On the Analysis of Bacterial Cooperation with a Characterization of 2D Signal Propagation

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Abstract—The exchange of small molecular signals within microbial populations is generally referred to as quorum sensing (QS). QS is ubiquitous in nature and enables microorganisms to respond to fluctuations of living environments by working together. In this work, a QS-based communication system within a microbial population in a two-dimensional (2D) environment is analytically modeled. Notably, the diffusion and degradation of signaling molecules within the population is characterized. Microorganisms are randomly distributed on a 2D circle where each one releases molecules at random times. The number of molecules observed at each randomly-distributed bacterium is analyzed. Using this analysis and some approximation, the expected density of cooperating bacteria is derived. The analytical results are validated via a particle-based simulation method. The model can be used to predict and control behavioral dynamics of microscopic populations that have imperfect signal propagation.

I. INTRODUCTION

A. Motivation

The number and variety of microorganisms are vast and they exist all over the earth, in and on living creatures, underground, and underwater [1]. Quorum sensing (QS) is a ubiquitous approach for microbial communities to detect and respond to the cell population density by coordinating behavior. For example, QS enables bacteria to work together by gene regulation to maximize their benefits (e.g., food and resources) when the density of bacteria is high. That is to say, the benefit from cooperation is only higher than being selfish if a minimal number of neighbouring bacteria is present. This is because cooperation is costly, e.g., cooperative bacteria consume energy to produce exofactor for gene regulation [2]. In QS, bacteria assess the number of other bacteria they can interact with by releasing and recapturing the molecular signal in the environment, as shown in Fig. 1. This is because a higher density of bacteria leads to more molecules that can be detected before they diffuse away.

Microscopic populations utilize QS to coordinate many collective behaviors, such as virulence, bioluminescence, biofilms, and the production of antibiotics. These behaviors play a crucial role in bacterial infections, environmental remediation, and wastewater treatment [3]. Since the QS process is highly dependent on signaling molecules, the accurate characterization of releasing, diffusion, degradation, and detection of such molecules is very important to understand and control QS, which can help us to prevent undesirable bacterial infections and lead to new environmental remediation methods [4].

B. Related Work

There are growing research efforts to study QS. Among them, [1, 5–9] mathematically modeled the bacterial interactions. [1, 5] considered a queueing model to analyze the dynamics of bacterial interaction. [6] considered an optimization-based framework to study QS as a networked decision system. [7] proposed a simple game to predict cooperation in bacterial population under population uncertainty. [8] introduced a game-theoretic model to show how individual links in a bacterial network could form. [9] studied the effects of cooperation and uncertainty on communication efficiency within a nanoscale network. Although [1, 5–9] stand on their own merits, we use a more sophisticated signal propagation model than [1, 5–9] by characterizing the propagation of signaling molecules. Modeling the signal propagation and analyzing the responsive behaviors of a spatially distributed microbial population is interesting yet computationally and analytically challenging.

C. Contributions

Despite the aforementioned challenges, we analytically model a QS-based communication system in an unbounded two-dimensional (2D) environment by characterizing the diffusion and degradation of signaling molecules. We consider bacteria that are randomly spatially distributed on a circle
according to a point process. Point processes are commonly used to model randomly-distributed locations, e.g., [10] used a homogeneous Poisson point process (PPP) to model locations of nano-transmitters and [11] used a PPP to model locations of bacterial populations. We also assume that each bacterium acts as both a point transmitter (TX) and a circular observer, which captures the features of emission and reception of QS molecules. Since bacteria may not emit molecules at fixed times, each bacterium continuously emits molecules according to a random process. Bacteria make decisions when they observe a stable molecule concentration (i.e., asymptotic observation). Due to random molecule release times and asymptotic observations at bacteria, perfect time synchronization is not required for tractability of our analytical results, although this is a widely adopted unrealistic assumption in the MC literature [12].

