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The novelty of the lamprey ear: Small sense organ, full motor control

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Abstract

The systematic position of the lamprey, as one of only two extant jawless vertebrate, makes its ear of particular interest from evolutionary, developmental and physiological standpoints. Studying the ear of the lamprey could give us insight into the morphology of the archetype/prototype ear of lamprey/jawed vertebrates' ancestor. Moreover, the seemingly simple neural circuits that relay information between the ear and brain to control gaze and posture could help us better understand the complex circuitry underlying vestibuloocular and vestibulospinal reflexes in a more derived vertebrates. Older morphological data on the lamprey ear, suggested a rudimentary ear lacking some basic elements of the ear present in other jawed vertebrates. However, this observation did little to explain the agility of the locomotor behavior in lampreys. More recent findings suggested that the lamprey ear is not rudimentary, and although different, has an anatomical substrate, a horizontal canal, for full range of movement detection around the yaw plane that was once believed to be a novelty in jawed vertebrates.

Review

The vestibular system in vertebrates is the body's motion sensor that allows an animal to detect self-motion in a stationary environment [1-2]. Through elaborate connections with motor system, the vestibular sense organs can finely tune body and eye muscle activity to allow animals to gracefully navigate their environment and keep their eyes on targets while chasing a prey or fleeing a predator [3]. Equipped with three semicircular canals deployed in the three orthogonal coordinates, the canals serve as accelerometers for angular movements in all planes, and two otolith sensory organs; the utricle and saccules, also orthogonally deployed, serve as accelerometers for linear movements and tilt in the vertical and horizontal planes, respectively. Inputs from all five sense organs converge to create central estimate of the sense of position and movement in a three-dimensional space, and a three-dimensional motor response ensues. It is note worthy that the vestibular system works silently but diligently beyond conscious level to control many aspects of the animal behaviors.

Extant jawless vertebrate's cyclostomes (hagfish and lamprey) are aquatic vertebrate which acrobatically swim and burrow [4]. Their locomotor behaviors entail a requirement for a

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full complement of peripheral sensory organs movement detectors in their ears to meet with their central demand to keep close tabs on their muscles for proper postural control and gaze fixation on their targets while on the move, like those present in their jawed vertebrate aquatic counterparts. Although hagfish has no functional eye nor extraocular muscles like other vertebrates, both lamprey and hagfish move predominantly by undulatory swim movements in a three-dimensional space, with ensuing rhythmic sinusoidal head movements, the need for an anatomical substrate, a canal or duct deployed in horizontal plane in particular, should intuitively be believed an existential feature for proper motor control of swim behavior through vestibulospinal reflexes [5-7].

In contrast to intuitive expectations on how the morphology of the ear of cyclostomes in general and lamprey in particular should look like, the ear in cyclostomes was described as primitive and lacks some core morphological components deemed necessary for proper ear functioning. The early description of the ear in cyclostomes by Retzius et al. [8] followed later by deBurlet and Versteegh [9] and later Lowenstein et al. [10] described the ear of the hagfish as exhibiting one vertical semicircular canal and that of the lamprey as exhibiting two vertical canals (anterior and posterior). In both species, the horizontal canals were believed to be missing. These morphological observations posed a tremendous challenge in our understanding of how the cyclostome ear operates. How the lamprey senses movement in the yaw plane and how the hagfish senses movement in the roll and yaw planes to bring about appropriate reflex responses remained unanswered questions.

It is unlikely that cyclostomes have some unique locomotor behavior that obviates the need to sense movements in the planes where there are no canals positioned. Behavioral studies suggest that the lamprey swims acrobatically in three-dimensional space and robustly responds with a three-dimensional reflex utilizing both vestibuloocular and vestibulospinal systems, even to movements in planes that lack canals [11-15]. What are the stimuli that trigger those reflex responses and where are the peripheral mechanisms that process those movements? The lamprey has four otolith sensory organs deployed in vertical and horizontal planes. These organs can sense the tangential (linear) components of turns in the three planes but not the angular components of the turn, and cannot account for the robust, agile responses to a turn in different planes. In fact Lowenstein et al. [10], proposed that the trifid crista of the vertical canal has a vertical arm that may be capable of sensing rotational acceleration force in horizontal plane. However, without a toroidal-shaped duct in horizontal plane, there will be no endolymph inertial vector in this plane [16].

