

# Tooled for the Task: Vision in the Opossum

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*Comparative analysis of the functional and morphological characteristics of the central nervous system of extant vertebrates can shed light on the evolutionary forces that have shaped different vertebrate brains, which, although sharing similar elements and a basic plan, have had to cope with extremely diverse environments. We chose the *Didelphis opossum* as an experimental model because of its putative resemblance to cretaceous mammals. This marsupial can be quite accurate in performing activities that rely on visual skills. The existence of an oculomotor system that stabilizes the image on the opossum's retina is of primary importance, compensating for movements of the head and providing this species with a framework to stabilize the retinal image while foraging for food. We review evidence for how the nucleus of the optic tract, a key structure involved in this function, is organized to provide an appropriate blending of form and function to bring about this basic behavior.*

*Keywords: opossum, vision, brain, binocularly, optokinetic reflex*

**F**ossil records indicate that the split between mammals and their closest relatives, small therapsid reptiles, occurred about 300 million years ago, at the end of the Triassic period of the Mesozoic era. At first unimpressive and relatively small, mammals coped with extremely diverse environments, eventually giving rise to the huge variety of extant species. Two hundred million years later, in the age of dinosaurs, a succession of adaptative radiations gave rise to the three main living groups of mammals: the monotremes (Prototheria), marsupials (Methateria), and placentals (Eutheria). Marsupials evolved into a great variety of forms, including small opossum-like creatures, flying squirrels, wolf-like carnivores, and bipedal herbivores; they now live both in the New World and in Australia (Preuss and Kaas 1999).

Neuroscientists trying to trace the evolutionary processes that shaped the mammalian brain are faced with a difficult task, since brains, like other soft tissues, do not fossilize. One very limited solution to this problem is to analyze endocranial casts, or endocasts, of the brain created by the hardening of sediment material. However, this method gives researchers access only to fragmentary data on the gross surface anatomy of the brain. Another, more efficient solution is the use of comparative studies. This approach rests on the assumption that brain characteristics shared by extant mammals were present in the brain of their common ancestor. How successful this approach is depends on the thoughtful selection of extant models from the phylogenetic tree.

Comparative studies suggest that the American opossums have retained some of the morphological and physiological characteristics that are believed to have existed in the early mammals. Among these ancestral features, nocturnal habits and frontal eyes, present in the extant opossums, may have played a large part in the success of the mammalian radiation (Pettigrew 1986). Furthermore, the opossum's brain has features that resemble those found in brain endocasts of Cretaceous mammals (Jerison 1990). This ancestral mammalian condition has also been inferred by cladistic analysis (Kirsch and Johnson 1983).

Among opossums, the visual system of *Didelphis aurita* has been by far the most studied. For many years, a group of neuroscientists at the Federal University of Rio de Janeiro has explored the anatomy and electrophysiology of the cortical and subcortical structures involved in this opossum's visual processing. There is considerable evidence that the visual system of the opossum is well tooled for the task. Vision-

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related areas occupy a large part of this species' brain, about half of the total area of the neocortex (see Martinich et al. 2000). Also, the functional properties of neurons in the primary visual cortex are very similar to those of cats and primates (Rocha-Miranda et al. 1976, Oliveira et al. 2002). The superior colliculus, which is thought to be involved in animals' orientation toward novel visual stimuli, is a large structure in this opossum, with about the same dimensions as the corresponding structure in carnivores and with a precise topographic representation of the visual field in its superficial layers (Volchan et al. 1982). Type  $\beta$  retinal ganglion cells, which are believed to carry information for high-acuity vision and which have previously been described only in primates and carnivores, are also present in the opossum retina (Moraes et al. 2000). Thus equipped, opossums of the genus *Didelphis* can be very accurate in catching a small snake by its neck (Oliveira and Santori 1999) and preying on small insects (Santori et al. 1995, Freitas et al. 1997). Marsupials of this genus can also climb trees and walk over fine branches (Cunha and Vieira 2002). All of these activities rely on vision. As Milner and Goodale (1995) point out, vision first evolved in animals not to enable them to see the world, but to guide their movements around the world.

