

## Poly(ADP-Ribose) Polymerases in Aging – Friend or Foe?

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**Abstract:** Poly(ADP-ribose) polymerases were originally described as DNA repair enzymes. PARP-1, PARP-2 and PARP-3 can be activated by DNA damage and the resulting activation of these enzymes that facilitate DNA repair, seems to be a prerequisite of successful aging. PARP activation helps to maintain genomic integrity through supporting DNA repair systems; however, in parallel these enzymes limit metabolic fitness and make the organism more prone for metabolic diseases. In addition, several other pathways (e.g., proteostasis, nutrient sensing, stem cell proliferation or cellular communication) all contributing to aging, were shown to be PARP mediated. In this review we aim to summarize our current knowledge on the role of PARPs in aging.

**Keywords:** PARPs, mitochondria, DNA repair, aging, healthspan, energy stress.

### AGING, AGING-RELATED PATHOLOGIES

With increases in lifespan, Western countries face an ever-growing number of aging people and growing number of aging-related diseases. Aging is a natural process that is characterized by genomic instability, telomere attrition, epigenetic alterations, loss of proteostasis, deregulated nutrient sensing, mitochondrial dysfunction, stem cell exhaustion, cellular senescence and altered intercellular communication [1]. On the course of aging the prevalence of certain diseases increase as compared to the younger or mixed-age population, such as metabolic diseases (type II, diabetes, obesity), certain malignancies, macular degeneration, osteoporosis, hearing loss - just to list a few. It is evident that identifying molecular targets that improve healthspan or the quality of life during aging has obvious advantages for the society.

Poly(ADP-ribose) polymerases (PARPs) were originally described as DNA repair proteins and in the late '90s Muir and Bürkle [2] have shown that centenarians as compared to the average population have higher PARP activity in leukocytes suggesting that higher PARP activity is associated with successful aging. In the past years our understanding of the relationship between PARP activity and aging has greatly improved and in this review we try to provide a comprehensive picture of the role of PARPs in aging.

### THE ENZYMOLOGY OF POLY(ADP-RIBOSYL)ATION

In humans poly(ADP-ribose) polymerases (PARPs) form a family of 17 that share the same catalytic domain. PARPs

are multidomain proteins containing additional domains – among others – domains for protein-protein interactions (e.g., zinc fingers, BRCT domain, ankyrin repeats, etc.), macrodomains for binding or cleavage of ADP-ribose, DNA/RNA binding domains (zinc finger or SAP domain) and nuclear or nucleolar localization signals [3-6].

Poly(ADP-ribosylation (PARylation) is an evolutionarily conserved biochemical process. Activated PARP-1 binds and cleaves NAD<sup>+</sup> to ADP-ribose and nicotinamide (NAM) then conjugates ADP-ribose to glutamate or aspartate side chains [3, 5]. To the first ADP-ribose moiety the enzyme can subsequently join new ADP-ribose units forming large, branched polymers counting up to 200 individual ADP-ribose residues [3]. To date PARP-1, PARP-2 and tankyrases (TNK) are known to perform PARylation, the rest of the family performs oligo- or mono-ADP-ribosylation (inefficient or no elongation), can be inactive (mutation of catalytic amino acids) or its activity had not been characterized [5-11]. It must be noted that single ADPR units can be further elongated by PARPs capable of performing polymerization steps [7] 85-90% of the basal and DNA break-triggered PARP activity is covered by PARP-1, PARP-2 is responsible for the remaining 10-15%, while the activity conferred by the rest of the family is negligible as compared to the total activity [12, 13]. PARP-1, PARP-2 and PARP-3 are activated by DNA strand breaks; however, different posttranslational modifications may also modulate the activity of PARPs (for review see [14, 15]).

PAR molecules can be joined onto PARP-1 or PARP-2 (autoPARylation) or onto other acceptor molecules (trans-PARylation). AutoPARylation inhibits PARP-1 activation and therefore inhibits PARP-1 overactivation, while removing PAR reactivates PARP-1 [16, 17]. The PAR polymer is rapidly degraded in cells to ADPR. There are several em-

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