Summary of thesis for Ph.D.

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Neural Control Mechanisms of the Heart Beat in the African Giant Snail, *Achatina fulica* Férussac*

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軟体動物アフリカマイマイの心拍動調節機構

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SUMMARY

The purpose of this work was to understand the neural control of the heart activity in the African giant snail, *Achatina fulica* Férussac. Although the neural network for the control is fairly complex and needs further studies to clarify the whole aspects, the present work revealed several important features of the neural control mechanisms of the heart in this snail.

Heart regulatory network of

Seven heart regulatory neurones (PON, TAN, TAN-2, TAN-3, d-RCDN, d-LCDN, and VG1) were identified in the central nervous system of *Achatina*. Among these neurones, PON was the most effective heart excitor and it produced heart excitation at rather low firing frequencies. TAN, TAN-2 and TAN-3 were tonically firing neurones and their spontaneous activity was found to produce tonic heart excitation which supplemented the myogenic heart activity. There were some evidences that two cerebral ganglion cells (d-RCDN and d-LCDN) were also likely to be heart excitors although the direct connection to the heart was a little doubtful in some specimens. No direct inhibitory neurone was found, but the firing of VG1 at a high frequency usually produced heart inhibition.

Two cerebral ganglion cells, d-RCDN and d-LCDN, were found to have monosynaptic excitatory connections with several neurones in the suboesophageal ganglia (PON, TAN, TAN-2, TAN-3 and VIN). VIN had a weak electrical coupling with PON. VIN inhibited TAN, TAN-2

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and TAN-3, and the connections were considered to be monosynaptic. At the same time, TAN, TAN-2, TAN-3 and VG1 inhibited PON and VIN although the connections seemed to be polysynaptic. Another neurone in the pedal ganglia, d-LPeLN, was found to excite PON, VIN, TAN, TAN-2 and TAN-3. These connections were not monosynaptic.

There were the inhibitory pathways originating from the periphery in the heart regulatory network and many inhibitory inputs which depressed the activity of PON and VIN were considered to arise from these pathways. The mechano-afferents in the pericardium were found to be the components in these inhibitory pathways. Such mechano-afferents may be important as the pericardium is known to be essential for the hemodynamics.

The heart regulatory network of *Achatina* was somewhat different from that of the previously investigated gastropods (*Aplysia* and *Helix*) in that the heart regulatory motoneurones are connected mono- and poly-synaptically. Thus, in *Achatina*, the higher order neurones can not activate a single motoneurone without affecting other motoneurones.

Synaptic mechanisms between PON and the two cerebral neurones (d—RCDN and d—LCDN)

Under voltage-clamp, activity of the cerebral neurones usually produced an inward shift in the holding current of PON with a decrease of conductance. Ionic substitution experiments and injection of Cs^+ into PON showed that the response was mainly due to a decrease in K^+ conductance. In some cases, this inward shift showed two components : an early component with increased conductance and a late one with decreased conductance. The early component was not decreased by Cs^+-injection but was augmented by EGTA-injection into PON, suggesting the involvement of a Ca^{2+} conductance in this synaptic response.

Application of 5-HT produced a similar inward shift in holding current, which was also mainly the result of a decrease in the background K current. Two different 5-HT-sensitive K channels (SL-channel & SS-channel) were identified by the patch-clamp experiments, and the behavior of 5-HT-sensitive K current in the whole-cell clamp could be explained by the activity of these two channels at least qualitatively. 5-HT was also found to increase the voltage-dependent Ca current by the whole-cell clamp and the single channel recording. The Ca^{2+}-dependent K current and the inward rectifying K current were also increased by application of 5-HT. A presumed Ca^{2+}-dependent K channel current was recorded by the patch clamp.

The slow depolarization of PON induced by the activity of the cerebral neurones was blocked by the 5-HT antagonist, methysergide. Bath application of 5-HT to the axotomized PON produced a similar slow depolarization and it was also blocked by methysergide. These results as well as the similarity of the ionic mechanisms of both responses suggest that the neurotransmitter of d-RCDN and d-LCDN is 5-HT.

These synaptic and 5-HT actions increased the excitability of PON and produced the spike broadening. As PON is the strongest heart excitatory neurone and its activity may be usually depressed by the inhibitory inputs from the periphery, the modulation of the activity of this cell would have significant effect on the heart regulation.

Conclusion

In this work, nine neurones have been identified to be involved in heart regulation of *Achatina*. They are giant neurones of more than 100 μm in diameter and can be easily identified. These situations are contrast to those in previously studied two other snails (*Aplysia* and *Helix*), in which most identifiable heart regulatory neurones are not giant except for some interneurones. Thus, the nervous system of *Achatina* is a promising system for future analysis of the neural control of heart regulation and the relationships between heart regulation and other behaviors, and also for the detailed biophysical and biochemical analyses of the neuronal membrane.