We consider a 2D environment since the theoretical results of molecular communication must be validated experimentally [12]. Biological experiments, especially with bacteria, are usually conducted in a 2D environment, e.g., bacteria residing on a petri dish and the formation of biofilms [13]. Therefore, the consideration of a 2D environment facilitates future experimental validation of our current theoretical work. Our contributions are summarized as follows:

1) We analytically derive the asymptotic channel response (i.e., the expected number of molecules observed) at a circular RX due to continuous emission of molecules at a) one point TX and b) randomly-distributed point TXs on a circle in a 2D environment.

2) We derive an approximate expression for the expected density of cooperative bacteria by first analytically deriving the asymptotic channel response at each bacterium.

3) We validate the accuracy of our analytical results via a particle-based simulation method where we track the motions of signaling molecules over time due to diffusion and degradation.

We emphasize that contribution 1) can generally be applied to any context where a TX is continuously releasing molecules into a 2D environment.

D. Notations

We use the following notations: $|\hat{x}|$ denotes Euclidean norm of vector $\hat{x}$. $\bar{N}$ denotes the mean of $N$ and $E\{N\}$ denotes the expectation of $N$ over a spatial random point process. $K_n(Z)$ denotes modified $n$th order Bessel function of the second kind.

II. System Model

We consider an unbounded two-dimensional (2D) environment and a population of bacteria existing on a circle $S_1$ with radius $R_1$ centered at $(0,0)$. We consider that bacteria are spatially distributed on the circle according to a 2D point process (e.g., PPP) with constant density $\lambda$, as shown in Fig. 2. We denote $\bar{x}_i$ as the location of the center of the $i$th bacterium. We denote $\Phi(\lambda)$ as the random set of bacteria locations.

We consider that bacteria try to maximize their benefits by deciding whether to cooperate. We assume that the bacteria closer to $(0,0)$ are more likely to cooperate than those further away from the population center. This is because as bacteria approach the population center, they are surrounded by more bacteria and are more likely to obtain a higher reward from cooperation. As shown in Fig. 3(a), a bacterium receives more signaling molecules when it is closer to the population center. Inspired by this observation, we assume that bacteria estimate their position relative to $(0,0)$ by detecting the signaling molecules. In the following, we detail the emission, propagation, reception, and detection of signaling molecules, and decision marking by the bacteria.

Emission: We model bacteria as point TXs. The $i$th bacterium continuously emits $A$ molecules from $\bar{x}_i$ at random times according to an independent random process, e.g., continuous Poisson process, with constant rate $q$ molecule/s, as shown in Fig. 4.

Propagation: All $A$ molecules diffuse independently with constant diffusion coefficient $D$ and they can degrade into a form that cannot be detected by the bacteria via a reaction.
mechanism that can be described as
\[ A \xrightarrow{k} 0, \]
where \( k \) is the reaction rate constant in \( \text{s}^{-1} \). If \( k = 0 \), then this degradation is negligible. Since we consider a single type of molecule, we only mention “the molecules”, instead of “A molecules” in the remainder of this paper.

**Reception:** We model the \( i \)th bacterium as a circular receiver (RX) with radius \( R_0 \) and area \( S_0 \) centered at \( \vec{x}_i \). We model the bacteria as passive observers since the analytical expression of hitting rate for an absorbing RX in a 2D environment does not exist in current literature [12]. We assume that bacteria perfectly count A molecules if they are within \( S_0 \). Since the molecules released from all bacteria may be observed by the \( i \)th bacterium, the number of molecules observed at the \( i \)th bacterium at time \( t \), \( N_{\text{agg}}^i (\vec{x}_i, t|\lambda) \), is given by
\[
N_{\text{agg}}^i (\vec{x}_i, t|\lambda) = \sum_{\vec{x}_j \in \Phi(\lambda)} N (\vec{x}_i, t|\vec{x}_j),
\]
where \( N (\vec{x}_i, t|\vec{x}_j) \) is the number of molecules observed at the \( i \)th bacterium at time \( t \) due to the \( j \)th bacterium. The mean of \( N_{\text{agg}}^i (\vec{x}_i, t|\lambda) \) and \( N (\vec{x}_i, t|\vec{x}_j) \) is denoted by \( \bar{N}_{\text{agg}}^i (\vec{x}_i, t|\lambda) \) and \( \bar{N} (\vec{x}_i, t|\vec{x}_j) \), respectively.

