clearly could abandon this area and move on to presumably better hunting grounds.

Evidence is beginning to accumulate from ethnographic studies of other Yąnomamö subpopulations that protein consumption is more than adequate and that levels of protein consumption do not correlate with patterns of warfare intensity. The work of Lizot is the most detailed on this score (*14, 15*). He recently conducted a very complete dietary study of two Yąnomamö villages located about 25 miles to the east of the villages on which we are here reporting. He found that, although consumption of animal protein varied between the two groups (36 and 77 g per capita per day), their patterns of warfare were identical (*14, 15*).

Protein consumption data on other Amazonian populations is emerging and likewise calls into question the often repeated suggestion that Amazonia is a protein desert. The earlier survey conducted by Gross (*9*) has been superseded by protein consumption studies in which superior data collection methods were used. Table 2 presents a compilation of dietary surveys for a number of Amazonian tribes, most of which were not available at the time of Gross' publication. Although we had to estimate some of the data because of differences in individual reporting techniques, a number of generalizations are possible: (i) The average per capita consumption in our sample (Table 2) is slightly greater than that given for the society with highest consumption in Gross' entire sample, (ii) the average per capita consumption in our sample is 80 percent higher than the average reported in Gross' survey, and (iii) our figure for average per capita consumption is higher than that found in the world's most developed nations (*8*, p. 430, figure 20-2). Ironically, the Jívaro and Bari, aside from the Yąnomamö, are considered by most anthropologists to be very warlike tribes, yet they consume more meat than the more peaceful tribes described (Table 2).

In conclusion, where quantified data on animal protein consumption has been collected in Amazonian native populations characterized by relatively intense warfare patterns, there appears to be little support for the hypothesis that a shortage of protein in the native diet explains intergroup warfare. Past attempts at such explanations have often advocated the existence of a protein shortage, and to the extent that empirical evidence has any bearing on these kinds of explanations of, for example, Yąnomamö warfare, the explanations fail. They would probably be inadequate explanations even if there were significant protein deficiencies, for warfare in any society is sufficiently complex that no single variable can account for its ultimate or proximate causes, its character, timing, duration, and consequences.

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Accessory Optic Projections upon Oculomotor Nuclei and Vestibulocerebellum

Abstract. *Displaced retinal ganglion cells in birds are the sole source of the retinal projection onto the nucleus of the basal optic root, the main component of the accessory optic system. This nucleus has direct bilateral axonal projections onto the oculomotor nuclear complex, the trochlear nucleus, and folia IXc,d and paraflocculus of the vestibulocerebellum. The cerebellar projection terminates within a superficial band of the granule cell layer adjacent to the Purkinje cell layer as a mossy fiber system. This bisynaptic projection onto oculomotor neurons and the cerebellum may play a functionally distinct and specific role in oculomotor reflexes.*

The accessory optic system had been recognized as a constituent of the visual system as early as 1881 by Gudden (*1*) and has been described in all vertebrate classes (*2*). The accessory optic system is characterized by the accessory optic nuclei, which are located at the meso-diencephalic border, and a distinct fascicle of retinal axons that terminate on these nuclei (*2*). Recently, in birds, a unique class of retinal ganglion cells, the displaced ganglion cells of Dogiel, have been demonstrated to be the sole source of a retinal projection onto the main component of the accessory optic system, the nucleus of the basal optic root (nBOR) (*3*). Dogiel (*4*) and Cajal (*5*) first characterized displaced ganglion cells as large retinal ganglion cells located at the border of the inner nuclear layer and in-

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ner plexiform layer and as having dendrites that ramify only within the first stratum of the inner plexiform layer. These cells are prominent in birds although they have been identified within the retina of all vertebrate classes (*4–6*).

Little information is currently available concerning the efferent projections of the accessory optic nuclei. Recent physiological and anatomical studies, however, have provided some evidence that the accessory optic nuclei project either directly (*7–10*) or indirectly (*11*) (via the inferior olivary complex) onto the vestibulocerebellum. We now report direct experimental evidence of the efferent projections of the avian accessory optic nucleus (the nBOR complex) onto the oculomotor nuclear complex, the trochlear nucleus, and folia IXc,d and paraflocculus of the vestibulocerebellum. The cerebellar projection terminates within the external regions of the granule cell layer adjacent to the Purkinje cell layer as a mossy fiber system.

