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Guaranteeing a captive audience: coordinated regulation of gene transfer agent (GTA) production and recipient capability by cellular regulators

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Gene transfer agents (GTAs) are bacteriophage-like particles produced by many prokaryotes. Several members of the *Alphaproteobacteria* produce a class of genetically-related GTAs that is best studied in *Rhodobacter capsulatus.* DNA transfer by the *R. capsulatus* GTA (RcGTA) combines aspects of both transduction and natural transformation, as recipient cells require a natural transformation-like system to incorporate donated DNA. The genes involved in RcGTA production and recipient capability are located at multiple loci in the bacterial genome; however, a conserved phosphorelay containing the response regulator CtrA and a quorum sensing system regulate both RcGTA production and recipient capability. This review highlights recent discoveries in RcGTA biology, and focuses on the co-regulation of genes involved in RcGTA production and recipient capability.

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Introduction

Horizontal gene transfer (HGT; also called lateral gene transfer) is the transfer of a gene to an organism by means other than classical (vertical) inheritance to from a parent progeny. HGT is a common occurrence among prokaryotes and several examples of HGT have also been reported for multicellular organisms [1,2]. Several functions beneficial to the organism, including antibiotic resistance, production of virulence factors, or new metabolic mechanisms, have been documented as transferred by HGT [2].

The most common mechanisms of HGT between prokaryotes are conjugation, natural transformation and transduction [3,4]. Conjugation is the transfer of genetic material, typically a plasmid, by direct cell–cell contact [4,5]. Natural transformation is the uptake and recombination of naked DNA from the environment, a process that requires a conserved set of proteins collectively called Com proteins [4,6]. Transduction is HGT mediated by bacteriophages (phages) or phage-like particles. Phages can transduce genetic material as a by-product of their life cycle, either by taking a part of the host genome along with their genome during excision from the prophage state (specialized transduction) or by "erroneous" packaging of host DNA in place of phage DNA (generalized transduction) [3].

In addition to the classical mechanisms above, several prokaryotes produce small phage-like particles termed gene transfer agents (GTAs) that appear to be specific for HGT. GTAs have in common that they package short pieces of random DNA from the genome of the producing organism, and that this DNA is insufficient to encode the genes required for production of the GTA [7,8••]. Phage-like particles produced by several phylogenetically unrelated prokaryotes have been proposed to be GTAs based on the presence of DNase I-protected, non-discrete segments of DNA, and their ability to transduce genetic markers (Table 1). Because the DNA contained in the capsid is protected from nucleases present in the environment and appears specifically targeted to related cells (see below), GTAs may be an effective mechanism of HGT between closely related members of a community.

This review is limited to the class of genetically related GTAs found in several members of the *Alphaproteobacteria* with a focus on the genetic regulation of the model GTA from *Rhodobacter capsulatus* (RcGTA). It has recently become clear that RcGTA mediates HGT by combining aspects of both transduction and natural transformation (Figure 1a), and that both processes are regulated by the same bacterial regulatory systems, including a quorum sensing system and a conserved phosphorelay containing the response regulator CtrA (Figure 1b; Box 1).

Table 1

GTAs and GTA-like particles

Organism(s)	Element/particle	References
Rhodobacter capsulatus and several *Rhodobacteraceae*[a]	RcGTA	[9•,12••]
Brachyspira hyodysenteriae	VSH-1	[49]
Desulfovibrio desulfuricans	Dd1	[50]
Methanococcus voltae	VTA	[51]
Bartonella spp.	BaGTA (BLP)	[52–54]

[a] Several members of the *Rhodobacteraceae* contain an RcGTA-like gene cluster [8••] and RcGTA-like particles have been reported produced by *Ruegeria pomeroyi* [24], *Rhodovulum sulfidophilum* [27], *Roseovarius nubinhibens* and the *Rhizobiales* member *Nitratireductor* 44B9 [25].

Box 1 The CckA-ChpT-CtrA phosphorelay.

The CckA-ChpT-CtrA phosphorelay, composed of the hybrid histidine kinase CckA, the phosphotransferase ChpT and the DNA-binding response regulator CtrA, is conserved throughout the *Alphaproteobacteria* [55,56•]. It has been extensively studied for its essential role in controlling DNA replication and cell division in the stalked bacterium *Caulobacter crescentus* [57••].

CckA-ChpT-CtrA is also a regulator of cell division in several other *Alphaproteobacteria*, including the plant symbiont *Sinorhizobium meliloti* and the zoonotic pathogen *Brucella abortus*. In *S. meliloti*, it further appears to have an important role in cellular differentiation into nitrogen-fixing bacteroids, and in *B. abortus* for efficient infection of phagocytic cells [58–60].