**Detection and Decision Making:** We assume that the expected number of molecules observed at the \( i \)th bacterium is constant after some time; as an example to illustrate the mechanism that can be described as
\[
A \xrightarrow{k} 0,
\]
where \( k \) is the reaction rate constant in \( \text{s}^{-1} \). If \( k = 0 \), then this degradation is negligible. Since we consider a single type of molecule, we only mention “the molecules”, instead of “A molecules” in the remainder of this paper.

In this section, we derive the channel response, i.e., the expected number of molecules observed at RX, due to continued transmission of molecules from TX(s), in the following cases: 1) a point TX and 2) randomly distributed TXs. These analyses lay the foundations for our derivations of the observations at bacteria and expected density of cooperators in Sec. IV.

To derive the channel response due to continuous emission, we first review the channel response at the point defined by \( \vec{r} \) at time \( \tau \) due to an impulse emission of one molecule from the point at \( (0, 0) \) at time \( \tau = 0 \) in an unbounded 2D environment based on [14, Ch. 4], which is given by
\[
C (\vec{r}, \tau) = \frac{1}{(4\pi D \tau)} \exp \left( -\frac{|\vec{r}|^2}{4D \tau} - k \tau \right).
\]

We next derive the asymptotic channel response based on (5) and we assume that the RX is a circular passive observer \( S_0 \) centered at \( \vec{b} \) with radius \( R_0 \).

**A. One Point TX**

In this subsection, we present the asymptotic channel response due to one point TX. We also present the special case when the TX is at the center of the RX, since each bacterium receives the molecules released from not only other bacteria but itself. We finally simplify the asymptotic channel response using the uniform concentration assumption (UCA) [15].

1) **Any \( \vec{b} \):** The asymptotic channel response can be obtained by multiplying \( C (\vec{r}, \tau) \) by the emission rate \( q \), integrating over \( S_0 \), and then integrating over all time to infinity. By doing so, the asymptotic channel response at the circular RX with radius \( R_0 \) centered at \( \vec{b} \), due to continuous emission with rate \( q \) from the point \((0,0)\) since time \( t=0 \), is given by
\[
\bar{N} (\vec{b}) = \int_{r=0}^{\infty} \int_{\theta=0}^{2\pi} q C (r_1^* \vec{r}, \tau) r d\theta dr d\tau,
\]
where \( B (\vec{x}_i) \) is the decision of the \( i \)th bacterium, “1” denotes cooperation, and “0” denotes non-cooperation, and \( \eta \) is a decision threshold. For compactness, we remove \( \infty \) in all notation in the reminder of this paper since we assume that bacteria use asymptotic observations to make decisions.
2) $|\tilde{b}| = 0$: We have the following theorem:

**Theorem 1**: The asymptotic channel response at the circular RX with radius $R_0$, due to continuous emission with rate $q$ from the center of this RX since time $t = 0$, is given by

$$
\mathbb{N}_{self} = \lim_{|\tilde{b}| \to 0} \mathbb{N}(\tilde{b}) = q/k \left( 1 - \sqrt{kR_0 K_1 \left( \sqrt{k/D} R_0 / \sqrt{D} \right)} \right). \tag{7}
$$

