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REVIEW PAPERS

Distant Interactions in Bacteria

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Abstract—Exchange of information between bacteria via physical signals, referred to as "distant interactions" (DI), is the subject of this review. All cases of DI reported to date are discussed, as well as the history of these studies and the place of DI in bacterial communication. Bacterial DI are a particular case of DI occurring in nature (in plants, animals, and fungi). Along with the chemical signals of intracellular communications, DI play a significant role in the life of microorganisms, especially during critical and transitional periods.

Key words: distant interactions, transmission of information, bacteria

Like other living organisms, bacteria can glean and process information about both the living and inanimate environment. Perception and adequate responses to various ambient physicochemical parameters are well studied in bacteria [1, 2]. Three ways of exchanging information (*communication*) between living subjects are known [3]. *Chemical communication*, mediated by chemical compounds, is the best studied of all [4, 5]. Mechanical, or *contact* communication, has been little investigated in bacteria. The third way is the communication *through physical fields*, also referred to as communication involving distant interactions [6], mitogenetic radiation [7], secondary biogenic radiation [8], or physical signals [9]. Unlike in higher organisms, this mode of communication was little studied in bacteria. Moreover, some researchers doubt the corresponding findings and consider the very possibility of such communications questionable [10, 15, 45]. The arguments against the transmission of physical signals between bacteria will be discussed further. However, since A.G. Gurwitsch and coworkers described the phenomenon of mitogenetic radiation in the 1920s [7, 12, 19], numerous studies have demonstrated that bacteria communicate between themselves and with other organisms by means of physical fields. However, the reports were often separated by considerable time intervals; many were published in nonmicrobiological journals and were written in German or French, which are nowadays not very popular within the scientific community. For these reasons, data on the bacterial communication by means of physical fields should be pooled together and reviewed, which is the goal of this work. The only recent review, published in 1994 [11], was extremely brief. I have also reviewed the works published from 1994 through 1999.

The terms used for the description of the communication through physical fields need to be considered first. An *emitter* is the source of a radiation signal. A *detector* is the organism sensitive to a signal. By the response of the detector, the signal itself can be revealed and its biological implication can be evaluated. At present, the use of biodetectors is the only way through which one can prove the existence of an exchange of information between organisms. *Distant interaction* (DI) [6] is the interaction between organisms that are distant from each other. It is implied that, in higher organisms, the organs specialized in the perception of information are not involved in DI; in microorganisms, DI is not chemically mediated. The signal is meant to be transmitted through physical fields (this term is the most appropriate).

ON THE HISTORY OF THE PROBLEM

In the 1920s, A.G. Gurwitsch and his school were the first to predict and then demonstrate that living organisms exchange information by means of physical fields. These researchers used onion roots as biodetectors to show that growing roots emit some rays stimulating cell division (mitoses) in the roots of another plant not far from the first one [12]. The novel radiation was denoted *mitogenetic radiation* (MGR), i.e., mitoses-generating radiation. Gurwitsch's discovery stimulated extensive investigations of the novel phenomenon in his own and other laboratories of the Soviet Union and throughout the world. By 1940, more than 600 reports had been published [11]. MGR proved to be an extremely weak ultraviolet light with an intensity of several tens of photons per second and a wavelength from 200 to 300 nm [7]. Even at that time, such a weak UV light could be detected instrumentally (Geiger pulse counter), although on the limits of the resolving power. Only the method of biodetectors was adequate to evaluate the biological implication of MGR. With onion roots serving as detectors, it was found that MGR is emitted by plant seedlings, insect and sea urchin eggs, hydra cells, frog and mammalian blood, dissected muscles, bacteria, and yeast. In total, more than 30 bio-