Twenty white Carneaux pigeons were studied. They were anesthetized with intramuscular Ketamine (Parke-Davis) (0.15 ml per 100 g of body weight), and the wound edges were infused with xylocaine. Unilateral stereotaxic injections of 0.5 to 1.0 μl of a 1:1 mixture (*12*) of [^{3}H]proline and [^{3}H]leucine were injected into the nBOR complex. Between 1 and 4 days later the pigeons were anesthetized and perfused transcardially with 0.75 percent saline followed by Carnoy's fixative. The brains were then embedded in Paraplast, sectioned at 10 μm in either horizontal, transverse, or parasagittal planes, and processed according to standard autoradiographic procedures (*13*).

Subsequent to the anterograde autoradiographic experiments, retrograde studies with horseradish peroxidase (HRP) were conducted to verify the projection patterns of the nBOR complex. Unilateral injections of 0.05 to 0.1 μl of a 40 percent solution of HRP in distilled water were made into the oculomotor nuclear complex and the trochlear nucleus or folia IXc,d and paraflocculus of the vestibulocerebellum. Between 1 and 2 days later, the pigeons were anesthetized and perfused transcardially with 6 percent dextran followed by 1 percent paraformaldehyde and 1.25 percent glutaraldehyde in 0.1*M* phosphate buffer (*p*H 7.2). The brains were removed, blocked, stored overnight in a 30 percent sucrose fixative mixture at 5°C, and then cut at 40 μm in either horizontal, transverse, or parasagittal planes. Sections were treated for HRP by the benzidine dihydrochloride method (*14*).

The anterograde autoradiographic experiments demonstrated bilateral labeling of the oculomotor nuclear complex and the trochlear nucleus. Labeled axons were traced from the injection site dorsomedially along the lateral margin of

