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Signaling pathway underlying the octopaminergic modulation of myogenic contraction in the cricket lateral oviduct

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ABSTRACT

Octopamine (OA), a biogenic monoamine, is a neurotransmitter and neuromodulator in invertebrates. Here, we report the effect of OA on the spontaneous rhythmic contractions (SRCs) of the lateral oviduct of the cricket *Gryllus bimaculatus* and the possible signaling pathway involved. Application of OA increased both the frequency and amplitude of SRCs in a dose-dependent manner. The effect of OA was inhibited by subsequent application of the OA receptor antagonist epinastine, indicating that the action of OA is mediated by OA receptor. To investigate the predominant signaling pathway underlying the action of OA, we first examined a possible involvement of the cAMP/cAMP-dependent protein kinase A (PKA) signaling pathway. Application of the membrane-permeable cAMP analog 8-Br-cAMP had little effect on SRCs and the effect of OA was not influenced by subsequent application of the PKA inhibitor H89, indicating that the cAMP/PKA signaling pathway is not the predominant pathway in the action of OA. Next, we examined a possible involvement of the second messenger inositol 1,4,5-trisphosphate in the action of OA. The effect of OA on SRCs was inhibited by subsequent application of the phosphoinositide-specific phospholipase C (PLC) inhibitor U73122, indicating that the PLC pathway is involved in the action of OA. The OA-induced increase in the frequency of SRCs was inhibited by pretreatment of the cell with the ryanodine receptor antagonist tetracaine but was not significantly affected by the IP_3 receptor antagonist 2-aminoethoxydiphenyl borate (2-APB). On the other hand, the OA-induced increase in the amplitude of SRCs was inhibited by pretreatment of the cells with 2-APB but was not significantly affected by tetracaine. Taken together, these results suggest that the OA-induced excitatory effect on SRCs is mediated by the PLC signaling pathway: Ca^{2+} release from IP_3 receptors may contribute to the modulation of the amplitude of SRCs, whereas Ca^{2+} release from ryanodine receptors may contribute to the modulation of the frequency of SRCs.

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1. Introduction

Octopamine (OA) is the invertebrate homolog of vertebrate noradrenaline and acts as a neurotransmitter (Nathanson, 1979), neuromodulator (Lange and Orchard, 1986), and neurohormone (Orchard, 1982). OA is involved in regulating many physiological phenomena, such as initiation and maintenance of rhythmic behaviors (flying and walking) (Sombati and Hoyle, 1984), memory (Dudai et al., 1986; Menzel et al., 1988), circadian rhythms (Muszynska-Pytel and Cymborowski, 1978), and oviduct contraction (Orchard and Lange, 1985; Lange and Tsang, 1993).

Many studies have been performed in *Locusta migratoria* on the role of OA in the control of lateral oviduct spontaneous rhythmic contractions (SRCs). OA strongly inhibits both the neurogenic and myogenic SRCs of the locust oviduct (Orchard and Lange, 1985; Lange and Tsang, 1993). A recent study further clarified that OA not only acts peripherally by relaxing the lateral and common oviducts to enable egg laying, but also acts centrally by altering the motor pattern responsible for the egg-retention central pattern generator (Wong and Lange, 2014). The inhibitory action of OA on oviduct muscle is mediated by an increase in cAMP via binding to OA-2B receptors, which are G-protein coupled and are linked to adenylate cyclase (Lange and Nykamp, 1996; Nykamp and Lange, 1998).

In contrast to this inhibitory action of OA, we found that OA has opposite modulatory effects on SRCs in the cricket *Gryllus bimaculatus*. Exposure of cricket lateral oviduct to OA increased both the frequency and amplitude of SRCs. Therefore, we hypothesized that the types of OA receptors that are responsible for the modulation of oviduct contraction might differ between the locust and cricket. Various types of OA receptors have been identified in

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insects according to their coupling to different G proteins and their effects on second messengers. According to the recent classification of OA receptors by Evans and Maqueira (2005), OA receptors are grouped into three classes: α-adrenergic-like (OCTαR), β-adrenergic-like (OCTβR), and octopaminergic/tyraminergic (OCT/TYR-R) or tyraminergic (TYR-R). Activation of OCTαR by OA increases intracellular Ca^{2+} via activation of phospholipase C (PLC) enzyme, which hydrolyzes phosphatidylinositol 4,5-bisphophate into inositol 1,4,5-trisphosphate (IP_3) and diacylglycerol (DG). IP_3 then causes intracellular Ca^{2+} release from intracellular Ca^{2+} stores and DG activates protein kinase C (PKC), which regulates physiological responses by phosphorylating various signaling proteins. OCTαR also associated with a small increase in intracellular cAMP levels via the stimulatory G proteins (Gs), which in turn stimulate protein kinase A (PKA) (Farooqui, 2007, 2012).

In the present study, we investigated the signaling pathways activated by OA receptor activation by using the most commonly used secondary messenger-specific antagonists. Our results indicated that the OA-induced excitation of SRCs of the cricket lateral oviduct is not mediated by cAMP/PKA, but by the PLC/IP_3 signaling pathway. Ryanodine receptors (RyRs) in the intracellular Ca^{2+} store were involved in the modulation of the frequency of SRCs and were probably associated with plasma membrane Ca^{2+} channels, whereas IP_3 receptors (IP_3Rs) in intracellular Ca^{2+} stores were found to be involved in modulation of the amplitude of SRCs.

