SUMMARY AND CONCLUSIONS

4.1 SUMMARY AND CONCLUSIONS OF THE STUDY

The activity of Na^+/K^+-ATPase has been found to be inhibited by not only cardiac glycosides ouabain and digoxin but also other factors such as a PKC-delta inhibitor, rottlerin, and detergent DOC. Both ouabain and digoxin showed similarly inhibitory effects on Na^+/K^+-ATPase activity in rat kidney whereas ouabain failed to block the activity of Na^+/K^+-ATPase in rat astrocytes compared to the potential effects of digoxin. This observation could be explained by studying the conformation of Na^+/K^+-ATPase in rat astrocytes by a stopped-flow technique. The results indicated that Na^+/K^+-ATPase is initially unsaturated in $E_1(Na^+)_3$ conformation in the presence of Na^+ ion and other conformations such as E_2P and $E_2(K^+)_2$ conformations may also be present. These conformations of the enzyme, if existed, can interpret the differences of the inhibitory effects between ouabain and digoxin on Na^+/K^+-ATPase in rat cultured astrocytes.

Rottlerin has been found to inhibit the activity of Na^+/K^+-ATPase in a dose-dependent manner in both rat kidney and cultured astrocytes. In rat kidney, rottlerin showed a potential inhibition of other ATPase (i.e. Mg^{2+}-ATPase) and had various effects on the activity of Na^+/K^+-ATPase. At low concentrations, rottlerin stimulated the activity of the enzyme whereas at high concentrations, rottlerin inhibited the enzyme activity. The effects of rottlerin on the activity of Na^+/K^+-ATPase measured by the production of P_i generation in a cell-free preparation demonstrated that rottlerin had a directly inhibitory effect on the Na^+/K^+-ATPase activity.

The variety of rottlerin effects on the activity of Na^+/K^+-ATPase was further investigated by using a DMPC monolayer technique. The effects of DOC on the activity of Na^+/K^+-ATPase (Cortas et al., 1989) were also found to be similar to rottlerin. Therefore, both rottlerin and DOC were used to test possible interactions of these compounds on the membrane lipids because the activity of Na^+/K^+-ATPase has been claimed to be regulated by the properties of the lipid membrane (Kimelberg, 1975; Sinensky et al., 1979). The results showed that both rottlerin and DOC decreased the surface pressure of DMPC monolayers and increased the surface area per DMPC molecule. The findings indicate

that both rottlerin and DOC penetrated into the DMPC monolayers. A range of low concentrations of rottlerin used to test the interaction of the drug with the lipids was the same concentrations that caused the activity of Na^+/K^+-ATPase to be increased. It is suggested that changes in rottlerin-induced properties of lipid membrane result in stimulating the activity of Na^+/K^+-ATPase. The concentrations of DOC that showed to inhibit the Na^+/K^+-ATPase activity were used to test this proposal. The results found that at high concentrations of DOC (10 mg/ml), the formation of DMPC monolayers was replaced by DOC monolayers, suggesting that the activity of Na^+/K^+-ATPase in DOC environment results in inhibiting the enzyme activity. However, the exact cause for changes in the Na^+/K^+-ATPase activity is recommended further investigation. In addition, the property of DMPC monolayers has been found to be independent on the ionic strength of Na^+ and Mg^{2+} ions but the phase transition of the DMPC monolayers could be induced by increasing temperature.

The trafficking of glutamate transporter GLAST between the cytoplasm and the membrane has been claimed to be induced by excitatory amino acid glutamate and this effect was associated with the activity of glutamate- or D-Asp-stimulated GLAST (Duan et al., 1999). The present study examined the distribution of glutamate transporter GLAST in two compartments: the membrane and the cytoplasm of rat cortical cultured astrocytes by using deconvolution microscopy and image analysis. The distribution of GLAST between the membrane and the cytoplasm was estimated as a ratio of fluorescence intensity (RFI) of GLAST between the membrane and the cytoplasm. The results showed that non-metabolizable glutamate analogue D-Asp stimulated the movement of GLAST from the cytoplasm to the membrane. The finding suggests that the expression of glutamate transporter GLAST is proportional to the activity of excitatory neurotransmitter-induced GLAST.

