Binocular Vision and Ipsilateral Retinal Projections in Relation to Eye and Forelimb Coordination

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Key Words

Optic chiasm · Evolution · Dexterity · Ipsilateral retinal projection · Nonmammalian vertebrate · Binocular vision · Primate

Abstract

It is commonly proposed that the number of fibers that do not cross in the optic chiasm (OC) is proportional to the size of the binocular visual field, and that the major advantage of binocular vision is acute depth perception. I present an alternative, an 'eye-forelimb' (EF) hypothesis, suggesting that alterations in the OC influence the length of neural pathways that transmit visual information to motor nuclei and somatosensory areas involved in forelimb coordination. Evolutionary processes resulting in increased ipsilateral retinal projections (IRP) are of adaptive value in animals that regularly use the forelimbs in a frontal position, while evolutionary change towards reduced IRP is of value for animals that mainly use the forelimbs in lateral positions. Primates and cats, to a large extent, use visually guided forelimb maneuvers, and both groups have high proportions of IRP. The fact that vertebrates' IRP arise exclusively from the temporal retina supports the hypothesis, since IRP from the nasal retina would increase the length of neural pathways involved in forelimb coordination. The EF hypothesis offers new perspectives on why a high proportion of IRP among early limbless verte-

brates became reduced during the evolution of laterally situated limbs, and why reptiles that lost their limbs (snakes) evolved more IRP. Anatomical, neurophysiological, phylogenetic, ontogenetic and ecological data suggest that mutations changing the proportions of ipsilateral visual connections in the OC may have selective value for EF coordination.

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Introduction

Harris [1904] wrote: 'Binocular vision is clearly of great assistance in the accurate use of the hand for fine movements ...', and several authors after that have proposed a significant association between binocular vision and eye-hand control, e.g. Elliot Smith [1928], Le Gros Clarke [1934] and Hughes [1977]. However, the architecture of neural pathways between the eye and the brain in relation to forelimb control, which is the focus of this review, has been little discussed. The structure of the ventral diencephalon midline, where retinal ganglion cell (RGC) axons partially decussate, or cross, is called the optic chiasm (OC). In primates, approximately 45% of RGCs project to targets on the same side [Fukuda et al., 1989]. Many predatory mammals, such as the Felidae, have frontally positioned eyes and a significant degree of ipsilateral retinal projection (IRP) [Jeffery and Erskine,

2005]. Domestic cats display 30% IRP [Herrera and Mason, 2007], while the ferret possesses approximately 8% IRP [Henderson, 1985; Morgan et al., 1987]. Mammals with laterally positioned eyes have a low degree of IRP [Herrera and Mason, 2007]. In rodents, the uncrossed component is about 2–3% [Petros et al., 2008]. Newton argued that binocular vision requires that fibers from each retina allocate to both sides of the brain [Soury, 1899; Newton, 1931; Polyak, 1957]. Johannes Müller proposed that this could be achieved either by splitting each retinal fiber or by partial decussation of the optic nerve in the OC [Polyak, 1957]. Bernhard von Gudden showed that the OC contains both crossed and uncrossed retinal fibers, and Ramon y Cajal [1972] observed that the degree of hemidecussation varies among species [Polyak, 1957; Ramon y Cajal, 1972]. Walls [1942] formalized the law of Newton-Müller-Gudden (NGM), which proposes that the number of fibers that do not cross the midline is proportional to the size of the binocular visual field. That is, the degree of optic fiber decussation in the chiasm is inversely related to frontal orientation of the optical axes of the eyes. A controversial aspect of the NGM law is the considerable interspecific variation in ipsilateral visual projections in nonmammalian species [Ward et al., 1995]. This variation has not been shown to be related to an overlap of visual fields, mode of life, or taxonomic position. I present an eye-forelimb (EF) hypothesis, based on the idea that alterations in the OC will influence the length of neural pathways that transmit visual information to motor nuclei and somatosensory areas involved in forelimb coordination. Mutations resulting in increased IRP should be of adaptive value in animals that regularly use their forelimbs frontally, while mutations towards reduced IRP will be of adaptive value for animals that mainly use the forelimbs laterally. The aim of this review is to evaluate the EF hypothesis in vertebrates in relation to OC formation, hemidecussation, binocular vision, and motor behavior.

