

## Mechanisms of Phospholipase C Activation by the Vasoactive Intestinal Polypeptide/Pituitary Adenylate Cyclase-Activating Polypeptide Type 2 Receptor

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### ABSTRACT

The vasoactive intestinal polypeptide/pituitary adenylate cyclase-activating polypeptide type 2 (VPAC<sub>2</sub>) receptor was shown to induce both [<sup>3</sup>H]inositol phosphate ([<sup>3</sup>H]IP) and cAMP production in transfected COS7 cells and in GH<sub>4</sub> cells where it is natively expressed. Neither cholera toxin nor forskolin could elicit an equivalent [<sup>3</sup>H]IP response, suggesting independent coupling of the two pathways. The VPAC<sub>2</sub> receptor-mediated [<sup>3</sup>H]IP response was partially inhibited by pertussis toxin (Ptx) and by the G $\beta\gamma$ -sequestering C-terminal fragment of G19C2 (G19C2-ct) in COS7 and GH<sub>4</sub> cells, whereas responses of control receptors were unaffected. Blockers of receptor-activated Ca<sup>2+</sup> influx pathways (Ca<sup>2+</sup> and SKF 96365) also partially inhibited

VPAC<sub>2</sub> receptor-mediated [<sup>3</sup>H]IP responses. This inhibition was not present in the component of the response remaining after Ptx treatment. A range of blockers of voltage-sensitive Ca<sup>2+</sup> channels were ineffective, consistent with the reported lack of these channels in COS7 cells. The data suggest that the VPAC<sub>2</sub> receptor may couple to phospholipase C through both Ptx-insensitive and Ptx-sensitive G proteins (G<sub>12/13</sub> and G<sub>q/11</sub>, respectively) to generate [<sup>3</sup>H]IP. In addition to G $\beta\gamma$ , G<sub>12/13</sub> activation appears to regulate receptor-activated Ca<sup>2+</sup> entry. This is consistent with the possibility that not only G<sub>12/13</sub>-responsive and G $\beta\gamma$ -responsive isoforms of phospholipase C but also Ca<sup>2+</sup>-responsive forms may contribute to the overall [<sup>3</sup>H]IP response. (*Endocrinology* 142: 1209–1217, 2001)

THE 28-AMINO acid vasoactive intestinal peptide (VIP) belongs to a family of structurally related hormones that include pituitary adenylate cyclase-activating polypeptide (PACAP), secretin, GH-releasing hormone, and glucagon. VIP has well documented effects as a potent vasodilator and stimulator of electrolyte secretion and smooth muscle relaxation. In the central nervous system it is involved in regulating cerebral blood flow and circadian rhythms. It is a secretagogue for melatonin synthesis and release from pineal gland, PRL release from pituitary, insulin release from pancreas, and catecholamine release from adrenal medulla. VIP has a protective role in limiting oxidative damage in various tissues. Furthermore, dramatic changes in the amounts of VIP, PACAP, and their receptors in the spinal cord after peripheral nerve injury suggest an important role in neuropathic pain states (1–5).

The pleiotropic effects of VIP are mediated through G protein-coupled receptors that may activate several signal

transduction pathways in addition to cAMP production. Two distinct receptors for VIP have been cloned, the vasoactive intestinal polypeptide/pituitary adenylate cyclase-activating polypeptide type 1 (VPAC<sub>1</sub>) from rat lung (6) and the VPAC<sub>2</sub> from rat pituitary and olfactory bulb (7). The neuropeptide PACAP<sup>38</sup> and its 27-residue amino-terminal form PACAP-27 (which shares approximately 68% identity with VIP) are similarly potent at these receptors in stimulating cAMP production. Receptors for VIP/PACAP belong to group II of the G protein-coupled receptor family, which includes receptors for secretin, PTH, and calcitonin (8). Members of this family couple to adenylate cyclase (AC), and a number have been shown to couple additionally to phospholipase C (PLC) (9, 10).

Preliminary studies indicated that the VPAC<sub>2</sub> receptor-mediated activation of [<sup>3</sup>H]inositol phosphate ([<sup>3</sup>H]IP) formation in transiently transfected COS7 cells occurred through a mechanism that was in part pertussis toxin (Ptx) sensitive (11). Here we investigated the hypothesis that this response is due to the stimulation of a PLC isoform by a mechanism involving the  $\beta\gamma$ -subunits of the Ptx-sensitive G proteins, G<sub>i</sub> and G<sub>12/13</sub>, and whether there is any role for receptor-operated Ca<sup>2+</sup> entry in the response. As well as in transfected COS7 cells, studies were carried out in GH<sub>4</sub> cells, which natively express the VPAC<sub>2</sub> receptor at low levels.

### Materials and Methods

#### Drugs and chemicals

Tissue culture media were obtained from Life Technologies, Inc. (Paisley, UK); diethylaminoethyl (DEAE) dextran was obtained from

Received August 15, 2000.

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