil into the anterior chamber where it is drained into the venous circulation at the edge of the cornea by the canal of Schlemm. If the pecten also secretes fluid, a bulk flow through the vitreous would produce a "sweeping" effect that might facilitate the removal of retinal metabolic wastes.

Fluid secretion by the pecten may have an additional role in the vegetative physiology of the eye. For at least 20 years, it has been known that chicks (*G. domesticus*) reared under continuous illumination develop a glaucomatous condition characterized by bulbar enlargement, raised intraocular pressure, reduced corneal curvature and aqueous volume (Fig. 4), and eventual blindness (Lauber 1974). Curiously, eye enlargement precedes a measureable increase in intraocular pressure by several weeks, and no primary lesions of the sort usually associated with glaucoma, such as reduced outflow of aqueous humor

caused by the iris adhering to the lens or by blocking of the corneal angle, are found in the early stages of the disease. All known human glaucomas are the result of impaired outflow facility; a theoretically possible "hypersecretion glaucoma" has never been found (D. R. Anderson, pers. comm.). However, investigations by Bawa and YashRoy (1972) demonstrated that alkaline phosphatase, an enzyme implicated in some forms of active transport, shows decreased activity in the pecten upon dark adaptation of the eye. Although purely speculative at the present, it would be most interesting if fluid secretion by the pecten were directly influenced by light, making the "primary lesion" of light-induced avian glaucoma a hypersecretion by an overstimulated pecten. Assuming that the outflow facility of the eye is relatively fixed, hypersecretion beginning soon after hatching might cause the rapidly growing eye to "balloon" in response to a chronic but small elevation in intraocular pressure which becomes measurable only after the eye is no longer able to enlarge.

The question might well be asked, "Why has a pecten-like structure evolved in the avian eye in lieu of the more conventional retinal vascularization found in most other vertebrates?" Actually, the presence of blood vessels on and within the mammalian retina is an impediment to sharp vision, and one finds that in those mammals having the best vision, the foveal region is supplied from the choriocapillaris and is devoid of blood vessels. Walls (1942), Hughes et al. (1972), Krebs (1972), and Brach (1975b) argued that the evolution of the pecten may be one of a suite of several adaptations for improving retinal image quality and transparency, including the loss of blood vessels and mitochondria from the retina. In this regard it is interesting to recall that the eyes of most diurnal lizards are served by the histologically similar conus papillaris (Brach 1976). However, both nocturnal birds and lizards have a reduced pecten or conus, perhaps the result of retinal "nocturnalization" (sensu Walls 1942). The typical "nocturnalized" retina sacrifices visual acuity for photic sensitivity and is relatively thinner than the diurnal retina due to the reduced number of retinal ganglion cells. In those nocturnal birds and lizards which have come to depend largely upon tactile and olfactory senses (e.g., kiwis and the Gila monster, *Heloderma suspectum*), both the pecten and the eye itself have become greatly reduced.

Although the enigma of the pecten is far from solved, future research, especially that

involving experimental surgery, may produce a satisfactory answer within the next few years. In my opinion, the functional significance of the avian pecten holds considerable interest for medicine as well as ornithology and is well-deserving of intensive study.

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