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logical objects from all kingdoms were examined [13]. Thus, the novel radiation was not species specific, but rather a universal means of communication between living organisms of various taxonomic groups. Yeast became thereafter the most convenient MGR detector [7, 13]. For a short time, the role of MGR in bacterial life was also under study (see the following section of this review). It was soon found that MGR has an effect not only on cell division; it also causes changes in the morphology, biochemistry, and growth rate of organisms [13]. It should be noted that, although there were numerous reports in support of MGR, some authors questioned this phenomenon and considered it "pathologic" [14]. In 1937, Hollander and Claus published a fundamental study against MGR [10]. Some authors believe that it was exactly this publication that caused the interest in MGR to wane [11]. More likely, however, this was a consequence of the onset of the Second World War: the bulk of these studies was conducted in the Soviet Union and Germany.

In the postwar period, MGR investigations resumed. The physical aspect of MGR was extensively studied [17]; the existence of the electromagnetic radiation of living objects was confirmed by the methods available, and its unique physical properties were reveled (coherence) [18]. In the Soviet Union, investigations were continued in A.G. Gurwitsch's laboratory [19]; several reports on the MGR phenomenon were published [20]. In the 1980s, MGR was extensively studied at the Departments of Embryology and Bioorganic Chemistry of the Biological Faculty of the Moscow State University [21]. In our country, the studies of the communication between living organisms by means of physical fields went far beyond the scope of *mitosis*-stimulating radiation. Note that A.G. Gurwitsch pointed out that MGR is not a very appropriate term; it was coined according to the phenomenon which was the first to be revealed (stimulation of mitoses). This phenomenon in fact includes an entire class of various radiations with diverse biological effects [7]. Physical fields were found to induce various pathological changes in the tissue cultures of higher animals. Not only UV, but also visible light, IR, and radiowaves [6, 22] were found to form the basis for these fields. Thus, the concept of MGR merged with that of secondary biogenic radiation (SBR) [8]. The first postwar report on DI in bacteria also appeared in our country [23].

However, some researchers failed to reveal the biological effects of the radiation emitted by growing cultures (the idea of the radiation itself was not rejected). In the 1970s, Qhickenden and Tilbury failed to detect the exchange of information between *Saccharomyces cerevisiae* cultures [15], although they did find that these cultures emitted weak UV and visible light [16].

A REVIEW OF EXPERIMENTAL STUDIES WITH BACTERIA

Since pertinent experimental studies are not numerous, they will be discussed in chronological order. Some reports that are not easily accessible will be considered as they are cited in the comprehensive Rahn's review [13].

Soon after Gurwitsch's discovery, extensive studies of bacterial MGR were launched. Baron's report was published in 1926 [24], and several more appeared soon after [25–27]. Sewertzowa found that the MGR emitted by a *Nadsonia* yeast culture caused a 13 to 120% increase (27% on average) in the population density of *Bacillus mesentericus* and *B. lactis aerogenes* cultures (as compared to control cultures) during 2 to 3.5 h of incubation [25]. It should however be noted that in three out of fourteen experiments, the values were lower than in the controls. Table 1 presents the results of four experiments. Similar results were obtained by Acs, who used *Bacillus murimoris* as a detector culture [26]. The emitter culture was either *Bacillus murimoris* grown on solid medium or a yeast culture, which produced a lesser effect. The effect of a culture on a detector culture of the same species was referred to as *mutoinduction.* I think that it is convenient to term the radiation producing an effect on a culture of the same species *isogenic MGR* and of a different species—*xeno-* or *heterogenic* MGR. When liquid media, especially nutrient broth one has to use thin culture layers (< 1 mm) and diluted media (1 : 10), because of the high UV absorption characteristic of water and organic compounds. An important observation was made by Wolff and Ras [27], who used *Staphylococcus aureus* both as an emitter and detector. These authors revealed no stimulating effect of an exponential-phase detector culture, whereas lag-phase cells produced maximal effect. They also revealed the effects of "exhaustion" and "overradiation," when growth of a culture permanently exposed to MGR was initiated earlier than that of the control one, although, subsequently, its growth decelerated so that the control culture growth was ahead. This is the reason why many researchers failed to reveal the MGR effect [10, 15]: they tried to detect a difference between the experimental and control cultures when this difference had already disappeared. In addition, Wolff and Ras showed that the effect of MGR directly depended on its intensity. As the distance between the emitter and detector cultures diminished from 12.5 to 2 cm, the lag phase was reduced from 1 to 0 h (the lag phase of the control culture lasted for 2 h, Table 2). This example well illustrates that the effect of MGR is capricious, with a consequent low reproducibility of the results.