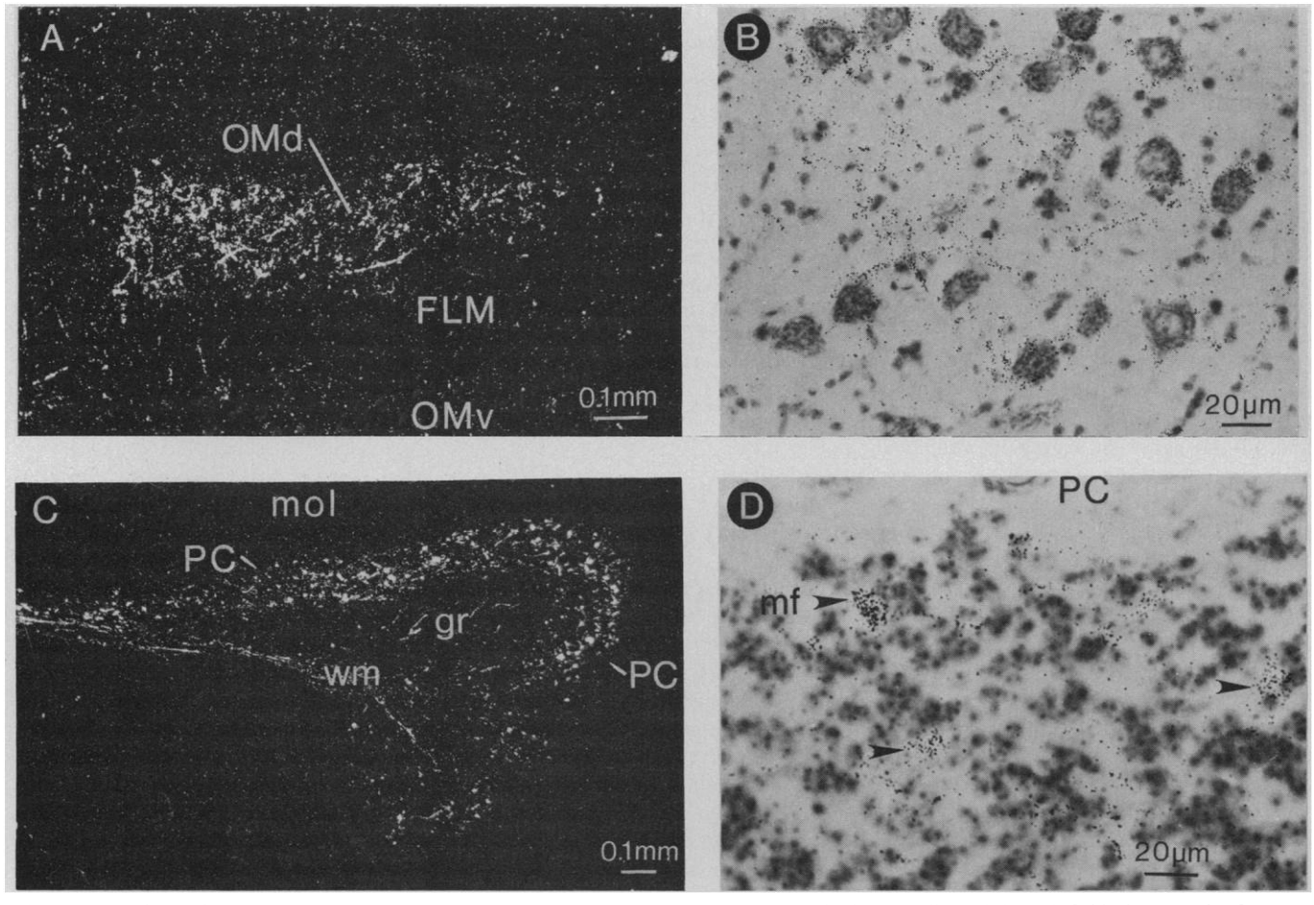

Fig. 1. Projections of the nBOR complex onto the oculomotor nuclear complex and vestibulocerebellum. (A) Dark-field photograph of a parasagittal section through the contralateral dorsolateral division of the oculomotor nuclear complex illustrating the termination of nBOR on this nucleus. (B) Higher-power, bright-field photograph illustrating the distribution of silver grains near and around the soma of oculomotor neurons within the contralateral dorsolateral division of the oculomotor nuclear complex. (C) Dark-field photograph of a parasagittal section of folia IXc,d illustrating labeled axons within the white matter and the distribution of mossy fiber terminal labeling only within the external regions of the granule cell layer adjacent to the Purkinje cell layer. (D) Higher-power, bright-field photograph of mossy fiber rosettes within the granule cell layer. Abbreviations: *gr*, granule cell layer; *mol*, molecular layer; *OMd*, dorsolateral division of oculomotor nuclear complex; *FLM*, fasciculus longitudinalis medialis; *OMv*, ventral division of oculomotor nuclear complex; *PC*, Purkinje cell layer; *mf*, mossy fiber rosette; and *wm*, white matter.

the oculomotor nerve (nerve III) to the oculomotor nuclear complex. Label was observed predominantly over the ipsilateral ventral and the contralateral dorsolateral divisions of the oculomotor nuclear complex (Fig. 1A). No labeling was observed over either the ipsilateral or contralateral dorsomedial division of the oculomotor nuclear complex. A light bilateral projection was also observed over the trochlear nucleus (nucleus IV). Labeling was absent over the abducens nucleus (nucleus VI). The silver grains were clustered immediately adjacent to the somata of neurons within the oculomotor nuclei (Fig. 1B), which suggests that axon terminals of nBOR cells synapse onto perikaryons and proximal dendrites of oculomotor neurons. Unilateral injections of HRP into the oculomotor nuclear complex and trochlear nucleus resulted in retrograde labeling of cells within the contralateral nBOR and the ipsilateral nBOR pars dorsalis (nBORd), which are subdivisions of the nBOR complex. These retrograde HRP studies confirmed the autoradiographic experiments and further clarify the organization of the nBOR complex (Fig. 2B).

The anterograde autoradiographic experiments also demonstrated a descending fascicle of axons joining the ipsilateral brachium conjunctivum (BCP) to enter the cerebellum. Labeled axons distribute bilaterally within the cerebellum, crossing to the contralateral cerebellar folia via the commissura cerebellaris dorsalis. The nBOR efferents distribute predominantly to the uvula, specifically folia IXc,d, and paraflocculus, and terminate within superficial regions of the granule cell layer as a mossy fiber system (Fig. 1C).

The label is distributed bilaterally with an apparent equal density within the cerebellum. Very few mossy fiber terminals or rosettes were observed in more rostral cerebellar folia (folia VI, VII, VIII, IXa, and IXb), which indicates a sparse accessory optic projection upon these folia. No evidence of a climbing fiber system was observed in any experiment. Unilateral injections of HRP confined to folia IXc,d, or the paraflocculus resulted in approximately the same number of retrograde-labeled cells within both the ipsilateral and the contralateral nBOR complex. Thus, these experiments are in agreement with earlier retrograde studies (*7*) and the present anterograde autoradiographic studies.