The regulation of the distribution of GLAST between the membrane and the cytoplasm was further investigated in the presence of other systems such as Na^+/K^+-ATPase, purinergic receptors, dopamine receptors and ammonia (hyperammonia). A number of studies have been reported that inhibition of Na^+/K^+-ATPase activity resulted in blocking

the activity of glutamate transporters in rat cortical cultured astrocytes (Stanimirovic et al., 1997; Volterra et al., 1994). The present study observed that Na^+/K^+-ATPase inhibitors caused the distribution of D-Asp-induced GLAST away from the cell-surface membrane, suggesting that Na^+/K^+-ATPase decreased the activity of glutamate transporters via a cause of a reduction of the expression of GLAST at the surface membrane. This effect, at least, was the action of Na^+/K^+-ATPase α2-subunit isoform.

The activation of purinergic receptors via $P2X_1$ and $P2X_3$ receptor subtypes and adenosine-mediated P1 receptors has been found to enhance the distribution of glutamate transporter GLAST at the surface membrane of rat cultured astrocytes in the absence of D-Asp. This effect is suggested to be independent on Ca^{2+} transition in a glutamate-independent manner. However, those effects of purinergic receptors on the redistribution of GLAST between the membrane and the cytoplasm were failed in the presence of D-Asp, suggesting that the redistribution of glutamate transporter GLAST at the membrane is induced by D-Asp but not by purinergic receptor activation.

The treatment of schizophrenia by two types (classical and atypical) of neuroleptic drugs has been reported to produce various effects, particularly, on the regulation of the extracellular glutamate concentration (Daly and Moghaddam, 1993). The present study found that a classical antipsychotic drug, haloperidol, decreased the expression of D-Asp-induced GLAST at the surface membrane of rat cortical cultured astrocytes whereas an atypical antipsychotic drug, clozapine, had no effect on the distribution of D-Asp-induced GLAST between the membrane and the cytoplasm. The findings suggest that in an initial period of the treatment, haloperidol could reduce the activity of GLAST because in a longer period, haloperidol had no effect on the extracellular concentration of glutamate in vivo (Daly and Moghaddam, 1993). The results also indicated that glutamate transporter GLAST played no role in the elevation of the extracellular glutamate concentration in a schizophrenic treatment with clozapine. In addition, clozapine has been found to stimulate the shifting of GLAST towards the membrane in the absence of D-Asp.

The redistribution of glutamate transporter GLAST towards the membrane was induced by ammonia at physiological concentrations and toxic concentrations (10 mM) in the absence of D-Asp. The findings suggest that the movement of GLAST from the cytoplasm to the membrane may be independent on pH_i (acidification) in a glutamate-independent manner. Hyperammonia has been found to increase the uptake of L-glutamate but have no influence on the uptake of D-Asp (Bender and Norenberg, 1996). The present study demonstrated that hyperammonia had no effect on the distribution of D-Asp-induced GLAST, suggesting that hyperammonia stimulates the activity of glutamate transporters via glutamate but not non-metabolizable glutamate analogue D-Asp because of a demand for the generation of glutamine inside astrocytes.

In conclusion, Na^+/K^+-ATPase is inhibited by ouabain, digoxin, DOC and rottlerin. Rottlerin can inhibit the enzyme directly but the effect can be via changes in the properties of the lipid membrane. The redistribution of glutamate transporter GLAST from the cytoplasm to the membrane of rat cultured astrocytes is induced by D-Asp, α,β-methylene ATP, adenosine, clozapine and ammonia (100 μM, 10 mM). However, Na^+/K^+-ATPase inhibitors decrease the distribution of D-Asp-induced GLAST at the membrane.

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