Santori and colleagues (1995) and Freitas and colleagues (1997) observed that, in the wild, opossums search for food in the litter mass and eat a wide spectrum of invertebrates, mainly insects. In the opossum, visual acuity for light and dark sinusoidal ratings has an average value of 1.25 cycles per degree (Silveira et al. 1982); as a rule, the animals are myopic, with an average eye refractive rate of  $-2.27$  diopters (Picanço-Diniz et al. 1983). Although its acuity is quite poor when compared with that of primates, the opossum can easily discriminate an insect comprising one degree of visual angle (i.e., 1 centimeter [cm] in length, or the size of a small cockroach) at a distance of 57 cm. Using its near vision, at a distance of 10 cm, the opossum can discriminate an insect measuring only 0.2 cm.

Researchers have also shown that the opossum, like other mammals, has a well-developed system to stabilize the image in the retina (Nasi et al. 1997). Our studies have focused on the nucleus of the optic tract, or NOT (Volchan et al. 1989, 1992, Pereira et al. 1994, 2000, Vargas et al. 1996, 1997, 1998, 2001), which detects the horizontal wavering of the retinal image and generates, through several steps downstream, a compensatory eye movement called the horizontal optokinetic reflex. In this article we review the functional and anatomical data for the circuitry underlying the horizontal optokinetic reflex and propose that it is well suited to provide this species with a framework to stabilize the retinal image while the opossum forages for food.

### **The optokinetic reflex and the pretectal nucleus of the optic tract**

Optomotor reflexes are mechanisms by which animals hold their eyes in a stable orientation relative to their visual surroundings, regardless of changes in head and body position.

Optomotor responses have been studied in different animals (see Tauber and Atkin 1968) and show remarkable similarity across species.

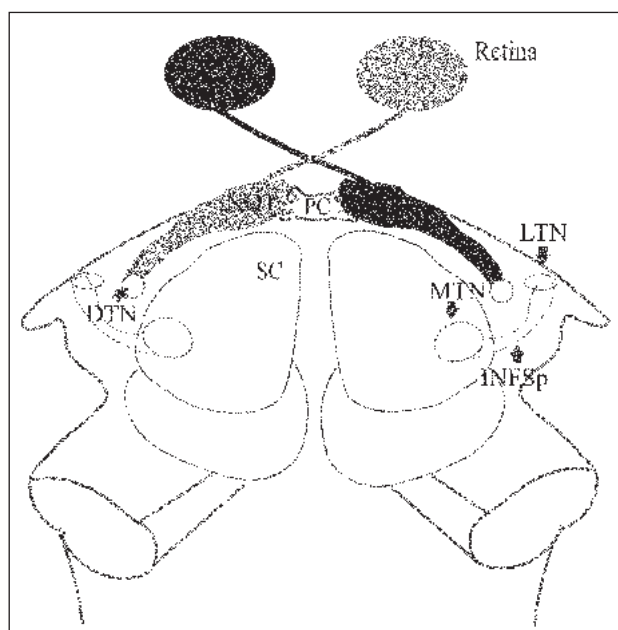
When an animal is walking, any movement of the head produces a retinal slip of the whole visual background. In vertebrates, angular movement of the head also stimulates the semicircular canals of the labyrinth in the inner ear. Compensatory eye movements quickly restore a steady image so that the effects of stimulus "jitter" are minimized. This compensation is brought about by the vestibulo-ocular reflex and the optokinetic reflex, which together cover the whole range of head displacements. The compensatory eye movement elicited by both reflexes occurs with a stereotypic pattern consisting of an initial period when both eyes follow the moving stimulus very closely, at least for a certain velocity range, and a second, fast-resetting phase. The eye movements that occur during the initial tracking phase resemble those that occur during the voluntary pursuit of small stimuli across the visual field. The resetting phase is a ballistic movement similar to a saccade. Saccades are the most frequent eye movements; they occur when the eyes fix on one point after another in the visual field.

