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THE STATOCYST-OCULOMOTOR REFLEX OF CEPHALOPODS AND THE VESTIBULO-OCULOMOTOR REFLEX OF VERTEBRATES : A TABULAR COMPARISON

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HAIR CELL
STATOCYST
VESTIBULAR
OCULOMOTOR
EVOLUTION
CEPHALOPODA

ABSTRACT. – In cephalopods, the control system for compensatory eye movements, the statocyst oculomotor reflex, attains the highest level of complexity among invertebrates. In a large table, all its major components, from the receptor input to the effector output, are compared step-by-step with the equivalent components of the vertebrate vestibulo-oculomotor reflex. This direct comparison highlights the many parallels in structure and function of the two systems, and underlines the importance of the cephalopod system as an alternative invertebrate model for comparative vertebrate vestibular research.



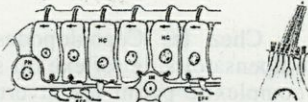
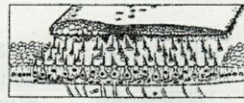
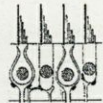


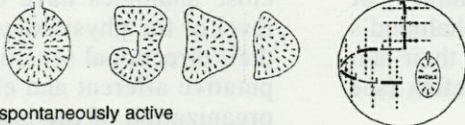

CELLULE CILIÉE
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OCULOMOTEUR
ÉVOLUTION
CEPHALOPODA

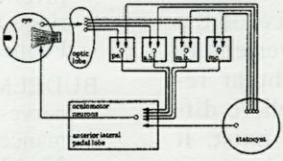
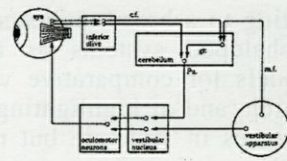
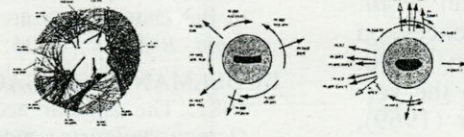
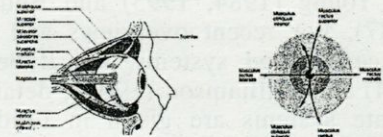
RÉSUMÉ. – Chez les Céphalopodes, le système contrôlant les mouvements oculaires compensatoires, le réflexe dit statocyste-oculomoteur, atteint son plus haut niveau de complexité parmi les invertébrés. Tous les composants majeurs, allant du récepteur à l'effecteur, sont comparés étape par étape avec les composants correspondants du réflexe vestibulo-oculomoteur des vertébrés dans un tableau. Cette comparaison directe démontre les nombreuses similitudes de structure et de fonction dans les deux systèmes, et souligne l'intérêt du système Céphalopode en tant que modèle invertébré pour les recherches comparatives consacrées au système vestibulaire des vertébrés.

Cephalopods are one of the most highly evolved invertebrates. With only a few exceptions (e.g., *Nautilus*), they are voracious, visually-oriented and very mobile predators. Such a lifestyle necessarily requires sophisticated sense organs and an elaborate nervous system. Not surprisingly, then, during the course of evolution cephalopods – though confined to their molluscan design – developed sensory and nervous systems that are the most sophisticated of all the invertebrates; some rival the equivalent vertebrate systems in complexity and are well-known examples of convergent evolution, such as the cephalopod's lateral line analogue system, their eyes, their statocysts, and their statocyst-oculomotor reflex (see Packard 1972; Budelmann 1994).

Over the past 25 years, the structure and function of the cephalopod statocysts and statocyst-oculomotor reflex have been intensively studied at all levels and have often been compared with the equivalent vertebrate systems, the vestibular apparatus and the vestibulo-oculomotor reflex.

Areas of comparison include : the linear (gravity) and angular acceleration receptor systems; the receptor hair cells; the brain areas and afferent and efferent brain pathways involved in oculomotor control; and the eye muscle system and compensatory eye movements (compare Budelmann 1990, 1994; Williamson 1995). Although basic differences primarily in gross morphology exist between the cephalopod and vertebrate systems due to the fact that they have evolved along different evolutionary lines, a striking number of close analogies have been described, e.g., at the level of the physiology of the hair cells (including their directional sensitivity and ionic currents), the putative afferent and efferent transmitters, and the organization of the brain pathways. The main differences, despite in gross morphology, relate to : the structure of the receptor hair cells with regard to the number and arrangement of kinocilia and the presence (vertebrates) and absence (cephalopods) of stereocilia; the presence (cephalopods) and absence (vertebrates) of somata of first-order