The recent study by Maklad et al. [17] that re-evaluated the morphology of the ear in the lamprey made several interesting observations. First, the anterior and posterior vertical canals in lampreys are orthogonal to one another and can equally and accurately resolve movements in pitch and roll planes. Second, and more importantly, a horizontal canal system exists in lampreys and provides a peripheral sense organ to respond to movement in the yaw plane. Interestingly, and unlike all jawed vertebrates with one horizontal canal, the lamprey has two horizontal canals in each labyrinth. These structures are located on anterior and posterior aspects of the ear with mirror-image symmetry between the two horizontal canals (**Figure 1**). The implication of that mirror image arrangement of the horizontal canals is that with any given lateral turn, the input from one canal will be activated, whereas, the input from the other canal will be deactivated, i.e, coupled activation/deactivation inputs from one ear. Conversely, a similar pattern of activation/deactivation occurs for the contralateral ear [4]. Therefore, the right anterior and left posterior horizontal canals are a similarly tuned physiological pair that is activated in response to leftward head turns. In contrast, left anterior and right posterior horizontal canals are activated and respond to right ward head turns. The later hypothesis, driven by our recent morphological finding [17], is supported by physiological data. Lowenstein [4] reported that electrophysiological recordings revealed some neurons in VIII respond with activation to the ipsilateral turns while others respond with deactivation, supporting the presence of two oppositely tuned sense organ (presumably canals) responsive to lateral turn in one ear.

How is the redundancy of two horizontal canals handled centrally to control the vestibulospinal and vestibuloocular reflex? Jawed vertebrates have one horizontal canal on each side. When one is activated the other is deactivated. Consequently, each side of the brain receives a uniform input, albeit antagonistic to the contralateral side. However, in the lamprey with two canals, each side of the brain would receive mixed (activation/deactivation) input. The lamprey evolved a simple solution to the problem of mixed contradictory inputs. The anterior branch of the VIIIth nerve, supplying the anterior horizontal canal afferents project to the anterior area of octavomotorius nucleus [18]. This nucleus, in turn, projects ipsilaterally to the reticulus nucleus that represents the main motor input to the spinal motor neurons via reticulospinal tract. In contrast, the posterior division of the VIIIth nerve, supplying the posterior horizontal canal afferents project to the posterior area of the octavomotorius nucleus that projects to the contralateral reticular nucleus to control the activity of the contralateral spinal motor neurons [18]. With this connectivity pattern, the mixed (activation/deactivation) input from the two canals segregate centrally to discretely activate or antagonize groups of muscles, i.e, right versus left side of the body in case of vestibulospinal reflex in yaw plane [17].

The connectivity pattern between the horizontal canals and ocular motor neurons is different from those controlling spinal motor neurons. First, afferent information from the canals to the octavomotorius projects directly to ocular motor neurons with no involvement of other brainstem nuclei as reticular nuclei. Second, information from the canals splits roughly equally between direct and crossed pathways in a rather vectorially uniform fashion [14]. For example, when the head turns right, the activated physiological pair (the right posterior and left anterior horizontal canals) projects equally through direct and crossed pathways into both right rostral rectus and left caudal rectus, causing conjugate forward movement of right rostral rectus and backward movement of the left caudal rectus to affect the appropriate counter roll movement for rightward turn in a lateral eyed animal [7,9,11,14]. In contrast, the disfacilitatory inputs from the deactivated pair (right anterior and left posterior horizontal canals) project through equally direct and crossed pathways to turn off the activities in the right caudal rectus and left rostral rectus [17]. A summary of the connectivity pattern and neural circuits driving the vestibulospinal and vestibuloocular reflexes is outlined in **figure 2**.

Conclusion

In summary, the lamprey is endowed with an ear that is like no other ear in any living or extinct vertebrate ear studied to date. Although small and unique, the lamprey ear is far from primitive or rudimentary. It is astonishing that a mere simple cyst of cartilage, no more than 5 mm in it is longest dimension and containing a maze of chambers and shallow arcs of ducts, is so efficient at extracting information regarding position and movement. It is likely that this unique structure has equipped the lamprey to become an agile swimmer and fierce predator.