Five pairs of interconnected nuclei located in the brain stem (Giolli et al. 1984) are known to trigger the optokinetic reflexes in mammals: the NOT in the pretectum, the dorsal terminal nucleus, the medial terminal nucleus, the lateral terminal nucleus, and the interstitial nucleus of the superior fasciculus (figure 1; see Simpson and colleagues [1988] for a review of these nuclei and their functions). The pretectal NOT is the main afferent relay of the horizontal optokinetic reflex (Collewyn 1975a, Cazin et al. 1980a, Kato et al. 1986, Schiff et al. 1988). The NOT is formed by a small group of neurons scattered within the brachium of the superior colliculus (figure 1), receiving direct sensory innervation from the retina.

The directional selectivity of NOT neurons can be revealed by testing the visual stimulus in different directions. The head is restrained (thus excluding the vestibular contribution) and a checkerboard pattern mimicking the background is displaced in front of the animal. Direction-selective neurons with a bias toward ipsoversive movement of the visual background have been found in several mammals, including the rabbit (Collewyn 1975b), rat (Cazin et al. 1980b), cat (Hoffmann and Schoppmann 1981), monkey (Hoffmann et al. 1988), ferret (Klauer et al. 1990), and wallaby (Ibbotson et al. 1994); they are also present in the opossum's NOT (Volchan et al. 1989, 1996, Pereira et al. 1994, 2000). A rightward movement of the visual stimulus causes simultaneous excitation of the right NOT and inhibition of the left NOT, with the activity reversing when the stimulus moves horizontally to the left (figure 2).

Recordings of electrical activity in the opossum NOT showed that half of the neurons responded to stimulation of either eye (Pereira et al. 1994), even though only the contralateral retina projects to the NOT (Vargas et al. 1998). In other words, although both eyes are individually capable of modulating the activity of many NOT neurons, each eye

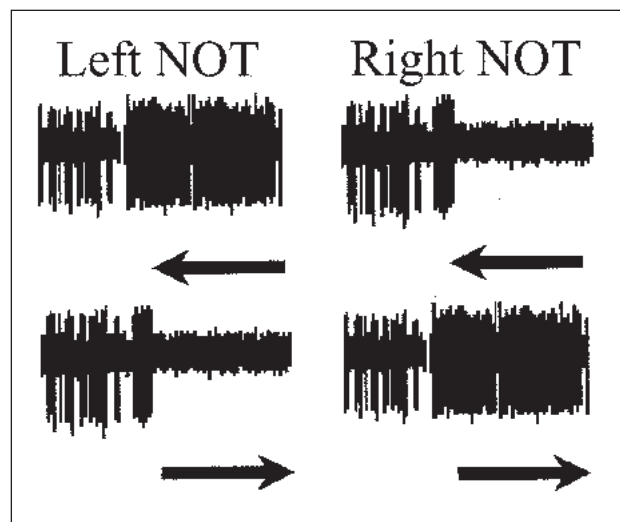
communicates directly with the nucleus only at the opposite side of the brain (figure 1). Projections from the primary visual cortex, demonstrated in rats (Schmidt et al. 1993), cats (Schoppmann 1981), and monkeys (Hoffmann et al. 1991), represent a possible source for the binocularity of NOT neurons. However, Pereira and colleagues (2000) systematically screened the projections from the visual cortex to the pretectum in the opossum and found no evidence for a projection to the NOT. What, then, is the source for the binocularity of the NOT in the opossum?



