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THEME ICT-2007.8.3 - FET proactive 3
"Bio-ICT convergence"

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(small or medium-scale focused research project)

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1. Introduction

The primary WP goal addressed during this period was to elucidate the descending command signals to the spinal locomotor networks during different locomotor behaviours exhibited by freely moving salamanders.

The second WP objective was to compare the data obtained in salamanders with those previously reported in the lamprey by KI, because this may shed light on the motor control processes related to the evolution of the locomotor modes in vertebrates.

2. Identification brain areas inducing rhythmic movements

Using electrical microstimulation in a semi-intact preparation, we have shown that simple signals from the brainstem can elicit either locomotion (swimming or stepping, depending on the level of activation), or rhythmic movements of a single hindlimb (Fig. 1). Furthermore, rhythmic movements restricted to the tail can be induced by electrical stimulation of the first spinal cord segment. These results support the view that some descending pathways can selectively activate subparts of the locomotor network.

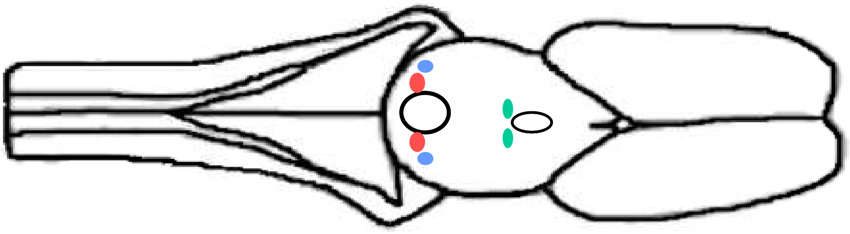

Fig. 1. Distribution of effective sites for evoking rhythmic movements. *Dorsal view of the salamander brain. Blue and green circles indicate sites in which electrical stimulation induced rhythmic movements of a single hindlimb (ipsilateral and controlateral, respectively). Red circles indicate sites for producing locomotion: stepping at low stimulus intensity, swimming at high stimulus intensity.*

3. Recording from descending motor pathways in freely behaving salamanders

3.1. Recording and stimulating electrodes.

We have developed tripolar electrodes suitable to record/stimulate from motor supraspinal structures in freely moving salamanders by modifying the MS333 electrodes manufactured by Plastics One, Inc. The electrodes consisted in a bundle of 2 twisted Teflon-coated platinum wires (50µm diameter) and 1 Teflon-coated stainless steel wire (70µm diameter) (Fig. 2, left panel). After penetration into the brain through a small hole drilled in the skull, the 2 platinum electrodes were fixed to the skull with dental cement. The stainless steel wire (ground) was fixed to the skull with a stainless screw. Thereafter the 3 wires were connected to an amplifier/constant-current stimulus isolation unit through a bipolar light flexible cable (length around 1m) (Fig. 2, right panel).

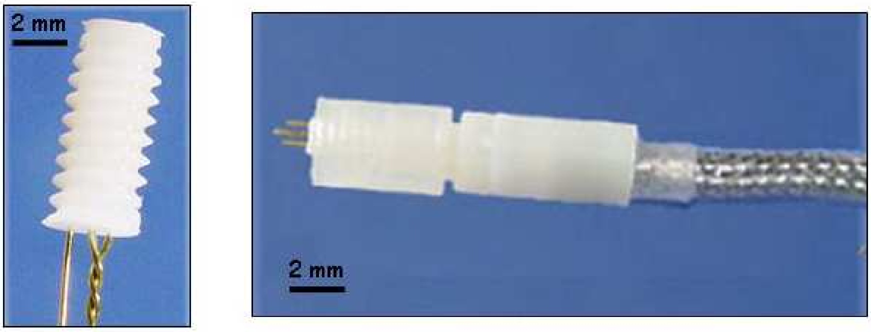

Fig. 2. Photographs of the electrodes (*left panel*) and of the plug and connecting cable (*right panel*).

3.2. Tectal activity, head and eye movements during locomotion in salamander

We have focused on the optic tectum because this structure plays a critical role for visuomotor coordination, and this further allowed a comparison with the data reported in the lamprey by KI. Moreover, we took advantage that both the retina projections to the optic tectum and the tectal efferents to the lower brainstem structures (e.g. the reticular formation) that control spinal motor centres have previously been described in detail in salamanders.

In a first step, using electrical microstimulation we have obtained an oculomotor map of the optic tectum which overlapped its retinotopic innervation (Fig. 3). Electrical stimulation of the lateral part of the left optic tectum (lower part of the visual field) induced a strong retraction of the left eyeball, and a weaker one of the right eyeball. Electrical stimulation of the medial part of the left optic tectum (upper part of the visual field) induced a strong retraction of the right eyeball, and a weaker one of the left eyeball.