**Proof**: The proof is given in the Appendix.

3) UCA: We simplify (6) by assuming that the concentration of molecules throughout the circular RX is uniform and equal to that at the center of the RX. This assumption is accurate if $|\tilde{b}|$ is relatively large and thus it is inaccurate when $|\tilde{b}| = 0$. Using this assumption, we rewrite (6) as

$$
\mathbb{N}(\tilde{b}) = \pi R_0^2 \int_{\tau = 0}^{\infty} q c \mathbf{r}(\tilde{b}, \tau) d\tau. \tag{8}
$$

We then employ [16, Eq. 3.471]

$$
\int_{0}^{\infty} x^{\nu - 1} \exp \left( -\frac{\beta}{x} - \gamma x \right) dx = 2 \left( \frac{\beta}{\gamma} \right)^{\frac{\nu}{2}} K_{\nu}(2\sqrt{\beta \gamma}), \tag{9}
$$

to solve (8) as

$$
\mathbb{N}(\tilde{b}) = q R_0^2 / 2DK_0 \left( |\tilde{b}| \sqrt{k/D} \right). \tag{10}
$$

**B. Randomly Distributed TXs**

In this subsection, we consider that many point TXs are randomly distributed on a circle $S_1$ according to a point process with density $\lambda$. The circle $S_1$ is centered at $(0, 0)$ with radius $R_1$. We represent $\tilde{a}$ as the location of an arbitrary point TX $a$ and the random set of TXs’ locations is denoted by $\Phi(\lambda)$. We denote the channel response at the RX at time $t$ due to TX $a$ by $\mathbb{N}(\tilde{b}, t|\tilde{a})$ and the aggregate channel response at the RX at time $t$ due to all TXs by $\mathbb{N}_{agg}(\tilde{b}, t|\lambda) = \sum_{\tilde{a} \in \Phi(\lambda)} \mathbb{N}(\tilde{b}, t|\tilde{a})$.

We denote $\mathbb{E} \left\{ \mathbb{N}_{agg}(\tilde{b}, t|\lambda) \right\}$ as the expected $\mathbb{N}_{agg}(\tilde{b}, t|\lambda)$ over the point process. We next derive $\mathbb{N}_{agg}(\tilde{b}, t|\lambda)$ and then simplify it using UCA. We have the following theorems:

**Theorem 2 (Any $\tilde{b}$)**: The expected aggregate asymptotic channel response at the circular RX with radius $R_0$ centered at $\tilde{b}$, due to continuous emission with rate $q$ since time $t = 0$ from randomly distributed TXs on circle $S_1$ with density $\lambda$, is given by

$$
\mathbb{E} \left\{ \mathbb{N}_{agg}(\tilde{b}, \tau|\lambda) \right\} = \mathbb{E} \left\{ \sum_{\tilde{a} \in \Phi(\lambda)} \mathbb{N}(\tilde{b}, t|\tilde{a}) \right\}
\approx \int_{|\tau|=0}^{R_1} \int_{\varphi=0}^{2\pi} \int_{|\tilde{r}|=0}^{R_0} \int_{\theta=0}^{2\pi} \frac{q \exp \left( -\frac{\tau|\tilde{b}|^2}{4D} - k\tau \right)}{4\pi D \tau} d\varphi d|\tilde{r}| d\tilde{r} d|\tilde{r}|^2
\times K_0 \left( \sqrt{k \Omega(\tilde{b}) / D} \right), \tag{11}
$$

where

$$
\Omega(\tilde{b}) = \sqrt{\Omega(\tilde{b}) + |r_0|^2 + 2\sqrt{\Omega(\tilde{b}) |r_0|^2} \cos \theta}, \tag{12}
$$

and $\Omega(\tilde{b}) = |\tilde{b}|^2 + |\tilde{r}|^2 + 2|\tilde{b}||\tilde{r}| \cos \varphi$.