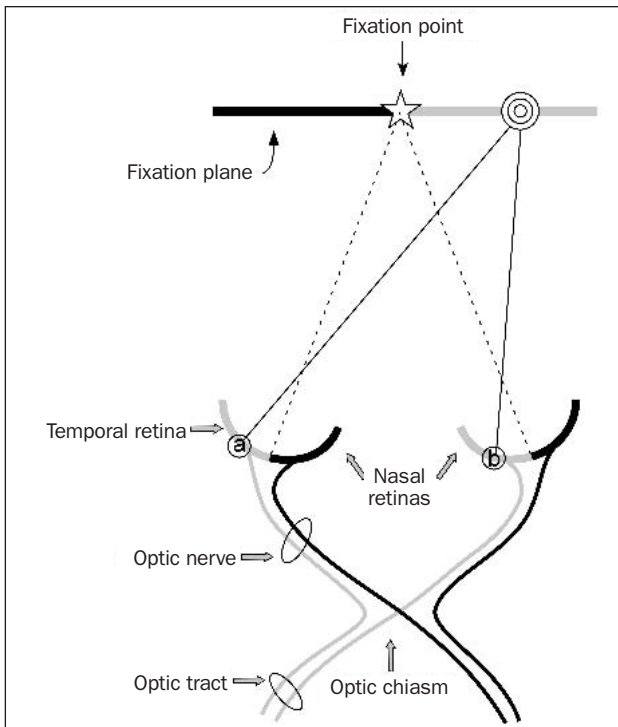
**Figure 1.** Subcortical nuclei involved in the stabilization of the retinal image. Five brain stem nuclei (shown in dorsal view) are known to participate in optokinetic reflexes: the nucleus of the optic tract (NOT), the dorsal terminal nucleus (DTN), the medial terminal nucleus (MTN), the lateral terminal nucleus (LTN), and the interstitial nucleus of the superior fasciculus (INFSp). The NOT consists of a group of scattered cells located in the brachium of the superior colliculus (SC). Each NOT receives a strong crossed projection directly from the retina. We propose that binocularity in this nucleus is achieved by a midline cross-talk through the posterior commissure (PC). The visual stimulus is captured and processed by specialized retinal cells that send this information through nerve fibers to the NOT on the opposite side (from the left retina to the right NOT and from the right retina to the left NOT). Hardly any direct retinal nerve fibers reach the NOT of the same side. Each NOT in turn processes the retinal signals and communicates with the nucleus on the opposite side. This configuration renders many neurons of the NOT “binocular,” because they receive direct input from one retina and indirect input from the other retina via the other NOT.

### Binocular vision and the nucleus of the optic tract

Strictly speaking, every animal with two eyes has binocular vision, since information from both eyes will eventually be integrated somewhere in the brain. The term, however, is generally employed for animals that display a large area of binocular overlap in the visual field, resulting from their having frontal eyes. Among the special advantages of binocular vision are increased signal-to-noise ratio, camouflage breaking, and the absence of a need to move in order to generate motion parallax, which is of significant value for predators. Sometimes the term *binocular vision* is loosely interchanged with *stereoscopic vision*, although the latter is a more generic term meaning the visual perception of the three-dimensional structure of the world. Stereoscopic vision, however, can be obtained even with only one eye, given the presence of clues such as perspective and motion parallax (the fact that the angular velocity of an object moving at constant linear velocity is inversely proportional to its distance from the eye). For binocular stereopsis, however, depth in visual stimuli is judged with the help of two exclusive clues: vergence position of the eyes and binocular disparity. Vergence is the coordinate movement made by the eyes when closing in on stimuli located somewhere in space. Depending on the position of the stimulus (i.e., whether it is close or not), the eyes can converge or diverge at different degrees. Binocular disparity, on the other hand, stems



**Figure 2.** Directionally selective activity of neurons in the nucleus of the optic tract (NOT). When a visual stimulus that simulates the complexity of the background in a natural environment is moved to the left in front of the animal, cell activity is increased in the left NOT and is simultaneously diminished in the right NOT. The black traces represent the electrical activity (spikes) of a typical NOT neuron. When the stimulus moves to the right (bottom row), cell activity is inversely modulated in each NOT. Horizontal arrows below the traces indicate the duration and direction of the stimulus movement.