The EF Hypothesis

Manual Performance in the Right and Left Visual Hemispheres

Berlucchi et al. [1971] suggested that the reactions of the hand to stimuli presented in the ipsilateral visual hemifield are integrated in the contralateral hemisphere. This means that when the right hand performs a task in the right visual field (RVF), the visual information of the right hand's location in space is processed in the left

hemisphere, which also processes motor reactions of the right hand. On the contrary, right hand maneuvers and visual stimuli in the left visual field require coordination of the visual cortex in the right hemisphere and the motor cortex in the left hemisphere; hence such crossed reactions should contain at least one more synaptic link. Thus the right hand should react faster to stimuli presented in the RVF and vice versa for the left hand. Fisk and Goodale [1985] verified that the laterality of the target was the single most important determinant of the manner in which a reaching movement is executed. Their research also demonstrated a remarkably close timing of eye and hand during a reaching movement. Aziz-Zadeh et al. [2006] showed that both brain hemispheres displayed more rapid motor responses to contralateral visual stimuli as compared to ipsilateral stimuli.

Evolutionary Change in the OC and Effects on Neural Pathways among Cooperating Brain Areas

In vertebrates, motor nuclei and somatosensory areas of the limbs are situated in the contralateral cerebral hemisphere. Figure 1 shows visual pathways to the superior colliculus in three types of animals, a vertebrate without limbs, a vertebrate with laterally situated limbs, and a primate. The superior colliculus is a component of the tectum, which integrates visual, somatosensory and auditory information. In addition, two other major targets of visual information from the retina, the suprachiasmatic nucleus of the hypothalamus and the pretectum, are involved in circadian rhythm and pupillary light responses. The proportion of IRP in these non-image forming visual pathways is not related to the degree of binocular vision [Magnin et al., 1989].

If the eyes are laterally positioned and if only crossed axons exist in the OC, visual information from the RVF will be processed in the left brain hemisphere (fig. 1b). Fish, birds, and reptiles, for anatomical or functional reasons, rarely use their forelimbs frontally. Thus, evolutionary changes towards ipsilaterality would have no selective value with respect to EF coordination in these animals. A consequence, for example in crocodilians, would be that an increased fraction of visual information about the right forelimb position is directed to the right cerebral hemisphere, where it is not likely to be especially useful in eye-directed forelimb coordination. However, a change in the opposite direction (i.e. less IRP and more crossed retinal projections) would increase transmission of visual information about the right forelimb to the left hemisphere, which theoretically could lead to improved EF coordination (fig. 1b). That may also be relevant for dol-

Fig. 1. Visual pathways in three principal types of vertebrates. The figures only show retinal pathways to the superior colliculus, but principles for neural pathway length to the primary visual cortex will be analogous. (Visual pathways to the suprachiasmatic nucleus of the hypothalamus and the pretectum are not presented.) **a** Schematic of optic pathways in limbless vertebrates, e.g. cyclostomes, snakes and cecilians. Limbless animals in general have relatively abundant IRP. Body movements in limbless animals will inevitably involve both sides. As a consequence, motor commands to either side must be coordinated with those of the contralateral body part. In addition, when a snake or cyclostome is curled, the eye may receive visual information about ipsilateral as well as contralateral body parts. **b** Schematic of optic pathways in a vertebrate with lateralized visual fields and laterally placed forelimbs. Lizards, crocodilians, chameleons and mice exemplify animals that have no or very small proportions of IRP and lateralized visual fields. These animals rarely use forelimbs in the binocular visual field. When the forelimb is used in the lateral visual field, visual information about the forelimb will be integrated in the same hemisphere that receives somatosensory information and processes motor commands for that limb. **c** Schematic of optic pathways to the superior colliculus in a primate. In primates approximately 45% of RGCs project to targets on the same side.

The combination of frontally directed eyes and abundant IRP from the temporal retina results in visual information about a limb's location in space being integrated in the same hemisphere that receives somatosensory information and processes motor commands for that limb. The figures are modified from Preuss [2007] based on Pettigrew et al. [1989]. VM = Visual field meridian.

phins, since the front flipper can be supervised only with the ipsilateral eye. Bottlenose dolphins, *Tursiops truncatus*, display only crossed projections [Tarpley et al., 1994]. In species that often use forelimbs frontally (e.g. to capture prey, pick fruit, manipulate food, or to grip a branch during locomotion) evolutionary changes towards ipsilaterality in the lateral retina result in corresponding visual, motor, and somatosensory areas being localized in the same hemisphere (fig. 1c). As Berlucchi et al. [1971] suggested, one result will be shorter neural pathways. Moreover, in humans and tree-climbing primates, frontally directed eyes and IRP from the lateral retina result

in shorter neural pathways in the visual cortex and motor area involved in visually guided maneuvers of the lower limbs.