**Theorem 3 (UCA)**: Using UCA, we approximate

$$
\mathbb{E} \left\{ \mathbb{N}_{agg}(\tilde{b}, t|\lambda) \right\} \approx \int_{|\tau|=0}^{R_1} \int_{|\varphi|=0}^{2\pi} \frac{q R_0^2}{2D} \lambda |\tilde{r}| d\varphi d|\tilde{r}|
\int_{|\tau|=0}^{R_1} \int_{|\varphi|=0}^{2\pi} \int_{|\tilde{r}|=0}^{R_0} \int_{\theta=0}^{2\pi} K_0 \left( \sqrt{k \Omega(\tilde{b}) / D} \right). \tag{13}
$$

**Proof**: The proof of Theorem 2 and Theorem 3 is omitted here due to space limitation. It can be proven using Campbell’s theorem, (6), (8) and (9).

The numerical results in Sec. V will demonstrate the accuracy of the approximation of the UCA in (10) and (13).

We note that time-varying channel responses are also of interest, so we discuss them in the following remark:

**Remark 1**: It can be shown that the time-varying channel response $\mathbb{N}(\tilde{b}, t)$ and $\mathbb{E} \left\{ \mathbb{N}_{agg}(\tilde{b}, t|\lambda) \right\}$ can be obtained by replacing $\infty$ with $t$ in (6) and (11), respectively.

**IV. ANALYSIS OF BACTERIAL COOPERATION**

In this section, we aim to evaluate the expected density of cooperators over the point process, $\mathbb{E} \left\{ \lambda \right\}$, where $\lambda$ denotes the density of cooperators. To this end, we first analyze the expected aggregate asymptotic number of observed molecules at the $i$th bacterium, $\mathbb{N}_{agg}(\tilde{x}_i|\lambda)$, for a given realization of the point process.

**A. Observation of Bacteria**

We recall that the $i$th bacterium observes molecules in the environment released from all bacteria (also including the molecules released from itself). Thus, we have

$$
\mathbb{N}_{agg}(\tilde{x}_i|\lambda) = \sum_{\tilde{x}_j \in \Phi(\lambda)} \mathbb{N}(\tilde{x}_i|\tilde{x}_j) = \mathbb{N}(\tilde{x}_i|\tilde{x}_i) + \sum_{\tilde{x}_j \notin \Phi(\lambda) / \tilde{x}_i} \mathbb{N}(\tilde{x}_i|\tilde{x}_j), \tag{14}
$$

where $\mathbb{N}(\tilde{x}_i|\tilde{x}_i) = \mathbb{N}_{self}$ and $\mathbb{N}_{self}$ is given in (7). We then approximate the second term of the second line in (14) as

$$
\sum_{\tilde{x}_j \notin \Phi(\lambda) / \tilde{x}_i} \mathbb{N}(\tilde{x}_i|\tilde{x}_j) \approx \mathbb{E} \left\{ \sum_{\tilde{a} \in \Phi(\lambda)} \mathbb{N}(\tilde{x}_i|\tilde{a}) \right\}, \tag{15}
$$

where $\lambda = (\lambda \pi R_1^2 - 1) / \pi R_1^2$. In (15), we use the expected channel response over the point process to approximate the channel response under one realization of this point process. Also, we consider a new density $\hat{\lambda}$ to keep the average number of bacteria the same after the approximation of (15). Our
numerical results in Sec. V will confirm the accuracy of the approximation of (15). We further re-write (15) as
\[
\mathbb{E}\left\{ \sum_{\vec{d} \in \Phi(\lambda)} \mathbf{N}(\vec{x}_i^*|\vec{d}) \right\} = \mathbb{E}\left\{ \mathbf{N}_{agg}(\vec{x}_i^*|\lambda) \right\},
\]
where \( \mathbb{E}\left\{ \mathbf{N}_{agg}(\vec{x}_i^*|\lambda) \right\} \) can be evaluated by replacing \(|\vec{b}|\) and \(\lambda\) with \(|\vec{x}_i^*|\) and \(\lambda\), respectively, in (11) or (13).