Ferguson and Rahn studied isogenic irradiation of *Bacillus coli* [28]. MGR had no effect on a detector culture grown for less than 24 h, whereas 2- to 3-day-old cultures always responded to MGR. In addition, MGR caused an effect only in diluted cultures (< 100000 cells/ml). The authors had also found that a maximal MGR effect was

Table 1. Effect of irradiation of a *B. mesentericus* culture through a quartz glass by a yeast culture placed at a distance of 12 mm; four different experiments (cited from [25])

Experiment no.	Incubation time, h	Cell concentration, thousand cells/ml			Effect, %
		initial	control	irradiated	
1	2	3168	11440	18290	60
2	2.5	528	7920	8976	13
3	3	4048	12496	16016	28
4	3.5	1584	10912	13552	24

observed after exposition for an optimal time (Table 3). The *effect of induction* (a percent ratio of the difference between the experimental and control values to the control values) was calculated from the data of Table 3.

As can be seen from the results in Table 3, the value of the MGR effect depended considerably on the mode of calculation: when calculated from the cell concentration, the MGR effect observed after a 15-min irradiation was 183%; when calculated from the doubling time, the same effect comprised only 27%.

In 1929, Christiansen had revealed morphological changes in yeast and bacteria subjected to the radiation of blood [29]. A recipient suspension was placed as a hanging-drop preparation above the emitter blood drop. Under the influence of MGR, the cells of *Bacterium coli* became three to five time longer; cells of *Bacterium vulgare* lost their capsule; and cells of *Lactobacillus bulgaricus* ceased division and grew as long filaments. Two streptococcal species, *S. lactis* and *S. cremoris* displayed no morphological changes. Rahn and coworkers had observed similar morphological changes in yeast and bacteria under the influence of saliva and plant MGR [30, 31].

As early as in the very first years of MGR study, some authors revealed its effect on yeast metabolism [32]. Gesenius detected an inhibition of respiration and stimulation of fermentation in a system yeast–yeast incubated for 4 h [32]. Reproducible positive results were observed in 70% of experiments; in 2 to 4% of experiments, the results were negative.

Thus, such important properties of MGR were described in the first years of its study: (1) MGR is an extremely weak UV light; (2) the emitters provide important information to the detectors (MGR regulates gene activity mitotic activity, in particular, and has an effect on cell metabolism and morphology); (3) MGR is universal and not species-specific: it was found in organisms of all taxonomic levels and causes cross-effects; (4) MGR is a capricious phenomenon dependent on many known and unknown factors.

As mentioned above, the number of reports published on the communication of organisms through physical fields dropped at the end of the 1930s. In the postwar time, some researchers (A.A. Gurwitsch) resumed these studies. In the 1970s, a number of new researchers took part in the investigation of this problem [15–23], including the effect of MGR on microorganisms.

Some authors used a device that may be designated as a "flask-in-flask." The emitter culture was placed in a big flask, whereas a smaller flask fixed within the big flask contained a recipient culture. The neck of the inner flask was either outside of the device [23], or tightly closed [35]. Liquid media were used for culture growth.

A culture of *Vibrio costicola* dying off because of the addition of an antibiotic was found to stimulate the growth of another culture of the same species that was in the neighboring compartment separated by quartz glass [23], which allowed any kind of electromagnetic waves to serve as a signal. The biomass increment was low (from 3 to 11%, 6 ± 2% on average) but reliable. Since the recipient culture passed through several developmental phases during the experiment, it is unclear whether MGR had an effect on the adaptation of the culture, or growth, or dying off.