The OC and Binocular Vision

Many of the molecules and mechanisms involved in OC formation are evolutionarily conserved [Herrera and Mason, 2007]. The formation of the OC in the mouse, the most investigated mammal, takes place in the following order: pioneer axons from the dorsocentral retina navi-

gate into the optic stalk and enter the hypothalamic area. The majority of these cross the midline. Subsequently, axons from the ventral temporal crescent arrive at the midline retina. These axons turn back to the ipsilateral brain hemisphere, while axons from the remainder of the retina cross the midline [Guillery et al., 1995; Mason and Sretavan, 1997]. In the third phase, all RGCs, regardless of origin, cross the midline [Sretavan, 1990; Herrera and Mason, 2007]. Transcription factors that play vital roles in the morphogenesis of the retina and the regionalization of the OC area have been identified, and alterations in transcription factors commonly cause abnormal OC phenotypes [Chung et al., 2004; Pak et al., 2004; Herrera and Garcia-Frigola, 2008]. Mutations in RGCs towards ipsilaterality have been frequently proposed as a mechanism facilitating binocular vision and acute depth perception, and the potential for stereoscopic depth perception is the most often cited advantage of binocularity in mammals [Williams et al., 2004; Heesy, 2008]. It is commonly suggested that animals with binocular vision use subtle differences between the images received by each eye to perceive stereoscopic depth [Heesy, 2009]. However, studies have failed to identify a cortical site primarily dedicated to stereoscopic depth perception [Parker, 2007]. Parker [2007] highlights a significant gap in knowledge concerning the stereo cues that are used by the parietal cortical regions during reaching and grasping movements.

Another potential advantage of binocular vision is enhanced light sensitivity, since it increases the likelihood of capturing light within the area of overlap [Pirenne, 1943; Williams et al., 2004; Heesy, 2008]. Binocularity is also proposed to improve contrast discrimination, defined as the ability to detect luminance differences in nearby objects or multiple parts of the same object [Pirenne, 1943; Campbell and Green, 1965; Heesy, 2009]. Many have proposed that an important function of hemidecussation is to obtain input from each retina and transmit the information to corresponding targets that are located more centrally. Stimuli from a point in the visual field received by each retina can be directed to the same location in the visual cortex, where two slightly differing images are integrated into a consistent three-dimensional representation [e.g. Jeffery and Erskine, 2005; Herrera and Mason, 2007]. The large overlap between the RVF and left visual field is a primate visual specialization [Cartmill, 1974]. A wide binocular field is related to high visual acuity, specialization of visual pathways in the brain, adaptations of the visuomotor system, and elaboration and differentiation of the visual cortex [Grantyn and

Moschovakis, 2004; Heesy, 2009]. It also correlates with the degree to which the bony orbits face in the same direction [Heesy, 2009]. Binocular vision is almost universal among vertebrates [Hughes, 1977]. All animals with two eyes have binocular vision, but the term is typically used only for animals that have a significant binocular overlap [Herrera and Garcia-Frigola, 2008]. Martin [2009] argued that stereopsis has been investigated in only a narrow range of species that have a moderately broad frontal binocular field, eyes that usually are widely spaced and forward-facing with parallel axes and conjugate movements, and that these are not typical traits of vertebrates. In the majority of vertebrates, eye position, eye movements, and binocular fields are quite different from hitherto investigated species [Martin, 2009].

The EF Hypothesis and Visual Projections in Nonmammals

In the following sections I review visual projections, eye direction, and motor behavior in nonmammal vertebrates. Supporting data are summarized in table 1.

Fishes, Reptiles and Amphibians

Cyclostomes, in general, exhibit IRP, leading Ward et al. [1995] to suggest that the ipsilateral contingent of fibers may be a phylogenetically primitive characteristic. The division of squamates that lost their limbs during evolution (snakes) possesses more abundant IRP than that of those with limbs (lizards) [Repérant et al., 1992]. When a cyclostome or snake (fig. 2) is curled, the eye may receive visual information about ipsilateral as well as contralateral body parts. Banihani [2010] proposed that locomotion and other body movements will inevitably involve both sides of the body in a limbless animal, i.e., motor commands to on one side of the body will also influence the contralateral body part. As a consequence, motor commands to either side must be coordinated with those of the contralateral body part. IRP in limbless animals may provide visual information that helps the brain to coordinate bilateral movements. Cyclostomes and snakes have relatively abundant IRP, which is in accordance with that premise, but why do nonteleost actinopterygians, such as sturgeon, possess extensive IRP [Repérant et al., 1982], and why are IRP frequent in cladistically primitive groups of teleosts and extremely rare in neoteleostans [Von Bartheld and Meyer, 1987; Medina et al., 1993; Ward et al., 1995]? Wilga and Lauder [1999] proposed that one of the most prominent features in the evo-

Table 1. Visual projections (VP) in nonmammalian vertebrates

(1) Cyclostomes

Extant representatives of these ancestral jawless vertebrates are hagfishes (myxinioids) and lampreys (petromyzontids). In spite of outward resemblances, they diverged early in vertebrate evolution [Forey and Janvier, 1993; Janvier, 2003].