The mossy fiber system from the nBOR is characterized by axons which course through the white matter and enter the granule cell layer as discrete fascicles within parasagittal bands. These fascicles pass through the internal regions of the granule cell layer before spreading and forming mossy fiber terminals (Fig. 1, C and D). Mossy fiber rosettes are located predominantly within the external one-half to one-third of the granule cell layer immediately subjacent to the Purkinje cell layer (Fig. 1C). At several locations there is an extensive horizontal spread of mossy fiber terminals giving the appearance of a continuous band of terminals within the granule cell layer.

The accessory optic mossy fiber system appears to be unique in its termination pattern when compared with other cerebellar afferent systems. Olivocerebellar, spinocerebellar, and pontocerebellar afferent systems have been reported to enter and terminate within the cerebellar cortex in parasagittally oriented bands in both birds and mammals (*15*). Moreover, the spinocerebellar and pontocerebellar mossy fiber systems appear to terminate throughout the entire depth of the granule cell layer within these parasagittal bands. In contrast, the accessory optic mossy fiber system, which also enters the granule cell layer within parasagittally oriented fascicles, spreads into and forms a horizontal band of mossy fiber rosettes only within the external portions of the granule cell layer.

Our report has further clarified the precise termination of the accessory optic nuclei of pigeon as a mossy fiber system within the vestibulocerebellum, ending predominantly on folia IXc,d, and the paraflocculus. The projection of the accessory optic nuclei onto the vestibulocerebellum has recently been reported in several vertebrate classes (*7–10*) studied by retrograde transport methods (HRP histochemistry). These retrograde studies have demonstrated an accessory optic projection onto the vestibulocerebellum in fish (*8*), reptiles (*9*), and mammals (*10*), thus emphasizing its common existence in several vertebrate classes. Our experiments suggest that the accessory optic nuclear projection upon the cerebellum in all vertebrates would terminate as a mossy fiber system and, therefore, would account for the rapid visual mossy fiber response recorded within the mammalian (rabbit) vestibulocerebellum following optic nerve stimulation (*16*). This suggestion is based on the similarity of the mammalian accessory optic nucleus, also known as the medial terminal nucleus, to the nBOR complex in birds (*2*) and this report demonstrating that the nBOR projects onto the vestibulocerebellum and terminates as a mossy fiber system.

A striking finding is the demonstration of a direct projection of the accessory optic system upon oculomotor nuclei. This projection is the shortest visual pathway ending on the oculomotor nuclei that has been so far described; it is

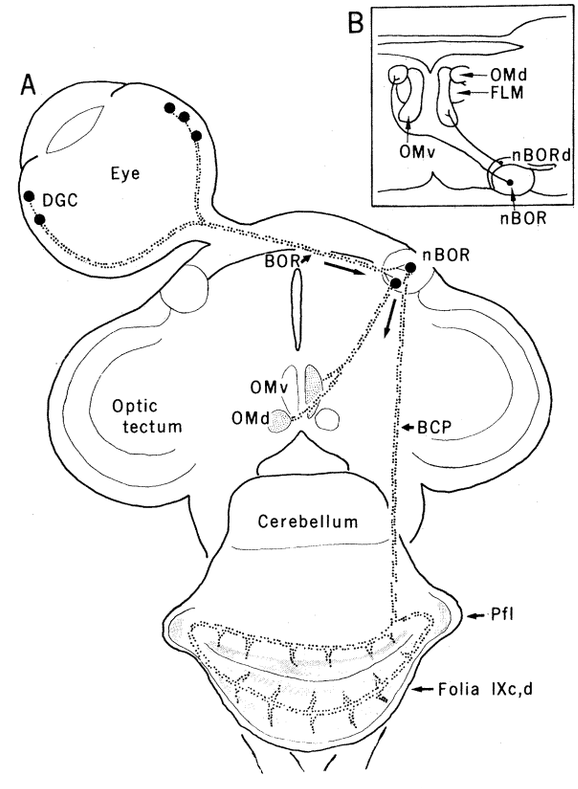

Fig. 2. Summary schematic of the displaced retinal ganglion cell projection onto the nBOR complex and the nBOR complex projections onto the oculomotor nuclear complex and the vestibulocerebellum. (A) Summary diagram. (B) Detail of the relationship of nBOR complex to the oculomotor nuclei. Abbreviations: *DGC*, displaced ganglion cell; *BCP*, brachium conjunctivum; *BOR*, basal optic root; *nBOR*, nucleus of the basal optic root; *nBORd*, nucleus of the basal optic root pars dorsalis; and *Pfl*, paraflocculus. Other abbreviations are as in Fig. 1.