	CEPHALOPODS	VERTEBRATES
GROSS MORPHOLOGY OF RECEPTOR ORGANS		
LINEAR ACCELERATION RECEPTOR SYSTEM	<p><i>Nautilus</i>: lower half of statocyst, no macula Octopods: 1 macula/statolith system, vertically oriented Decapods: 3 macula/statolith(statoconia) systems orthogonally arranged</p>	<p>2-3 macula/otolith(=statolith) and macula/otoconia(=statoconia) systems orthogonally arranged (utricle, saccule, lagena)</p>
ANGULAR ACCELERATION RECEPTOR SYSTEMS	<p><i>Nautilus</i>: no crista/cupula system, but statocyst sensitive to angular accelerations Octopods: 9 crista/cupula segments 3-dimensionally arranged Decapods: 4 crista/cupula segments 3-dimensionally arranged</p>	<p>3 semicircular canals 3-dimensionally arranged ampullae containing crista/cupula systems</p>
RECEPTOR HAIR CELLS	<p><i>Nautilus</i>: only primary sensory hair cells cristae: primary and secondary sensory hair cells maculae: only secondary sensory hair cells</p> <p>up to 200 kinocilia (9x2+2), no stereocilia/villi mechanical couplings: tip tight junctions, shaft connectors, basal connectors</p>	<p>only secondary sensory hair cells</p> <p>1 kinocilium (9x2+2), 50-60 stereocilia/villi mechanical couplings: tip links, shaft connectors, basal connectors</p>
LINEAR ACCELERATION RECEPTOR SYSTEM	 <p>1 hair cell type: 5,100 (<i>Octopus</i>) - 8,700 (decapods) hair cells 2 types of peripheral first-order afferent neurons: 2,000 (<i>Octopus</i>) - 5,000 (decapods)</p>	  <p>Type-I (50%) and Type-II (50%) hair cells fishes Type-I-like (?) and Type-II hair cells amphibians only Type-II hair cells utricle: 9,200 hair cells saccule: 7,500 hair cells</p>
ANGULAR ACCELERATION RECEPTOR SYSTEMS	 <p>3 hair cell types: primary, large, and small secondary sensory cells 2,100 (<i>Octopus</i>) - 2,600 (decapods) 2 types of peripheral first-order afferent neurons: 1,000 (<i>Octopus</i>) - 650 (decapods)</p>	 <p>Type-I (60%) and Type-II (40%) hair cells fishes Type-I-like (?) and Type-II hair cells amphibians only Type-II hair cells 4,500 (rabbit) - 7,600 (man) hair cells</p>
SENSITIVITY	<p>coding of angular velocity Octopods: two 10x differently sensitive systems hair cells with different sensitivity 0.5 mV/degree cilium displacement < 0.12 μm peak/peak cilia/cupula displacement gain: 3.6 imp.s⁻¹/deg sensitive to linear acceleration</p>	<p>coding of angular velocity</p> <p>hair cells with different sensitivity 3.0 mV/degree cilium displacement 0.01 μm peak/peak cilium displacement gain: 0.11-1.6 imp.s⁻¹/deg sensitive to linear acceleration</p>
HAIR CELL POLARIZATION AND ARRANGEMENT	<p>morphologically and physiologically polarized</p>  <p>spontaneously active sine-like stimulus/response correlation cosine-like directional sensitivity</p>	<p>morphologically and physiologically polarized</p>  <p>spontaneously active sine-like stimulus/response correlation cosine-like directional sensitivity</p>
HAIR CELL IONIC CURRENTS	<p>outward delayed rectifier (I_K) potassium current outward A-type potassium current no outward calcium activated potassium channel inward sodium current inward L-type calcium current</p>	<p>outward delayed rectifier (I_K) potassium current outward A-type potassium current outward calcium activated potassium channel inward sodium current inward L-type calcium current</p>

