



Long-term fate of terminally differentiated skeletal muscle cells following E1A-initiated cell cycle reactivation

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Abstract

We have previously shown that E1A reactivates the cell cycle in 'irreversibly' growth arrested, terminally differentiated (TD) cells. The molecular events following E1A-mediated reactivation of TD skeletal muscle cells have been extensively investigated. However, the long-term fate of the reactivated cells has not been directly determined. In this paper, E1A is used to reactivate TD myotubes derived from established cell lines or primary myoblasts. We show that the reactivated muscle cells continue proliferating beyond the end of the first cell cycle and progress through at least a second one. Experiments performed with an inducible E1A/estrogen receptor chimera indicate that the reactivated cell cycle is self-sustained, since E1A is exclusively necessary to reactivate TD cells, but is dispensable for both the continuation of the first cycle and the progression into the following one. Finally, we report that E1A-mediated reactivation of muscle cells results in apoptotic cell death that can be delayed by the antiapoptotic, adenoviral E1B 55 kDa oncogene. *Cell Death and Differentiation* (2000) 7, 145–154.

Keywords: terminal differentiation; mitosis; cytokinesis; time-lapse videomicroscopy

Abbreviations: TD, terminally differentiated; MSC, mouse satellite cells; Ara-C, β -D-arabinofuranoside; BrdUrd, 5-bromo-2'-deoxyuridine; MHC, myosin heavy chain; PI, post infection; TUNEL, terminal deoxynucleotidyl transferase-mediated dUTP nick end labeling; SF, serum free

Introduction

Terminally differentiated cells are defined by specialized properties, which are the result of tissue-specific gene expression, associated with a physiologically irreversible growth arrest. Terminal differentiation characterizes the majority of the cells in an adult mammal. The inability of TD cells to replicate poses strategic problems to the organism.

These cells must live as long as the organism itself, which requires extraordinary measures to ensure their survival. In addition, organs and systems devoid of stem cell compartments and whose parenchyma is composed exclusively of TD cells cannot renew their tissues by means of cell proliferation. This makes them especially vulnerable to irreplaceable cell loss caused by diseases or injuries. The ability to induce sustained proliferation of TD cells such as neurons, myocytes, or endocrine cells would potentially have a major impact on the therapy of diseases and traumas of such organs.

One example of terminal differentiation is provided by skeletal muscle cells.¹ The differentiation process of these cells can be recapitulated *in vitro*. Primary as well as established myoblasts can be cultured extensively. Mitogen withdrawal starts the differentiation program, which begins with irreversible exit from the cell cycle (commitment). Postmitotic myoblasts then express muscle-specific genes, turning into mononucleated myocytes (biochemical differentiation). The final stage of skeletal muscle differentiation *in vitro* involves fusion of myocytes into multinucleated structures called myotubes (morphological differentiation).¹

It has been shown that a number of DNA tumor virus oncogenes are able to reactivate the cell cycle in TD cells.^{2–6} Adenoviruses bear the E1A oncogene, which shares this ability.⁶ Adenoviruses are particularly well suited for cell cycle reactivation of TD cells, since they can infect almost all cell types^{7–9} across a wide range of species,⁶ irrespective of the proliferation status of the cells. In fact, we and others have shown that adenovirus infection and the consequent E1A expression can reactivate a variety of TD cells, including myotubes, adipocytes,^{4,9} myocardiocytes,¹⁰ and neurons (M. Crescenzi, unpublished). E1A exerts such activity by activating genes normally expressed at the G1/S boundary.¹¹ By this mechanism, E1A in effect bypasses the cell cycle block that prevents TD myotubes from proceeding beyond mid-G1 phase upon mitogenic stimulation.¹²

We have shown that E1A-reactivated myotubes undergo DNA replication, mitosis, and cytokinesis.^{4,9} However, the long-term fate of these cells has not been investigated in depth. Open questions include whether further cell cycles follow the first one, whether any fraction of the reactivated cells can survive indefinitely, and whether the activity of E1A is required to sustain the cell cycle or it is only needed to initiate it. All of these issues are relevant in view of potential therapeutic applications.

In this paper, we present evidence that TD skeletal muscle cells reactivated by E1A undergo more than one cell cycle. We show that the reactivated cells eventually die by apoptosis. Such outcome can be at least partially opposed by the antiapoptotic adenovirus E1B oncogene, which allows extended survival. Finally, making use of a

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