**Figure 3. Binocular representation of the visual field.** The part of the visual field on which the animal fixates its gaze is known as the fixation point (indicated with a star). It divides the visual field into the left (black) and right (gray) hemifields. The projection of the fixation point onto the retinas (dashed lines) also divides each retina into two sections, the temporal retina and the nasal retina. In this example, an object located in the right hemifield (concentric circles) has its image projected onto both the left temporal and the right nasal homologous retinal sites (labeled a and b, respectively). The nerve fibers arising from the nasal retina cross to the opposite side of the brain at the chiasm, and those arising from the temporal retina remain on the same side. Visual information is relayed from the left visual field to the right brain and from the right visual field to the left brain. Brain centers on each side can process information from an object seen by both eyes.

from the fact that the world is seen through sensors (the eyes) located at different positions on the head, resulting in objects' images being projected on slightly different sites in each retina. Stereopsis based on binocular vision seems to have appeared relatively early during mammalian evolution (Pettigrew 1986).

Apart from many hemispherical specializations, the brain can be schematically viewed as a symmetrical structure divided through the midsagittal plane into two halves. The visual field (as well as the sensory body surface) is decomposed into two hemifields by the brain, each represented in the opposite hemisphere. The visual-field split occurs through a partial segregation of retinal axons before they reach their brain

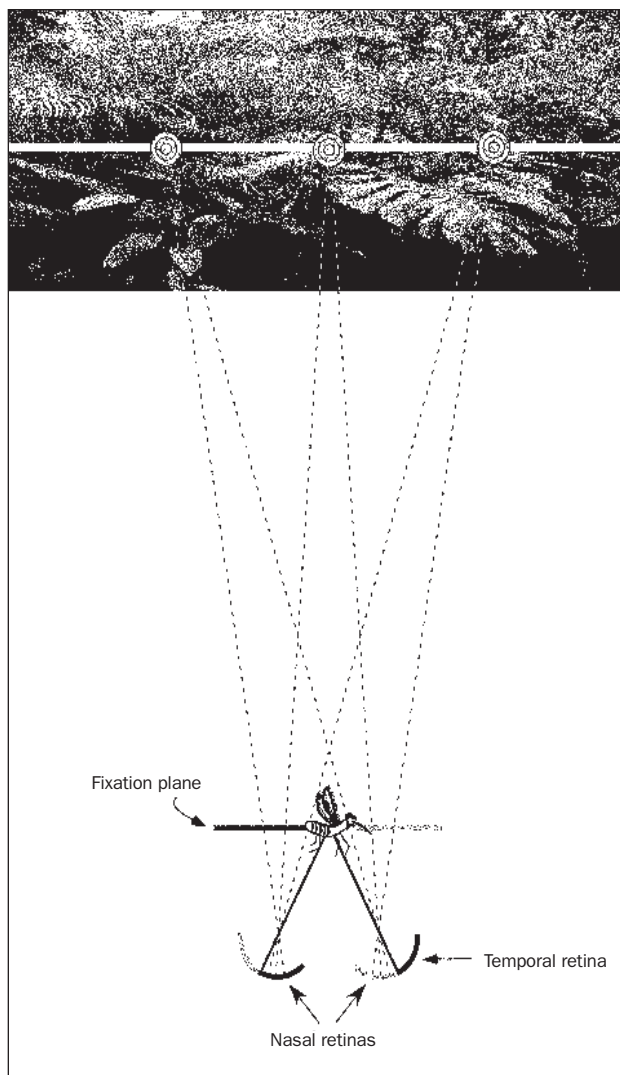
targets. The retina is divided vertically into two hemiretinas, designated as nasal and temporal (figure 3). All nerve fibers arising from the nasal retina cross to the opposite side of the brain at the optic chiasm. Uncrossed projections to the brain originate mostly from the temporal retina (in nonprimate mammals, such as the opossum [Hokoç et al. 1992], the temporal retina is also the source of some crossed projections). This way, each hemifield is projected into the opposite hemisphere with information derived from both eyes. The matching of homologous retinal sites, which lie on the nasal retina of one eye and the temporal retina of the other, gives rise to binocularity (figure 3).

