

## Profound differences in potassium current properties of normal and Rous sarcoma virus-transformed chicken embryo fibroblasts

(pp60<sup>src</sup> / patch-clamp technique / charybdotoxin / oncogenes)

HOLGER REPP, HENNING DRAHEIM, JÖRGEN RULAND, GÜNTHER SEIDEL, JOACHIM BEISE, PETER PRESEK, AND FLORIAN DREYER\*

Rudolf-Buchheim-Institut für Pharmakologie der Justus-Liebig-Universität Gießen, Frankfurter Strasse 107, D-6300 Gießen, Federal Republic of Germany

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**ABSTRACT** The membrane currents of chicken embryo fibroblasts (CEFs) transformed by Rous sarcoma virus (RSV) were compared with the currents of their nontransformed counterparts by using the whole-cell patch-clamp technique. In nontransformed CEFs, the main membrane current is a delayed outward K<sup>+</sup> current that is sensitive to tetraethylammonium ion but insensitive to 4-aminopyridine. This K<sup>+</sup> current is almost independent of the intracellular Ca<sup>2+</sup> concentration and becomes completely inactivated at positive membrane potentials with a time constant of about 10 s at +30 mV. In contrast, transformed CEFs exhibit a noninactivating K<sup>+</sup> current that strongly depends on the intracellular Ca<sup>2+</sup> concentration. This Ca<sup>2+</sup>-dependent K<sup>+</sup> current is blocked by the scorpion toxin charybdotoxin with an IC<sub>50</sub> value of 19 nM, whereas the K<sup>+</sup> current of normal CEFs is insensitive to charybdotoxin (up to 300 nM). The K<sup>+</sup> current properties of transformed CEFs were also found after microinjection of purified, enzymatically active pp60<sup>src</sup> into normal CEFs but not after infection of CEFs with the Rous-associated virus RAV5, which lacks the *v-src* oncogene. Our results suggest that the oncogene product pp60<sup>src</sup> modulates existing K<sup>+</sup> channel proteins, leading to profound electrophysiological and pharmacological alterations of the K<sup>+</sup> current properties in RSV-transformed CEFs. Furthermore, our experiments identify for the first time K<sup>+</sup> channels as possible substrates of pp60<sup>src</sup>.

Oncogenesis *in vivo* and transformation *in vitro* induced by Rous sarcoma virus (RSV) are linked to the expression of the *v-src* oncogene (for reviews, see refs. 1 and 2). The *v-src* oncogene product pp60<sup>src</sup> is the prototype of a nonreceptor tyrosine-specific protein kinase (for reviews, see refs. 3–5) located mainly on the cytoplasmic side of the plasma membrane of transformed cells (for review, see ref. 6). Cell transformation mediated by protein tyrosine kinases is associated with an increase in tyrosine phosphorylation of a large number of proteins, most of which, however, do not seem to be essential for the transformation process (7). Although it is widely accepted that those substrates of pp60<sup>src</sup> that might be crucial for transformation must be membrane-associated (for review, see ref. 8), the critical targets for pp60<sup>src</sup> action still await identification.

In several reports, a role of K<sup>+</sup> channels in cell proliferation has been described (9, 10). However, the role of K<sup>+</sup> channels in the event of cell transformation by oncogene products is far from being clearly established. In rat fibroblasts, an altered Na<sup>+</sup>/K<sup>+</sup> permeability ratio has been observed after *src*-transformation (11). In contrast, *src*-transformation of mouse astrocytes did not lead to changes in their K<sup>+</sup> membrane current (12). For the *ras* oncogene of the Kirsten sarcoma virus, it has been demonstrated recently that

its expression in mammalian fibroblasts is associated with the appearance of a Ca<sup>2+</sup>-activated K<sup>+</sup> current that is absent from nontransformed cells (13). Here, we report that the K<sup>+</sup> currents of normal chicken embryo fibroblasts (CEFs) and of RSV-transformed CEFs differ substantially in their electrophysiological and pharmacological properties. The same differences were found after microinjection of purified pp60<sup>src</sup> into normal CEFs. Our results suggest that the oncogene product pp60<sup>src</sup> of RSV profoundly modulates K<sup>+</sup> current properties.

### MATERIALS AND METHODS

**Cell Culture.** CEFs were isolated and maintained in primary tissue culture as described (14). After the second passage, the culture consisted almost exclusively of fibroblasts. At this stage, CEFs were infected with a temperature-sensitive mutant (ts-NY68) of RSV strain Schmidt-Ruppin A. After ts-NY68 infection, CEFs were maintained in humidified 10% CO<sub>2</sub>/90% air in Dulbecco's modified Eagle's medium containing 5% newborn calf serum. After confluence, cultures were trypsinized, and cells were plated at a density of  $2 \times 10^5$  cells per 35-mm dish and further incubated at 37°C for 2 days prior to patch-clamp recording. The *v-src* oncogene product pp60<sup>src</sup> of the conditional RSV mutant ts-NY68 is temperature sensitive for transformation, kinase activity, and membrane localization (4). At the nonpermissive temperature of 41°C, pp60<sup>src</sup> is mainly associated with the pp50–pp60 complex. At or below the permissive temperature of 37°C, it is active and can be translocated from the cytoplasm into the plasma membrane, inducing transformation events. The transformation can easily be followed by a marked phenotypic conversion—i.e., at permissive temperatures, the CEFs assume a round shape.

**Membrane Current Measurements.** The whole-cell recording configuration of the patch-clamp technique (15) was used to measure membrane currents under voltage-clamp conditions at 20–22°C. For optimal voltage-clamp conditions, normal and transformed CEFs were caused to assume a round shape by incubation with 0.025% trypsin for 1 min in Ca<sup>2+</sup>-free bath solution. The pipette solution was 140 mM K<sup>+</sup> glutamate/20 mM NaCl/2 mM MgCl<sub>2</sub>/10 mM HEPES-KOH, pH 7.3, EGTA at 5 mM and total Ca<sup>2+</sup> at 4.5, 2.5, 0.45, or 0.05 mM or no Ca<sup>2+</sup> were added to obtain free Ca<sup>2+</sup> concentrations of 10<sup>-6</sup>, 10<sup>-7</sup>, 10<sup>-8</sup>, 10<sup>-9</sup>, and 0 M. The bath solution was 140 mM NaCl/3 mM KCl/2 mM MgCl<sub>2</sub>/2 mM CaCl<sub>2</sub>/10 mM glucose/10 mM HEPES-NaOH, pH 7.4. All data presented have been corrected for the liquid-junction potential between the pipette and bath solution, which for the internal glutamate solution was 10 mV.

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Abbreviations: CEF, chicken embryo fibroblast; RSV, Rous sarcoma virus; RAV, Rous-associated virus; ChTX, charybdotoxin. \*To whom reprint requests should be addressed.

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