considerably shorter than the oligosynaptic visual projections onto the oculomotor nuclei reported to originate from cortical or brainstem regions. Our findings confirm earlier claims from study of normal material from birds, reptiles, and amphibians of the existence of a projection onto the oculomotor nuclear complex arising from the accessory optic nuclei (*17*). Recent retrograde studies have also confirmed the existence of an oculomotor projection in a teleost (*8*), further emphasizing the probable occurrence of this projection in several vertebrate classes. This bisynaptic retinal projection onto the oculomotor nuclei could result in rapid adjustments of the oculomotor muscles in response to a visual stimulus. Furthermore, our recent studies have demonstrated that the contralateral dorsolateral division and the ipsilateral ventral division of the oculomotor nuclear complex innervate the inferior and superior rectus of the same eye, which strongly suggests that the nBOR complex plays a significant role in vertical eye movements.

The recent demonstration that the input to the nBOR is derived exclusively from displaced retinal ganglion cells suggests that displaced retinal ganglion cells may be specifically involved in initiating rapid oculomotor responses to peripheral moving stimuli. This hypothesis is further supported by the finding that displaced retinal ganglion cells are distributed predominantly within peripheral retinal regions (*3*) and the accessory optic nuclei project directly onto oculomotor nuclei and folia IXc,d, and paraflocculus of the vestibulocerebellum (Fig. 2A). The lemniscal nature of a bisynaptic retinal pathway via the accessory optic nuclei indicates that this system has a specific functional role in the control of oculomotor reflexes in response to peripheral retinal stimulation.

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Dual Function of the Damselfly Penis: Sperm Removal and Transfer

Abstract. *The male of* Calopteryx maculata *(Beauvois) (Odonata) uses its penis not only to transfer sperm to the female but also to remove sperm deposited in the female's sperm storage organs from previous matings. Apparently, no such sperm removal function has previously been attributed to the intromittent organ of any animal.*

In most insects eggs are fertilized at oviposition, with sperm stored by the female from previous matings. When two or more males mate with a female before she oviposits, their sperms do not necessarily have equal chances to fertilize her eggs (*1*). Experiments with genetic markers or irradiated males have generally revealed a precedence of the sperm from the last male to mate (*2*); but lack of precedence (*3*) and mixing of sperm from successive matings (*4*) also occur. The mechanism of sperm precedence is poorly understood (*1*, *5*). In some species previous sperm may be forced to the rear of the female's sperm storage organs, resulting in a last in, first out phenomenon (*6*).

Males of the damselfly *Calopteryx maculata* defend ovipositing mates from disturbance and take-over attempts by other males (*7*). Multiple mating (*7*) and sperm storage (see Table 1) occur in females. Because these factors indicate the likelihood of sperm competition, I have investigated the fate of sperm deposited by males successively mating with the same female. No genetic markers are known for this species and females cannot be induced to oviposit under controlled conditions (*8*). Hence, evidence for sperm displacement is indirect and in my experiment restricted to three kinds.

1) I compared amounts of sperm in females after one and two matings, respectively, without oviposition to determine whether sperm from a second mating was simply added to that from the first. Females were collected on the stream, tethered, and presented to territorial males (*9*). Durations of the resulting copulations were timed, and the female abdomens were removed and immediately preserved in 70 percent ethanol. In the laboratory, the bursa copulatrix and spermatheca (Fig. 1A, *bc* and *st*) were removed from each female and the external dimensions of the sperm mass within them were measured with an ocular grid (×25 magnification). These measurements were used to calculate an index of sperm volume stored by a female.

The mean (± 95 percent confidence limits) volume index for females mated once (4.20 ± 0.59; $N = 14$) did not differ from that for females mated to two males within 10 minutes (4.38 ± 0.73; $N = 16$). Dissections of male sperm vesicles revealed that they had transferred sperm to the female (*10*). The duration (mean ± 95 confidence limits) of copulation for first and second matings also did not differ (79.0 ± 15.7 seconds; $N = 13$; 70.0 ± 11.6 seconds; $N = 16$). These results

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