DI were also found to occur between the bacterium *Pseudomonas corrugata* and the fungus *Gaeumannomyces graminis* [33]. The authors observed stimulation of bacterial development (as determined from chemiluminescence) in the presence of a growing fungal culture. This effect was recorded only if the cultures were separated by quartz but not by ordinary glass. This suggests that UV light served as the signal. The magnitude of the stimulating effect varied considerably (from sev-

Table 2. Effect of radiation emitted by *Staphylococcus aureus* on the growth of a culture of the same organism as dependent on the distance between the emitter and detector and duration of irradiation (cited from [27])

Incubation time, h	Cell concentration, cells/ml			
	control	12.2 cm	5.5 cm	2 cm
0	31200	31200	31200	31200
1	31400	32200	39700	50200
2	32100	55700	54000	48800
3	45000	57600	51700	46800
4	133000	128500	117000	51200
5	262000	237000	135000	79200

Table 3. Effect of radiation of a *B. coli* culture on the cell concentration and doubling time of a culture of the same bacterium (min; calculated for 2–6 h of growth) (cited from [28])

Incubation time, h	Cell concentration, cells/ml, $\times 10^4$					
	Control no. 1	Control no. 2	Exposition time, min			
			60	30	15	7.5
0	5050	6550	5650	6800	7250	6250
2	5700	7000	5800	7950	7750	5850
3	–	8500	11000	14350	14400	8300
4	23750	19550	24250	29000	35350	19150
6	188000	137000	223000	434000	457000	139000
Induction effect, %			37	168	183	–16
Doubling time	47.6	56	45.5	41.5	40.8	52.5
Induction effect, %			14	25	27	–1

eral percent to a 30-fold increase). Moreover, the effect was not always reproducible (it occurred only in two out of seven repetitions). According to high scientific standards these results should be considered negative; however, the authors insist that they revealed DI between bacterial and fungal cultures. These two reports [23, 33] seem to have escaped notice.

The most impressive results were obtained by Matsuhashi and coworkers [9, 34–37]. These authors used *Bacillus carbonifillus* cultures grown on solid media either on the same agar plates or in different Petri dishes placed close together or apart. Spore germination and development of this bacteria under unfavorable conditions (1% KCl and high temperature, 44°C) proved to be stimulated manifold under the influence of a physical signal transmitted from well-growing cultures of the same or other bacterial species. The efficiency of spore germination under unfavorable conditions reached 100% (!), whereas in the absence of physical signals, spore germination was not observed at all. Unfortunately, the excellent and convincing illustrations from this report cannot be reproduced in this review. The unfavorable effect of antibiotics, such as erythromycin and streptomycin, could also be reduced in the presence of another culture. The physical signals were transmissible through the air (over a distance of up to 40 cm), as well as through glass, plastic, or iron barriers (up to 2 mm thick). Using *B. carbonifilus* serving as the biodetector and well-growing cultures of *B. subtilis, Escherichia coli*, and *Micrococcus luteus* as emitters, organisms of various species were demonstrated to communicate each other by means of physical signals. Moreover, the authors also found that carbon materials, such as graphite and activated charcoal (but not diamond) promoted the growth of bacterial cells even in the absence of living biomass! [36]. The authors suggested that the physical factor involved was of sonic nature. However, this conclusion has been severely criticized [38]. Note that an enhanced stimulating effect of the emitter culture on the recipient culture was observed when they were both placed in a small acrylic box. This issue will be discussed below. Since the authors anticipated that many researchers would be skeptical about their findings, they asked researchers from independent laboratories to repeat their experiments; this has been successfully performed [35].