VP: IRP have been demonstrated in the myxinioids *Eptatretus burgeri* [Kusunoki and Amemiya, 1983] and *E. stouti* [Wicht and Northcutt, 1990] and in the petromyzontiforms *Lampetra fluviatilis* [Vesselkin et al., 1980], *L. planed* [Demiguel et al., 1990], and *Petromyzon marinus* [Northcutt and Przybyls, 1973; Kennedy and Robinson, 1977; Demiguel et al., 1990].

(2) Chondrichthyans

The cartilaginous fishes are separated into two major divisions, the elasmobranchii and the holocephali [Schaeffer and Williams, 1977]. Holocephali are rare, comprising only six living genera [Carroll, 1988]. The elasmobranchii include over 700 species and are divided into two superorders, the selachimorpha (sharks and dogfish) and the batoidimorpha (skates and rays) [Nelson, 1984]. VP: IRP are few in the spiny dogfish, *Squalus acanthus* [Northcutt, 1979], the spotted dogfish, *Scyliorhinus canicula* [Repérant et al., 1986], and the shark *Hemiscyllium plagiosum* [Jen et al., 1983]. In the batoid *Platyrhinoidis triseriata*, numerous IRP have been demonstrated [Northcutt and Wathey, 1980].

(3) Bony fish (Osteichthyes)

Ray-finned fishes

Subclass Brachiopterygii

VP: In *Polypterus senegalus*, IRP have been shown in a single hypothalamic site, the anterior portion of the optic tectum, two of five thalamic visual centers, and in one of three pretectal centers [Repérant et al., 1981].

The sturgeon, *Acipenser güldenstädti*

VP: Extensive IRP are present in all primary visual centers that receive a contralateral afferent supply [Repérant et al., 1982].

Subclass Actinopterygii

The subdivision Teleostei (infraclass Neopterygii and division Halecostomi) is the most important radiation with more than 20,000 species [Nelson, 1984].

VP: IRP are less frequently described in Teleostei compared to other Actinopterygii. IRP are more frequent in cladistically primitive groups of Teleostei and extremely rare in neoteleostans [Vonbartheld and Meyer, 1987; Medina et al., 1993; Ward et al., 1995].

Lobe-finned fishes

Subgroup of the sarcopterygians and thus a sister group of tetrapods. Include four living genera: the dipnoan lungfish (*Neoceratodus*, *Lepidosiren*, and *Protopterus*) and the cross-opterygian coelacanth, *Latimeria* [Nelson, 1984; Carroll, 1988]. VP: In *Neoceratodus fosteri*, generally considered to be the most primitive of the extant lungfish, IRP has been demonstrated [Moy-Thomas, 1971; Northcutt and Wathey, 1980], while studies in lepidosirenid lungfish have not revealed IRP [Northcutt, 1977; Ward et al., 1995].

(4) Amphibians

They include the Caudata (salamanders), the Gymnophiona (caecilians, a group of burrowing, limbless amphibians), and the Anura (frogs and toads) [Noble, 1931].

VP: Older studies [Herrick, 1925, 1948] commonly describe decussation as total in the amphibian OC, but more recent experimental works report IRP [Guillery and Updyke, 1976; Repérant et al., 1978; Rettig and Roth, 1986; Ward et al., 1995]. In caudate amphibians, IRP seem to be established early in development [Rettig et al., 1981; Rettig 1988; Ward et al., 1995]. In anurans, IRP emerge at the culmination of metamorphosis [Fritsch, 1990], roughly when the eyes shift to a more frontal location [Gaze, 1970].

(5) Chelonians

Modern turtles comprise 240 species [Bellairs, 1970] distributed among 12 families [Gaffney and Meylan, 1988].

VP: Of 12 species that have been examined by autoradiographic techniques, all but one, *Trionyx cartilagineus*, show IRP [Ward et al., 1995].

(6) Rhynchocephalians

This separate and rare order of reptilian can be found only on small islands close to New Zealand [Eisthen and Polese, 2006]. VP: A study in a single specimen of *Sphenodon* did not show IRP [Northcutt et al., 1974].

(7) Squamates

Snakes and the lizards form the two major divisions [Bellairs, 1970].