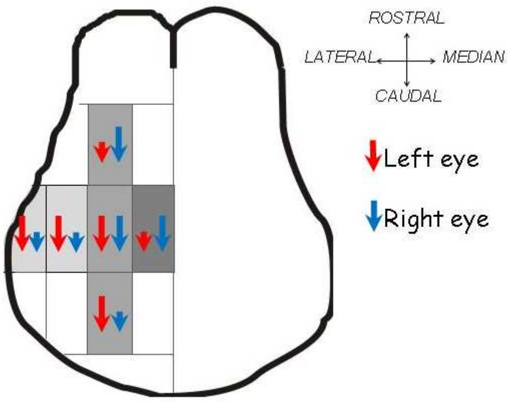

Fig. 3. Retraction eye movements elicited with electrical stimulations of the optic tectum in salamander. *Dorsal view of the salamander optic tectum. Each pair of arrows indicates the retraction of the left eye (red) and right eye (blue). Length of each arrow indicates the amplitude of eye movement.*

Thereafter, our kinematics and EMG recordings evidenced rhythmic yaw and pitch of the head and rhythmic retractions of the two eyes during land stepping along a straight track. Retractions of each eye occurred during protraction of the ipsilateral forelimb and yawing of the head towards the ipsilateral side. Interestingly, the coordination pattern between the two eyes depended on the environment: the left and right eyes alternatively retracted during stepping on ground, while they synchronously retracted during underwater stepping.

Finally, multiunit recording from the optic tectum evidenced: i) a double-bursting pattern of activation of the optic tectum during stepping (Fig. 4); ii) a correspondence of the activation pattern of the lateral/medial parts of the optic tectum to the oculomotor map. The main bursts in the medial part occurred during retractions of the controlateral eye, while the main bursts in the lateral part occurred during retractions of the ipsilateral eye.

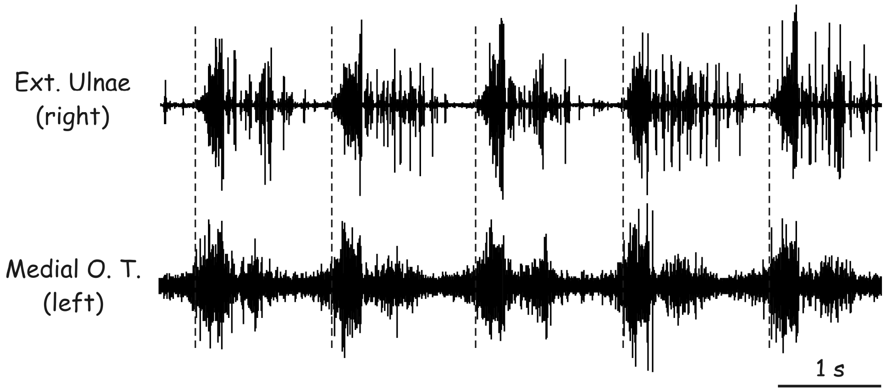

Fig. 4 Activation pattern of the medial optic tectum during land stepping in the salamander. Top trace: EMG recording from the right *extensor ulnae*. Bottom trace: multiunit recording from the medial part of the left optic tectum.

Altogether our results increase the current knowledge on the descending motor systems that control the spinal locomotor networks in salamanders, in line with the pursued WP first objective. They further emphasize the environment dependence of both the eye movement pattern and the tectal activation pattern during locomotion.

3.3. Comparison with the lamprey

Our results bridge over the two vertebrate models, in line with the second WP objective. Indeed, a comparison with the data previously reported in the lamprey by KI suggests strong similarities in the brainstem mechanisms that control the initiation and speed of locomotion.

In salamanders, each of the four limb CPGs and the body CPG can be activated independently of each other (e.g. just the CPG for one limb) by specific descending pathways. This is a potential mechanism which may explain the richer locomotor skills which appeared during evolution from limbless aquatic vertebrates to the first tetrapods which venture out onto land.

Comparison further reveals a more varied visuomotor control during locomotion in salamanders. This is related to the appearance of a more sophisticated extraocular musculature and a richer locomotor repertoire during evolution.

4. Conclusion

The results of this WP, which are crucial for the improvement of the salamander artefact, support the view that the new neuronal systems devoted to stepping in tetrapods were built on top of a primitive (i.e. lamprey-like) swimming circuit.