Remark 2: We analytically find that \( \mathbf{N}_{agg}(\vec{x}_i^*|\lambda) \) converges as time \( t \rightarrow \infty \), since \( \mathbf{N}_{agg}(\vec{x}_i^*|\lambda) \) can be obtained via (11)/(13) (and (7) and they all converge with time. This analytically proves that our assumption adopted in Detection and Decision Making in Sec. II is valid, i.e., \( \mathbf{N}_{agg}(\vec{x}_i^*|\lambda) \) does not vary with time \( t \) after some time.

### B. Density of Cooperators

In this subsection, we aim to evaluate \( \mathbb{E}\{\mathbf{N}\} \). To this end, we first analyze the binary decision at the \(i^{th}\) bacterium, \( B(\vec{x}_i) \), and its mean. Based on (4), \( B(\vec{x}_i) \) is a Bernoulli random variable (RV). The mean of \( B(\vec{x}_i) \) is denoted by \( \mathbf{B}_m(\vec{x}_i) \). We evaluate \( \mathbf{B}(\vec{x}_i) \) as
\[
\mathbf{B}(\vec{x}_i) = \Pr(B(\vec{x}_i) = 1) = 1 - \Pr(\mathbf{N}_{agg}(\vec{x}_i^*|\lambda) < \eta).
\]

We recall that \( \mathbf{N}_{agg}(\vec{x}_i^*|\lambda) \) is the sum of \( \mathbf{N}(\vec{x}_i^*|\vec{x}_j) \). We note that \( \mathbf{N}(\vec{x}_i^*|\vec{x}_j) \) is the sum of molecules observed at the \(j^{th}\) bacterium at time \( t = t_j^*\) released from the \(j^{th}\) bacterium since \( t = 0\). Thus, the observations at the \(i^{th}\) bacterium due to continuous emission at the \(j^{th}\) bacterium are not identically distributed since they are released at different times. Therefore, \( \mathbf{N}(\vec{x}_i^*|\vec{x}_j) \) is a Poisson binomial RV since each molecule behaves independently and has a different probability of being observed at \( t = t_j^*\) by the \(i^{th}\) bacterium. Since \( \mathbf{N}_{agg}(\vec{x}_i^*|\lambda) \) is the sum of \( \mathbf{N}(\vec{x}_i^*|\vec{x}_j) \), \( \mathbf{N}_{agg}(\vec{x}_i^*|\lambda) \) is also a Poisson binomial RV. We note that modeling \( \mathbf{N}_{agg}(\vec{x}_i^*|\lambda) \) as a Poisson binomial RV makes the evaluation of the cumulative density function (CDF) of \( \mathbf{N}_{agg}(\vec{x}_i^*|\lambda) \) in (17) very cumbersome, since we need to account for each probability for each molecule observed at the \(i^{th}\) bacterium released from all bacteria since \( t = 0\). Fortunately, using the central limit theorem [17], we can accurately approximate \( \mathbf{N}_{agg}(\vec{x}_i^*|\lambda) \) as a Gaussian RV. We further approximate the variance of \( \mathbf{N}_{agg}(\vec{x}_i^*|\lambda) \) by its mean \( \mathbf{N}_{agg}(\vec{x}_i^*|\lambda) \). By doing so and using CDF of a Gaussian RV [17], we have
\[
\mathbf{B}(\vec{x}_i) = \Pr(B(\vec{x}_i) = 1) = 1 - \frac{1}{2} \left[ 1 + \text{erf} \left( \frac{\eta - 0.5 - \mathbf{N}_{agg}(\vec{x}_i^*|\lambda)}{\sqrt{2\mathbf{N}_{agg}(\vec{x}_i^*|\lambda)}} \right) \right],
\]
where \( \mathbf{N}_{agg}(\vec{x}_i^*|\lambda) \) is as evaluated in Sec. IV-A. We next analyze the expected number of cooperators. We denote the number of cooperators and its mean for a given realization of the spatial point process by \( Z \) and \( \overline{Z} \), respectively. Due to \( Z = \sum_{\vec{x}_i^* \in \Phi(\lambda)} B(\vec{x}_i) \), we have \( \overline{Z} = \sum_{\vec{x}_i^* \in \Phi(\lambda)} \mathbf{B}_m(\vec{x}_i) \). Using Campbell’s theorem [18], we calculate the expected number of cooperators over the random point process as
\[
\mathbb{E}\{Z\} = \mathbb{E}\left\{ \sum_{\vec{x}_i^* \in \Phi(\lambda)} \mathbf{B}(\vec{x}_i) \right\} = \int_{|\vec{r}_i| = 0}^{R_1} \mathbf{B}(\vec{r}_i) \lambda 2\pi|\vec{r}_i| d|\vec{r}_i|,
\]
where \( \mathbf{B}(\vec{r}_i) \) can be obtained by replacing \( \vec{x}_i^* \) with \( \vec{r}_i \) in (18). Combining (19), (18), (14), (11)/(13), and (7), we rewrite \( \mathbb{E}\{Z\} \) as
\[
\mathbb{E}\{Z\} = \int_{|\vec{r}_i| = 0}^{R_1} \left\{ -\frac{1}{2} \left[ 1 + \text{erf} \left( \frac{\eta - 0.5 - \mathbf{N}_{agg}(\vec{r}_i^*|\lambda)}{\sqrt{2\mathbf{N}_{agg}(\vec{r}_i^*|\lambda)}} \right) \right] \ight. + 1 \} \lambda 2\pi|\vec{r}_i| d|\vec{r}_i|,
\]
where
\[
\mathbf{N}_{agg}(\vec{r}_i^*|\lambda) = \mathbf{N}_{agg}(\vec{r}_i^*|\lambda) + \mathbf{N}_{self},
\]
and \( \mathbf{N}_{agg}(\vec{r}_i^*|\lambda) \) can be obtained by substituting \( \vec{b} \) and \( \lambda \) with \( |\vec{r}_i| \) and \( \lambda \), respectively, in (11) or (13). We finally obtain \( \mathbb{E}\{\mathbf{N}\} \) by \( \mathbb{E}\{\mathbf{N}\} = \mathbb{E}\{\mathbf{Z}\} / \pi R_1^2 \).