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Figures

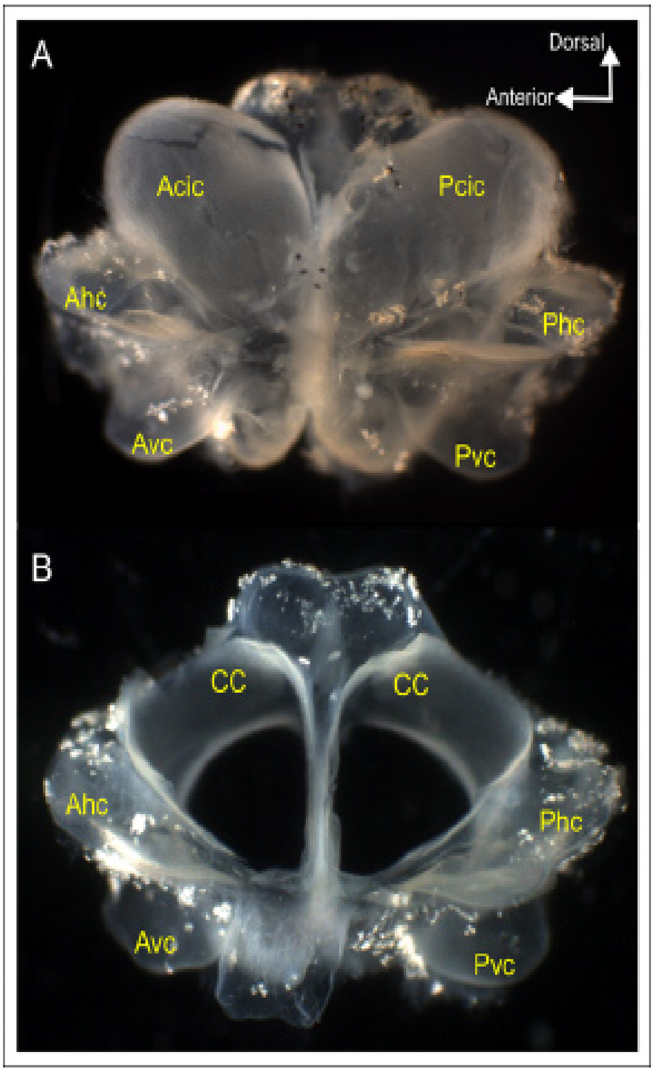

Figure 1: Shape of the ear in the lamprey A. A medial view of the whole ear in the lamprey after removing the cartilaginous capsule, showing the anterior and posterior ciliated chambers (Acic, Pcic; respectively) described by Retzius [8] and crus communis of the horizontal and vertical canals (CC) and anterior and posterior horizontal canals (Ahc, Phc; respectively, and anterior and posterior vertical canals (Avc, Pvc; respectively). B. A medial view of the ear after the two ciliated chambers removed showing only the anterior and posterior horizontal canals (AVC. PVC) and the anterior and posterior vertical canals (AVC, PVC), described in Maklad et al, 2014. Arrows indicate orientation for A & B.

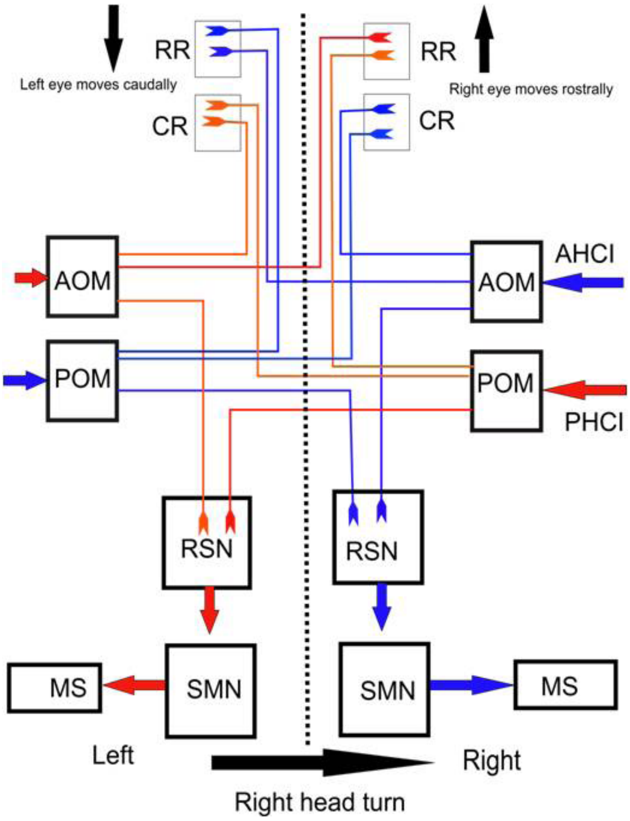

Figure 2: Neural pathways between the anterior and posterior horizontal canals and their effector body and eye muscle in the vestibulospinal and vestibuloocular reflex arcs and their activation/deactivation paradigm during right head turn. AHCI: anterior horizontal canal input; AOM: anterior octavomotorius; CR: caudal rectus; MS: muscles; PHCI: posterior horizontal canal input; POM: posterior octavomotorius; RR: rostral rectus; RSN: reticulospinal neurons; SMN: spinal motor neurons; activated neurons are coded in red, and deactivated neurons are coded in blue. This summary of pathways is after findings of Pflieger et al. [11, 14, 18-19] and Maklad et al, [17].

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