Snakes

VP: IRP are modest in the majority of squamates [Repérant et al., 1978]. IRP are regularly more extensive in snakes than in lizards [Repérant et al., 1992]. In two subterranean microphthalmic species, the boid *Calabaria reinhardtii* [Repérant et al., 1978] and the scolecophidian *Typhlops vermicularis* [Halpern, 1973], rudimentary eyes are associated with extensive IRP.

Lizards

VP: In the agamid *Uromastix acanthinurus* [Repérant et al., 1978] and in *Chameleo chamaeleon* [Bennis et al., 1994] IRP are entirely absent.

(8) Crocodilians

VP: One (*Caiman sclerops*) of seven species has been investigated. Autoradiography did not reveal IRP [Repérant, 1975].

(9) Birds

VP: Most data on ipsilaterality are derived from chickens and pigeons [Remy and Gunturkun, 1991; Ward et al., 1995].

(10) Monotremes

Mammals that lay eggs.

VP: Studies are scarce [e.g. Campbell and Hayhow, 1971, 1972] and show few IRP.

Table 1 (continued)**(11) Marsupials**

Extant marsupials comprise approximately 250 species [Matthews, 1971]. Australian marsupials are often divided into two main groups: Diprodontia, species with two incisors in the lower jaw, includes possums, gliders, kangaroos, wombats, and the koala. The remaining species belong to several orders which often are grouped together as the polypropodonts [Harman et al., 1990]. Due to unique morphological and other characteristics, the honey possum, *Tarsipes rostratus*, is classified as the single representative of a diprodont superfamily, Tarsipedoidea, family Tarsipedidae [Kirsch and Calaby, 1977].

VP: The pattern of retinal projections differ somewhat in the North American opossum, *Didelphys virginiana*, and the South American *Marmosa mitis*, but in both species, bilateral projections have been revealed [Royce et al., 1976]. The retinal projections of investigated Australian marsupials [Harman et al., 1990] are generally similar, reporting retinal projections to seven targets, and of these, only one nucleus shows an exclusively contralateral supply [Sanderson et al., 1987; Ward et al., 1995]. The pattern of retinal input to the dLGN is more variable [Harman et al., 1990]. An extensive overlap of visual projections in the dLGN is seen in the polypropodont family Dasuridae. In most diprodonts, the dLGN display terminal banding and segregation of input from the right and left eye, but with a notable difference in two species, the feather-tailed glider, *Acrobates pygmaeus*, and the honey possum, *Tarsipes rostratus*, which both display extensive overlap from the two eyes in the dLGN, and accordingly small monocular segments (e.g. 12% in the honey possum) [Harman et al., 1990]. Similarly, an arboreal South American opossum, *Marmosa mitis*, has a small monocular segment (17%) [Royce et al., 1976]. Ground-dwelling and herbivorous wombats [Triggs, 1996] have a large monocular segment, 66% of the dLGN, while other examined marsupial species have monocular segments between 25 and 35% [Harman et al., 1990].

lution of ray-finned fishes is the change in pectoral fin position and function. In most teleosts the pectoral fins extend laterally in a transverse plane and are located in a somewhat dorsal position on the side of the body [Rosen, 1982]. However, in the plesiomorphs, such as the sturgeon, the pectoral fins extend laterally from a ventral insertion on the pectoral girdle and are held in a generally horizontal orientation [Bemis et al., 1997; Wilga and Lauder, 1999]. As a result, the pectoral fins of sturgeon are relatively immobile, and there is typically no observable change in pectoral fin position during tail beats, while many teleosts utilize oscillatory motions of pectoral fins to generate propulsive forces [Wilga and Lauder, 1999]. Lepidosirenid lungfish also display complex movements of the pectoral fins, such as using them to raise the anterior part of the body and in conveying food into the

mouth [Janvier, 2003]. Studies of lepidosirenid lungfish have not revealed ipsilateral visual projections [Northcutt, 1977; Ward et al., 1995]. In the elasmobranchii, *Squalus* exemplifies a fish in which visual supervision is restricted to the ipsilateral forelimb (pectoral fin), thus its low numbers of IRP [Northcutt, 1979] are in accordance with the EF hypothesis. However, the phylogenetically more advanced batoid *Platyrrhinoidis* shows numerous ipsilateral projections [Northcutt and Wathey, 1980; Ward et al., 1995]. Ebbesson and Meyer [1980] suggested that the retinal projections in the batoid guitarfish, *Rhinobatidae*, differ from those of other elasmobranch species in that some parts of the body will be included in the visual field, since it has a flat body shape. However, whether the guitarfish eye and body morphology allows supervision of contralateral body movements remains to be studied.