In my recent report, I describe DI in a culture of *Pseudomonas fluorescence* [39]. In a "flask-in-flask" device, the DI effect on cell adhesion to glass was studied: the number of adhered and nonadhered free cells was determined. Not only the effect of DI but also the effect of volatile chemical substances transferred with air was studied. The number of nonadsorbed cells increased two- to thirtyfold (ninefold on average) due to exchange by chemical and physical signals between the emitter and recipient cultures (Table 4). No changes were found in the maximum specific growth rate or cell yield; the moment when the cells began to leave the glass did not change either.

A gaseous compound denoted volatile antiadhesin (VAA) caused a 6% decrease in cell adhesion; the number of nonadhesive cells increased by 10% (Table 4) [39].

When the emitter culture was separated from the recipient culture by both the flask glass and a rubber membrane so that the possibility of air exchange between the two cultures was eliminated, the number of adhesive cells increased by 50%.

These results suggest a synergistic effect of DI and chemical modulators.

The biological implication of DI revealed in this study lies in the fact that nonadhesive cells allow dissemination of the *P. fluorescence* population, although such cells are vulnerable to unfavorable factors. An equilibrium between adsorbed and nonadsorbed cells is important for the development, survival, and distribution of the population and the species in general. Both DI and chemical modulators are involved in sustaining this equilibrium. I was also able to reveal a positive effect of dead (autoclaved) cells on the number of free-

floating, nonadhered cells in the *P. fluorescence* recipient culture. This is consistent with the data of Matsuhashi and coworkers, who revealed the effect of inanimate carbon-containing materials on spore germination.

The fact that inanimate objects can also produce physical signals is consistent with the pioneering data obtained by A.G. Gurwitsch when he used solutions of various substances as a source of MGR [7]. In addition, this indicates that the DI of living objects is only a particular case of their perception of the environmental electromagnetic emission. This conclusion is consistent with Kuzin's suggestion that the natural radioactive background is a necessary condition for the normal functioning of living organisms [8].

As for the nature of DI revealed in a culture of *P. fluorescens*, a conclusion can be inferred that the physical signals were not mediated by UV light, since flasks made of ordinary glass rather than quartz glass were used in the experiments.

The list of publications concerning DI in bacteria is now over.

Thus, in postwar reports, the following additional characteristics of DI were revealed: (1) not only UV light can serve as physical signal, but also electromagnetic waves of visible and IR light [22, 39] and, possibly, acoustic waves [35]; (2) a synergistic effect of DI and volatile chemical compounds was revealed; i.e., DI are promoted by the presence of these compounds; (3) inanimate objects can also serve as a source of physical signals.

Some questions related to the DI problem should be discussed in more detail.

On the Biological Implication of DI

At first glance, it would seem that the biological role of DI is clear: it is an exchange of information and regulation. However, what are the processes regulated by DI? All cases of DI in bacteria revealed so far suggest that the role of DI is especially important during various transitions and critical periods, when cells have to overcome some problems. A pronounced effect of DI was revealed, e.g., after the transfer of old cells into a fresh medium [27, 28] (note that Wolff and Ras [27] failed to detect any effect of MGR when they used exponentially growing cells). Other examples include spore transfer to a fresh medium under extreme conditions [9, 34–37] (this model has been the most successful for revealing DI in bacteria) and adhesion–detachment of bacteria occurring in a novel habitat [39]. The morphological changes reported by some authors [29–31] can also be described as occurring under unfavorable (experimental) conditions.

Note that all attempts to reveal DI using recipient cultures growing under favorable conditions gave either negligible positive results [25, 26] or negative and insignificant results [10, 15, 33].

Table 4. Effect of the culture air and distant interactions on the number of adhered and nonadhered cells in a *P. fluorescens* population [39]

	Only VAA*	Only DI	Both factors
Decrease in adhesion	6	4	13
Increase in the number of nonadhesive cells	10	50	900

* Data in this column are from [40].