As noted earlier, we have observed neurons in the opossum's NOT that can be driven by either eye. In this sense, these neurons are binocular. However, quite unusually, these binocular neurons are activated predominantly by stimulation of the nasal retina in both eyes (Volchan et al. 1992). The nasal retina from each eye conveys information to neurons on the opposite side of the brain (figure 3). As shown by Vargas and colleagues (1998), each NOT receives a strong crossed projection directly from the retina (the left NOT from the right retina and the right NOT from the left retina). How, then, can an individual NOT neuron receive information from both nasal retinas if they are being projected to diametrically opposed sides? After carefully examining and comparing the response properties of binocular neurons in the opossum's right and left NOT, we advanced the idea that binocularity could be achieved by a midline cross-talk between the nuclei through the posterior commissure (figure 1; Volchan et al. 1990, 1992). Ibbotson and colleagues (2002) recently proposed a similar route for binocularity in the wallaby, an Australian marsupial. In the opossum (*D. aurita*), Vargas and colleagues (1997) have shown evidence for an anatomical connection between the NOTs across the midline, and Pereira and colleagues (2000) have demonstrated the critical importance of this connection for binocularity.

### Behavioral significance of binocularity in the nucleus of the optic tract

The binocularity found in NOT neurons may fulfill another function, one that is not directly related to stereoscopy. Stimuli located far away from the fixation plane are likely to stimulate both nasal retinas (figure 4). This is the optimal stimulus location to activate binocular neurons at the NOT. The main function of the NOT, as we have seen, is to capture the movement of the whole image of the distant visual background in order to maintain image stability. The pattern of termination of retinal projections in the NOT, along with the midline fusion of the visual field afforded by the connection between the two nuclei, provides the substrate for optimal performance in a system designed to stabilize the retinal image. The convergence of both eyes' simultaneous activation onto individual NOT cells augments the signal-to-noise ratio of neural information used for capturing the retinal slip of the distant background. The stabilization achieved with this process optimizes the extraction of visual features from near





**Figure 4.** Positioning of an opossum's eyes when fixating a proximal prey. The prey is represented by the contour of an insect. The projection of the fixation point onto the retinas divides each retina into two regions, nasal and temporal. The scene located behind the fixation plane (represented by a picture of woods) and between the prolongation of the fixation axes projects onto the nasal retinas of both eyes. Because of a connection across the midline between the nuclei of the optic tract, the movement of the distant background is processed binocularly by the nucleus on each side.

objects by other brain regions when, for instance, the opossum is foraging for food (figure 4).

Is this property unique to opossums, or could it apply to other mammals as well? Pereira and colleagues (2000) proposed that the oculomotor circuits subserving the optokinetic and vestibular-ocular reflexes are phylogenetically old and were probably present in early mammals. Thus, the commissural circuitry we have proposed for the opossum may also play a significant role in the control of the horizontal optokinetic reflex of other mammals. A strong reciprocal connection

between the two NOTs has been anatomically verified in rats (Terasawa et al. 1979), cats (Schmidt et al. 1995), and monkeys (Mustari et al. 1994). On the other hand, the predominance of the visual cortex as the main source of input to the mammalian NOT, which appeared more recently in phylogeny, may have added new functions mediated by circuits that are lacking in the opossum. With the emergence of retinal specializations, such as the central fovea, which subserves high-acuity vision, may have come the appearance of new ocular movements, such as the smooth pursuit and certain types of saccades, which joined the preexistent ocular motor reflexes. The visual cortex, already well developed in primates, provided the circuits responsible for the new ocular movements with its superior processing capabilities. Indeed, it has been proposed that the primates' NOT is also involved in the control of smooth pursuit, in which the eyes track the movement of small stimuli across the visual field (Ilg and Hoffmann 1991). Thus, the preexistent oculomotor circuits may have been used as a platform for the implementation of new functions compatible with the appearance of retinal specializations.

In conclusion, the circuitry underlying a visuomotor reflex in the opossum provides this marsupial with a framework to stabilize the retinal image while foraging for food. This is one of the features that may have contributed to the evolutionary success and the wide distribution of this genus in the Americas.

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