Ward et al. [1995] suggested that the considerable interspecific variation in the visual projections of the turtles (Testudines) cannot be explained in terms of taxonomic position or of mode of life, and constitutes a notable inconsistency in the NGM law. Among the investigated turtles, the only species lacking IRP, *Trionyx carolinianus*, has eyes notably more frontally placed and a larger binocular field than does *Chinemys*, in which the ipsilateral projections are among the most extensive [Hergueta et al., 1992].

RGCs project bilaterally with a contralateral dominance in most lizards, and projections are, on the whole, contralateral in crocodilians and completely contralateral in chameleons and uromastix lizards [Burns and Goodman, 1967; Repérant, 1975; Bennis et al., 1994; Tarpley et al., 1994; Ward et al., 1995; Derobert et al., 1999; Bruce, 2009]. Since these animals have little frontal use for their forelimbs, this is consistent with the EF hypothesis. In amphibians, the pattern is variable. Plethodontid salamanders have substantial numbers of IRPs [Wiggers, 1999; Dicke and Roth, 2009]. Plethodontid salamanders, in particular tropical climbing salamanders, *Bolitoglossa*, comprising 50% of extant salamanders, have developed a peculiar feeding apparatus specialized for tongue protrusion [Roth and Schmidt, 1993]. Wiggers et al. [1995] suggested that the substantial number of IRPs in *Bolitoglossa* is the basis for a fast computation of object distance. Notably, the projectile tongue of the *Bolitoglossa* is combined with a more frontal eye position relative to other salamanders [Roth and Schmidt, 1993]. The African clawed frog, *Xenopus laevis*, has only crossed projections until metamorphosis, when it develops binocularity, ipsilateral connections, and forelimbs with claws [Gaze, 1970; Fritzsche, 1990; Jeffery and Erskine, 2005]. Carreno

Fig. 2. When a snake is curled each eye may receive visual information about ipsilateral as well as contralateral body parts. In addition, body movements in eel- and snake-like animals (cyclostomes and caecilians) unavoidably engage both sides of the body, i.e., the left and right side must move in coordination. (Photo: Kveta Källmén).

and Nishikawa et al. [2010] showed that prior to capturing prey, the forelimbs of *X. laevis* are held in a forward flexed position, with each forelimb positioned in front of the head. During prey capture, the forelimbs are extended and used to capture prey and move it to the mouth. In a third amphibian group, the limbless caecilian *Ichthyophis kohtaoensis* displays contralateral retinal projections as well as IRP [Himstedt and Manteuffel, 1985].

In marsupials, the pattern of retinal input to the dorsal lateral geniculate nucleus (dLGN) is variable and has been extensively studied [Royce et al., 1976; Harman et al., 1990] (table 1). Abundant overlap of visual projections in the dLGN will be largely analogous to high proportions of IRP. Two species of diprodonts with an arboreal lifestyle, the feather-tailed glider, *Acrobates pygmaeus*, and the honey possum, *Tarsipes rostratus*, display extensive overlap in the dLGN from the eyes [Harman et al., 1990]. Similarly, an arboreal South American opossum, *Marmosa mitis*, displays extensive overlap in the dLGN [Royce et al., 1976]. Ground-dwelling herbivorous wombats are reported to have the least overlap [Triggs, 1996], while other investigated marsupials fall between these extremes [Sanderson et al., 1987].

Birds

Adult birds seem to have no or very few IRP [Remy and Gunturkun, 1991; Ward et al., 1995]. In bird embry-

os an important ipsilateral projection develops that is greatly reduced just before hatching [Thanos and Bonhoeffer, 1984]. Since birds are descendants of tetrapod reptiles, their ontogeny might reflect the phylogenetic development of birds, i.e. bird predecessors may have had more extensive ipsilateral projections. Avian predecessors had very long forelimbs, e.g., in *Archaeopteryx* the forelimb is 120–140% of the hindlimb length [Gauthier, 1986], which may have been compatible with frontal forelimb use. Birds do not display hemidecussation of retinal axons at the level of the OC, but they do show an interhemispheric crossing of visual fibers at the thalamotelencephalic level [Remy and Gunturkun, 1991]. The nucleus opticus principalis thalami is the equivalent structure to the lateral geniculate of mammals and receives a group of contralateral retinal fibers. This nucleus in turn projects bilaterally to the visual wulst, the equivalent avian structure of the V1 cortex. Thus, the bird primary visual cortex receives an IRP via the nucleus opticus principalis thalami [Remy and Gunturkun, 1991; Martin, 2009]. In particular, owls have a high degree of IRP [Pettigrew, 1986a]. Owls exhibit double decussation rather than the partial decussation of mammals. Pettigrew [1986a] suggested that owls have developed an elaborate neural substrate for binocular vision, and that most of the features described for the mammalian binocular visual pathway have a counterpart in the