### V. Numerical Results and Simulations

In this section, we present simulation and numerical results to assess the accuracy of our derived analytical results.

#### A. Simulation Details

We simulate using a particle-based method as described in [19]. We vary density \( \lambda \) and environmental radius \( R_1 \). We list other fixed environmental parameters in Table I. The molecules are initialized at the center of bacteria. The location of each molecule is updated every time step \( \Delta t \), where diffusion along each dimension is simulated by generating a normal RV with variance \( 2D\Delta t \). Every molecule has a chance of degrading in every time step with the probability \( \exp(-k\Delta t) \). In simulations, the locations of bacteria are distributed according to a 2D PPP. Each bacterium releases molecules according to a Poisson process, thus the times between the release of consecutive molecules at different bacteria are simulated as i.i.d exponential RVs. In Fig. 5, simulation results were averaged over \( 10^4 \) different realizations of randomly-generated releasing times of molecules. In Figs. 6 and 7, simulation results were averaged over \( 10^4 \) different realizations of randomly-distributed bacterium locations and randomly-generated releasing times of molecules.

### Table I

**ENVIRONMENTAL PARAMETERS**

| Parameter           | Symbol | Value  |
|---------------------|--------|--------|
| Radius of observer  | \( R_0 \) | \( 1 \mu m \) |
| Diffusion coefficient | \( D \) | \( 1 \times 10^{-3} \text{m}^2/\text{s} \) |
| Emission rate       | \( q \) | \( 1 \times 10^{10} \text{molecule/s} \) |
| Reaction rate constant | \( k \) | \( 1 \times 10^4 \text{molecule/s} \) |
Fig. 5. The expected number of molecules observed at the RX $N_{agg}(\vec{b}, t)$ due to continuous emission at one TX located at $(0, 0)$ versus time when the RX is located at (a) $(0, 0)$ and (b) $(5 \mu m, 0)$.