Synergistic Effect of DI and Chemical Modulators

All data reported demonstrate that the effects of DI and chemical modulators are synergistic. Thus, in the experiments of Matsuhashi and coworkers the maximal effect of DI was observed in the presence of some amount of the culture's air. When Petri dishes with "emitter" and "recipient" cultures were placed in a small acrylic box [35], a pronounced DI effect was observed. Note that when a growing culture is placed into an enclosed volume, the concentration of gaseous compounds released by this culture inevitably increases.

This property of DI has a considerable biological implication. Indeed, under conditions that are unfavorable but still permit growth (nutrients are available, etc.), the cell (or the spore) has to assess the degree to which the conditions are adverse and decide whether to grow further of wait for better times. The best evidence that the medium is adequate for growth (although the conditions are not optimal) is the presence of a neighboring growing culture. Signals from the latter can be physical and chemical. Since these signals may be weak, their concomitant occurrence is more informative, hence the synergistic effect.

Stempel was the first to suggest a combined effect of a volatile chemical signal and a physical one, although this suggestion was not supported experimentally [41]. Now, this suggestion has been proved. Strictly speaking, in none of the works published had the possibility been excluded that the researchers actually dealt with a combined effect of MGR and chemical modulators. Thus, in the first prewar works, emitter and detector cultures were placed not far from each other, so that the exchange of air was possible. Recently, gaseous hormones active at extremely low concentrations (10^{-9} M) have been described [42]. Such substances can easily pass from an emitter to the biodetector.

The synergistic effect of DI and chemical modulators can help explain the results of the experiments in which a mirror placed near the object produced a certain biological effect (e.g., on the developing eggs of fish and frogs [43]). I have also found that, when flasks with a growing culture of *P. fluorescens* were wrapped in foil, the number of nonadhesive cells increased [39]. Indeed, developing organisms produce chemical mod-

ulators and MDR, which is reflected by the mirror, simulating the presence of a neighboring population. Thus, both chemical and physical signals are present in the experiments with a mirror.

The Problem of the Validity of the Experiments on DI

One must be keenly aware of the validity problem when experiments with DI are discussed. In none of the studies (except for those performed by Japanese researchers) did the reproducibility of the results reach 100%. The results obtained were extremely variable (several times [33, 39]). The experiments had to be repeated many times to obtain the 95% level of significance commonly accepted in biological studies. Sometimes different experimental series differed by a value similar to the difference between control and experiment. This situation requires the use of the nonparametric Wikinson and sign criteria [23, 39]. Moreover, in some periods of time, these experiments were not reproducible [6, 13]. For these reasons, DI was denoted as a "pathologic effect" by some authors [11, 14]; others doubted the very existence of the DI phenomenon [10, 15].

On the Nature of the Emission

This problem has been well studied and the fact that all biological objects are surrounded by various physical fields is now beyond doubt. From the very beginning, Gurwitsch and other researchers demonstrated that the mitogenetic signal is transmitted by UV light [7]. In postwar time, this conclusion was supported by modern methods in the studies of Quickenden, Popp, and other researchers [16, 17, 44]. The cells were found to emit not only UV but also visible and IR light; this is clearly demonstrated by the experiments using flasks of ordinary glass [39]. Japanese researchers believe that acoustic signals are also involved in DI [9, 34–37].

Perspectives in DI Investigations

With the development of new methods for the study of bacterial fields, one might expect that the parameters of these fields will be used to describe the bacterial state, just as MGR can be used to characterize tissues of the higher organisms [7, 19, 21] and the physiological state of yeast [16]. The study of DI in bacteria may become a fascinating area of investigation and will find its practical applications. Investigations of distant interactions and their biological effects will be an important part of these studies.

Thus, the fact that bacteria communicate each other by means of physical fields is now beyond doubt. The reasons for the unsuccessful attempts by some authors to reveal DI are now clear: they are use of inadequate testing systems (test systems that are not in a critical state) and the occurrence of certain yet uncontrolled factors that affect the ultimate results.

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