binocular visual pathway of the owl. Martin [2009] reviewed binocular vision in birds and proposed that maximum binocular field width across most avian taxa ranges from 15° to 30°. In owls, maximum binocular field widths are typically almost twice this. The hypothesis that binocularity inevitably results in stereopsis in birds has been questioned [Davies and Green, 1994; McFadden, 1994]. Davies and Green [1994] suggested that too much time is required, especially during critical rapid flight maneuvers, to reach a sufficient level of accuracy in estimating depth through stereopsis. In filter-feeding ducks, the frontal binocular overlap is less than 10%, and in woodcock it is around 5%. In spite of this, woodcock are capable of rapid flight in complex habitats such as woodland [Martin, 2009]. Owls probably have the widest binocular fields of any avian species, but the binocular fields are narrower than the impression gained from casual observation and are not at the level of those of primates [Martin, 2009]. Since owls do not use wings for manipulation of objects, in the frontal position, their elaborate neural substrate for binocular vision appears to be at odds with the EF hypothesis. The decussation and binocular vision of owls may in theory improve eye-lower-limb coordination, which may have selective value in predation. Raptors normally take prey with their feet, approaching the target with feet brought up into the visual field just prior to capture [Martin and Katzir, 1999]. Several owl species have been observed foraging on foot [Johnsgard, 1988; Taylor, 1994; McMillian, 1998]; however, foraging on foot is common in many bird species. Owls seem to be an outlier group with respect to the EF hypothesis. Their acute vision and relatively unique hunting habits may be involved. Martin [2009] suggested that the primary function of binocular vision in birds is to extract information used in control of bill and foot position and the timing of opening the bill or feet, e.g. when pecking, lunging, taking prey, or feeding young birds.

Discussion

This EF hypothesis provides a novel, or complementary, approach to the question of why vertebrate species show differing proportions of IRP. In essence, it suggests that evolutionary processes may switch the direction of RGCs so that their axons may or may not cross the midline in the OC. An evolutionary change from the ancestral condition (with several IRP) towards reduced IRP proportions may be of adaptive value in animals that

exclusively or almost exclusively use the forelimbs in a lateral position, since increased contralateral IRP will result in additional visual information to the hemisphere that processes motor commands to the limb (fig. 1b). Evolutionary changes towards increased IRP result in shorter neural pathways and thus improve limb coordination in animals such as primates that regularly use the forelimbs frontally (fig. 1c). Evolutionary change in RGCs in limbless species is likely to influence supervision of body movements differently. When a snake is curled each eye may receive visual information about ipsilateral as well as contralateral body parts (fig. 2). In addition, body movements in eel- and snake-like animals inevitably involve both sides of the body, i.e., the left and right side must move in coordination. This might explain why a high proportion of IRP have been demonstrated in the so-called ancestral condition, e.g. in eel-like cyclostomes, and why phylogenetically diverse animal groups such as snakes and caecilians also display high proportions of IRP (fig. 1a). A strength of the hypothesis is that primates, an animal group characterized by superior eye-hand coordination, possess the most extensive IRP. Cats use visually guided forelimb movements during prey capture to a large extent [Hughes, 1977] and also display high proportions of IRP [Herrera and Mason, 2007]. An evolutionary change towards increased IRP involving RGCs in the nasal retina would give the contrary result with regard to visually guided movements, i.e. increase the distance between coworking visual and motor areas. In vertebrates, uncrossed projections arise exclusively from the temporal retina [Jeffery and Erskine, 2005], which is accommodated by the EF hypothesis. In mice, the number of uncrossed projections is low, and the corresponding RGCs are located in a crescent-shaped area bordering the inferior temporal retina [Dräger and Olsen, 1980]. Due to the anatomy of the snout in rodents [Hughes, 1977], it is likely that the only space in which the contralateral paw might be viewed is the upper quadrant of the visual field, which corresponds to the inferior temporal retina. Visual pathways to the suprachiasmatic nucleus of the hypothalamus and pretectum are unlikely to be involved in EF coordination, which may explain the many divergent functional and evolutionary characteristics of these ‘non-image-forming’ visual pathways [Magnin et al., 1989]. The EF hypothesis postulates no direct association with a nocturnal, euryphotoc, diurnal, or predatory mode of life, factors that, at least in nonmammals, have little or no association with the degree of IRP. The EF hypothesis might explain why IRP develop in *X. lae-*

vis, at metamorphosis simultaneously with their dexterous forelimbs. An ambiguity is that in mammals the visual thalamotelencephalic projections are uncrossed but that is not the case in many nonmammalian vertebrates [Heesy, 2009]. The elaborate neural substrate for binocular vision in owls cannot be explained in light of the EF hypothesis; on the other hand, the association between binocular vision and depth perception in birds has been questioned [Davies and Green, 1994; McFadden, 1994].