2. Materials and methods

2.1. Animals

Adult female *G. bimaculatus* were maintained in a colony at our institution's Department of Biology at 25–30 °C with a relative humidity of 65–85% under a 12:12 h light: dark cycle. Crickets were fed on an artificial insect diet (Oriental Yeast) and supplied with water.

2.2. Dissection of lateral oviduct

Animals were anesthetized using CO_2 before dissection and fixed in a dorsal side up position. The lateral oviduct was exposed by removing the surrounding muscles and connective tissues in normal saline containing (in mM): 140 NaCl, 10 KCl, 1.6 $CaCl_2$, 2 $MgCl_2$, 44 glucose, 2 HEPES, buffered to pH 7.4 with Tris (hydroxymethyl) aminomethane.

2.3. Recording of isometric contractions

The upper part of the lateral oviduct was attached to an FD Pickup SB-1T mechano-electrical force transducer (Nihon Kohden, Tokyo, Japan) using a fine thread and the anterior end of the ovaries was attached to the base of the trough in a Sylgard-coated dish (containing 400 μl saline). The preparation was attached horizontally to the force transducer to measure the isometric tension. The output signal of the force transducer was amplified by a carrier amplifier whose output signal was further amplified in turn by an AVH high-gain DC amplifier (Nihon Kohden). The final output signal was recorded by using a chart recorder (Omniace, NEC Sanei), monitored on the PC display, and stored by using a computer-based field recording unit (es8, TEAC Corporation, Japan) for later analysis. The amplitude of SRCs was measured from average 10–15 contractions. The frequency of the SRCs was measured from the time interval between successive contractions of lateral oviduct.

2.4. Solution

The normal saline contained (in mM): 140 NaCl, 10 KCl, 1.6 $CaCl_2$, 2 $MgCl_2$, 44 glucose, 2 HEPES, buffered to pH 7.4 with Tris–Cl. The Ca^{2+}-free EGTA solution contained (in mM): 140 NaCl, 10 KCl, 54.8 glucose, 2 HEPES, 5 EGTA, buffered to pH 7.4 with Tris–Cl. Incubations with both solutions were performed for 15 min.

2.5. Drugs

The following drug were used: DL-OA (Sigma), epinastine hydrochloride (Tokyo Kasei), 8-bromoadenosine 3′,5′-cyclic monophosphate sodium salt (8-Br-cAMP) (Sigma), H-89 (Wako), U-73122 hydrate (Sigma), 2-aminoethoxydiphenyl borate (2-APB) (Wako), tetracaine (Wako), GEDTA (EGTA) (Wako). U-73122 and 2-APB were prepared as a stock in DMSO; the final concentration of DMSO in the bath was less than 1:1000. All drug solutions were freshly prepared before use and were continuously perfused at a rate of approximately 5 ml/min.

2.6. Statistical analysis

Values are reported as the means ± SEM, with *N* representing the number of cells. For comparisons between two groups, a Student's *t* test, paired or unpaired, was used for statistical analysis. *P* values <0.05 were considered statistically significant.

3. Results

3.1. Effect of OA and the OA antagonist epinastine on SRCs

A representative example of the effect of OA on SRS of the lateral oviduct (0.6 μM) is shown in Fig. 1A. Application of OA increased the frequency and amplitude of SRCs (Fig. 1A and B). This potentiating effect was initially observed at a concentration of 0.01 μM OA. With increasing concentrations of OA, the frequency and amplitude of SRCs increased in the range between 0.01 and 10 μM (Fig. 1B). To investigate whether the excitatory action of OA is mediated by OA receptors, we examined the effect of epinastine (1 μM), a highly selective antagonist of insect OA receptors, on the OA-induced increase in the frequency and amplitude of SRCs (Fig. 2A_1). Epinastine significantly attenuated the OA-induced increase in the frequency ($P < 0.01$; Fig. 2B_1) and amplitude ($P < 0.01$; Fig. 2B_2) of SRCs. Fig. 2A_2 shows the effect of epinastine (1 μM) on SRCs. Application of epinastine alone had little effect on either the frequency (Fig. 2B_1) or amplitude (Fig. 2B_2) of SRCs. These results indicate that the action of OA is mediated by OA receptor activation.

3.2. Effect of 8-Br-cAMP

To determine whether the OA-induced increase in the frequency and amplitude of SRCs is mediated by cAMP/PKA signaling pathway, the effect of the membrane-permeable cAMP analog 8-Br-cAMP was investigated. Application of 8-Br-cAMP (1 mM) had little effect on either the frequency (Fig. 2D_1) or amplitude (Fig. 2D_2) of SRCs.

3.3. Effect of H89 on the action of OA

To further examine the possible involvement of PKA in the action of OA, we investigated the effect of the PKA inhibitor H89 on the effect of OA. The OA-induced increase in the frequency

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