The response regulator CtrA is essential in most, if not all, members of the *Caulobacterales* and *Rhizobiales* including *Caulobacter crescentus*, *Brucella abortus*, *Sinorhizobium meliloti* and *Agrobacterium tumefaciensis* [56•,58,60–63]. In contrast, CtrA is not essential among members of the *Rhodobacterales* and *Rhodospirillales* including *R. capsulatus*, *Rhodobacter sphaeroides*, *Ruegeria* sp. KLH11, *Rugeria* sp. TM1040, *Dinoroseobacter shibae*, *Magnetospirillum magneticum* and *Rhodospirillum centenum* [19•,42,64–68].

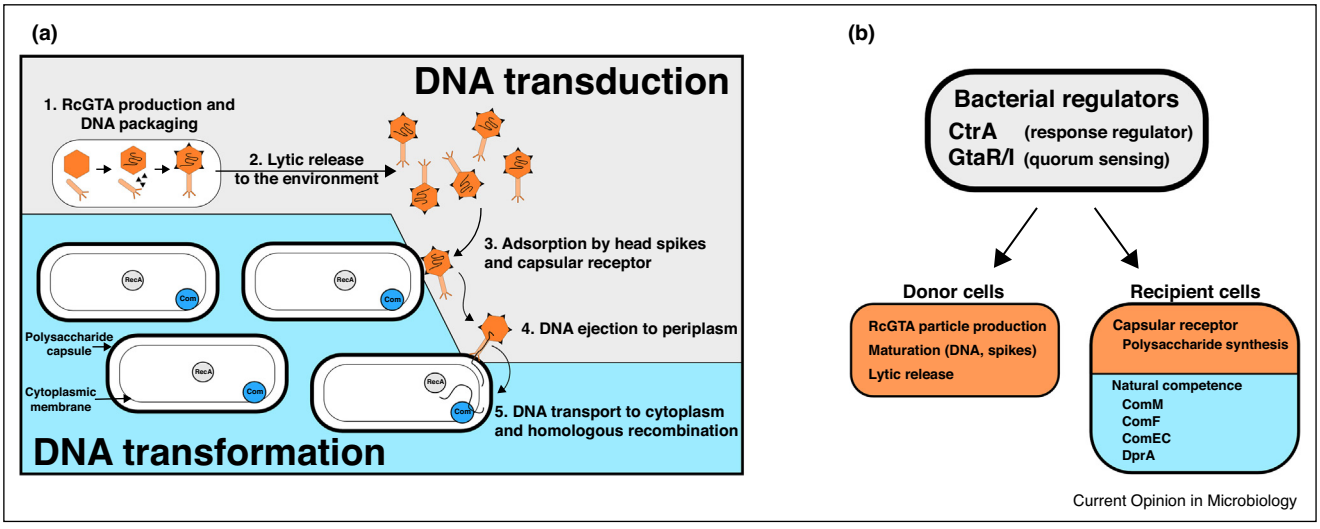
CtrA activity is highly regulated in *C. crescentus* and several additional regulators of CtrA activity have been described: phosphorylation of CtrA by CckA is controlled by response regulators and kinases, including DivL, DivK and PleC, and the CtrA protein is proteolytically degraded by ClpXP (for recent reviews, see Refs. [57••,69]).

The RcGTA-like gene transfer agents of the *Alphaproteobacteria*

The term 'gene transfer agent' was coined by Barry Marrs to describe the unknown agent responsible for genetic exchange in *Rhodobacter capsulatus* [9•]. This gene transfer was strain-dependent and was later shown to be carried out by a small, tailed phage-like particle that contains approximately 4.5 kb of essentially random DNA derived from the genome of *R. capsulatus* [10•,11,12••]. It is believed that RcGTA DNA is packaged by a headful mechanism [10•,13–15].

RcGTA production is highest in the stationary phase of laboratory cultures [16], but only a small subset of the cell population (quantified to between ~0.1% to 3%) produces RcGTA based on single-cell experiments [10•,17•]. Whether a cell will produce RcGTA appears to be

Figure 1



Regulated DNA transfer by RcGTA combines aspects of transduction and transformation.
(a) The model for DNA transfer by RcGTA combines aspects of both transduction (orange) and natural transformation (blue). RcGTA produced by a small subpopulation of the cells transfer DNA to the cells capable of receiving RcGTA-donated DNA (the majority of cells): 1. A donor cell turns on production of RcGTA proteins that assemble into a phage-like structure containing a random segment of genomic DNA. 2. RcGTA particles are released by cell lysis to the environment. 3. Head spikes on RcGTA facilitate adsorption to capsule-coated recipient cells. 4. DNA is ejected from RcGTA into the periplasm of a recipient cell. 5. DNA is transported to the cytoplasm and recombined into the genome using natural competence-like proteins (Com) and RecA. **(b)** Bacterial regulators control both RcGTA production (DNA donation) and the ability of cells to receive DNA donated by RcGTA (recipient capability). The CckA-ChpT-CtrA phosphorelay and/or GtaR/I quorum sensing system control(s) production and release of RcGTA particles in donor cells, and the production of a capsular polysaccharide receptor and natural transformation-like proteins in recipient cells.

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