A key role of binocular vision in vertebrates may be to provide the brain with accurate information about the position and timing of crucial body parts, such as digits/hands, forelimbs, bill, projectile tongue, or feet. An example may be the binocular field of artiodactyls and perissodactyls that is extended not in width but downwards along a narrow strip in the midsagittal plane to deal with ground near the feet [Pisa, 1939; Hughes, 1977]. Similarly, the unusual vertical orientation of the visual streak in the retina of the two-toed sloth [Andrade-da-Costa et al., 1989; Harman et al., 1990] may be linked to eye-limb coordination, since this species has the habit of hanging upside down.

Dexterity, in its strictest sense, reflects fine motor abilities. Under such a definition rodents are far more dexterous than felids [Whishaw et al., 1998]. However, it is not dexterity, but visually guided forelimb movements, dexterous or not, that would appear to correlate with a high degree of IRP. In accordance with this, cats, with high proportions of IRP [Herrera and Mason, 2007], are known to use visually guided forelimb movements during prey capture [Hughes, 1977], while rodents, animals with few IRP, can use fine-motor movements to manipulate food items without visual feedback [Whishaw et al., 1998]. In addition, rodents use olfaction for food identification while most primates use vision [Whishaw and Tomie, 1989]. Megabats use their long forelimbs (wings with a clawed thumb) in manual tasks such as picking and manipulating fruit [Vandoros and Dumont, 2004], and, since they have a high degree of binocular vision [Pettigrew, 1986b], such tasks may be performed under strictly visual control. Thus primate-like visual specialization in megabats, such as a highly elaborated visual cortex [Rosa et al., 1993] and a similar pattern of decussation in the retina [Pettigrew, 1986b; Pettigrew et al., 2008], conforms to the EF hypothesis. Among investigated marsupials, three arboreal species have the smallest monocular segment in the dLGN (analogous to a high proportion of IRP) [Royce et al., 1976; Harman et al., 1990], while the ground-dwelling and herbivorous wom-

bats have the largest monocular segment in the dLGN [Sanderson et al., 1987], indicating a low proportion of IRP.

Ross and Martin [2007] meant that dexterity and eye-hand coordination are important traits to distinguish primates. Fossil evidence implies that the first true primates emerged approximately 55 million years ago as specialized graspers [Bloch and Boyer, 2002]. Stem primates may have evolved manual grasping abilities and other specializations to feed on flowers, nectar, and leaves in the distal branches of trees [Bloch and Boyer, 2002]. These authors put forward that manual grasping abilities of primates evolved prior to their visual specialization. The hypothesis presented here implies that manual grasping abilities evolved in direct association with primate visual specializations through a common evolutionary mechanism, i.e. that increased IRP were selected for in species that regularly use the forelimbs in the frontal visual field. Improved eye-lower-limb coordination could have added to the selective value in tree-climbing primates.

It is difficult to draw firm conclusions, since acute depth perception, dexterity, binocular vision, and frontal forelimb use are overlapping traits in many animal groups. Much data on ipsilaterality is older and may be based on the law of NGM rather than direct studies of axon routing in the OC [Herrera, 2009, pers. commun.]. Iwaniuk et al. [1999] developed a list of brain sizes and scores for dexterity but found no significant correlation between forelimb dexterity and overall brain size in carnivores. They proposed that alterations in forelimb dexterity can be achieved through development of the connectivity among neural structures rather than through gross changes in the morphology of the central nervous system. A similar list with scores for EF coordination and accurate data on the degree of ipsilaterality in the OC in an assortment of nonmammal and mammal species could be of value to further validate the EF hypothesis. Studies of locomotion, feeding behavior, and EF coordination in the turtles *T. cartilaginosa* and *Chinemys* would also be of interest. In addition, the assumption that fish species such as sturgeon, with relatively immobile pectoral fins, have higher proportions of IRP relative to fish with bilaterally self-governing fin movements, may be tested empirically. Anatomical, neurophysiological, phylogenetic, ontogenetic, and ecological data suggest that evolutionary changes in the proportions of ipsilateral visual connections in the OC may have selective value with respect to EF coordination.

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