	CEPHALOPODS	VERTEBRATES
STATOLITH / STATOCONIA	Octopods: 1 statolith Decapods: 1 statolith + 2 statoconial layers calcium carbonate, statoliths with daily growth rings	otolith (= statolith) otoconial (= statoconial) layers calcium carbonate otolith (= statolith) with daily growth rings (fishes)
CUPULA	freely protruding into cyst cavity (swinging door) irregular shape and size (2 sub-systems) fibrillar (material ?)	diaphragm within ampullae; fibrillar (muco-polysaccharides, mucoproteins)
AFFERENT TRANSMITTERS and/or CO-TRANSMITTERS or MODULATORS	L-glutamate (non-NMDA) (excitatory)	L-glutamate (kainate-AMPA; few NMDA) (GABA, cAMP, adenosine ?)
EFFERENT TRANSMITTERS and/or CO-TRANSMITTERS MODULATORS	mostly inhibitory, few excitatory: acetylcholine (mus./nic.) (inhibitory) dopamine (excitatory and inhibitory) noradrenaline (α/β) (excitatory and inhibitory) GABA (GABA-A) (inhibitory) ATP (excitatory) NO (mostly inhibit, few excit) substance P - no effect ? CGRP (inhibitory)	mostly inhibitory, few excitatory: acetylcholine (inhibitory) noradrenaline GABA ATP (excitatory) NO substance P CGRP (calcitonin gene-related peptide) L-glutamate or aspartate (few reports) m-ENK (met-enkephalin), proenkephalin
AFFERENT AND EFFERENT CONNECTIONS BETWEEN HAIR CELLS AND BRAIN	non-myelinated fibers diameter between $<1 \mu\text{m}$ and $>12 \mu\text{m}$ 15%-25% afferent, 75%-85% efferent	myelinated fibers diameter between $<1 \mu\text{m}$ and $>10 \mu\text{m}$ 90% afferent, 10% efferent
MACULAE CRISTAE	9,200 (<i>Octopus</i>) - 25,300 (<i>Sepia</i>) fibers 8,700 (<i>Octopus</i>) - 9,500 (<i>Sepia</i>) fibers	3,000 - 5,400 fibers (utricle + saccule) 4,950 (pigeon) - 11,200 (monkey) fibers
BRAIN AREAS AND PATHWAYS INVOLVED IN INFORMATION PROCESSING	direct and indirect pathways  cerebellum analogue: peduncle, ant./med. basal, and magnocellular lobes	direct and indirect pathways  cerebellum
OCULOMOTOR NEURONS: LOCATION	anterior lateral pedal lobe	III. Nerve: ipsi/contralateral Oculomotor nucleus IV. Nerve: contralateral Trochlear nucleus VI. Nerve: ipsilateral Abducens nucleus
OCULOMOTOR NEURONS: TRANSMITTERS	acetylcholine (N-type; also M-type ?)	acetylcholine (N-type)
EYE MUSCLES	obliquely striated  <i>Nautilus</i> : 4 muscles Octopods: 7 muscles (* recti, * oblique) Decapods: 13-14 muscles (* recti, * oblique)	cross striated  6 muscles (4 recti, 2 oblique)
EYE MUSCLE INNERVATION	Octopods: 7 nerves Decapods: 4 nerves	3 cranial nerves: Oculomotor (III) nerve: med., sup., inf. rectus, inf. oblique Trochlear (IV) nerve: sup. oblique Abducens (VI) nerve: lat. rectus
COMPENSATORY EYE MOVEMENTS	'linear' movements: postrotatory and optokinetic nystagmus rotatory movements: counterrolling, up to $\pm 45^\circ$	'linear' movements: postrotatory and optokinetic nystagmus rotatory movements: counterrolling, up to $\pm 10^\circ$

afferent neurons at the level of the receptor epithelia; the complexity of the efferent innervation; and the number and arrangement of the extraocular muscles. Surprisingly, in some aspects the cephalopod systems exceed the vertebrate systems in complexity, such as in the cellular organization of the receptor epithelia of the angular acceleration receptor systems, in the efferent innervation of the receptor epithelia, and in the extraocular eye muscles.

The arrangement of the cephalopod and vertebrate data in a concise table form highlights all these similarities and differences. The tables have their limits, however, because uniform cephalopod and uniform vertebrate data do not exist. Also, all the known variations within closely-related taxonomic groups cannot be included and, consequently, "averaged" data often have to be used. Although the tables put special emphasis on cephalopods and, if available, describe the differences between the nautiloid, octopod and decapod systems, they neglect the differences (though much smaller) that exist between the systems of fishes, amphibians, reptiles, birds and mammals, and completely exclude the limited data that are available on the unusual systems (by vertebrate standards) of cyclostomes (hagfishes and lampreys).

Variability granted, the presentation of the data in table form has the advantage of easily demonstrating to a broad audience the importance of the cephalopod systems as alternative invertebrate models for comparative vertebrate vestibular research, and of highlighting those areas where differences in structure but not in function exist. It is the comparative research specifically in those areas that can contribute to our understanding of the basic morphological and physiological principles that underlie statocyst/vestibulo-oculomotor reflexes.

For details on the figures presented in the tables, see Lindeman (1969), Budelmann (1979, 1988, 1989, 1992), Grüsser (1983), Budelmann and Young (1984, 1993) and Budelmann *et al.* (1987). For recent overviews and references on the cephalopod systems, see Budelmann (1990, 1994) and Williamson (1995); details on the vertebrate systems are given in Lindeman (1969), Wersäll and Bagger-Sjöbäck (1974), Henn *et al.* (1980) and Lewis *et al.* (1985).

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The data shown in the tables stem from more than 100 publications. Because of space constraints, given below are only a few key references and all the sources of the illustrations used. Please contact the authors for a complete list of references.

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