Fig. 6. The expected number of molecules observed at the RX $N_{agg}(\vec{b}, t)$ due to continuous emission at randomly-distributed TXs for different environmental radius $R_1$. The average number of TXs is fixed at 100 and the RX's location is fixed at $(10 \mu m, 10 \mu m)$. We set $R_1 = 30 \mu m$, $R_1 = 40 \mu m$, $R_1 = 50 \mu m$ and corresponding density is $\lambda = 3.5 \times 10^{-2}/\mu m^2$, $\lambda = 2.0 \times 10^{-2}/\mu m^2$, and $\lambda = 1.3 \times 10^{-2}/\mu m^2$, respectively.

B. Channel Response

In Fig. 5, we plot the expected number of molecules observed at the RX due to continuous emission by one TX in two cases: a) the TX is at the center of the RX and b) the distance between the TX and the RX is $5 \mu m$. In Fig. 6, we plot the expected number of molecules observed at the RX due to continuous emission by a circular field of TXs for different environmental radii and we keep the average number of bacteria fixed as 100. The asymptotic curves in Fig. 5(a) and Fig. 5(b) are evaluated by (7) and (10), respectively. The asymptotic curves with UCA and without UCA in Fig. 6 are obtained via (13) and (11), respectively. We first note that the expected number of molecules observed in Figs. 5 and 6 first increases as the time increases and then becomes stable after time $t \approx 0.5$ s. Second, we note that all asymptotic curves perfectly match with simulations, thereby validating the accuracy of (7), (10), (13), and (11). Third, in Fig. 6, we note that the asymptotic curves with UCA and without UCA almost overlap with each other. This demonstrates the accuracy of the UCA in the derivation of the channel response where a circular field of TXs continuously emit molecules. Finally, we note that when the environmental radius $R_1$ decreases, the expected number of molecules increases, which is not surprising since the density of TXs is higher when $R_1$ is smaller.

C. Bacterial Cooperation

In Fig. 7, we plot the expected density of cooperators over spatial PPP $E\{\lambda_c\}$ versus threshold $\eta$ for different population radius $R_1$ and density $\lambda$: (a) $R_1 = 50 \mu m$ and $\lambda = 1.2 \times 10^{-1}/\mu m^2$ (b) $R_1 = 50 \mu m$ and $\lambda = 1.2 \times 10^{-2}/\mu m^2$ (c) $R_1 = 10 \mu m$ and $\lambda = 3.18 \times 10^{-1}/\mu m^2$.

In Fig. 7, we plot the expected density of cooperators over spatial PPP $E\{\lambda_c\}$ versus threshold $\eta$ for different population radius $R_1$ and density $\lambda$: (a) $R_1 = 50 \mu m$ and $\lambda = 1.2 \times 10^{-1}/\mu m^2$ (b) $R_1 = 50 \mu m$ and $\lambda = 1.2 \times 10^{-2}/\mu m^2$ (c) $R_1 = 10 \mu m$ and $\lambda = 3.18 \times 10^{-1}/\mu m^2$. The expected number of molecules observed in Figs. 5 and 6 first increases as the time increases and then becomes stable after time $t \approx 0.5$ s. Second, we note that all asymptotic curves perfectly match with simulations, thereby validating the accuracy of (7), (10), (13), and (11). Third, in Fig. 6, we note that the asymptotic curves with UCA and without UCA almost overlap with each other. This demonstrates the accuracy of the UCA in the derivation of the channel response where a circular field of TXs continuously emit molecules. Finally, we note that when the environmental radius $R_1$ decreases, the expected number of molecules increases, which is not surprising since the density of TXs is higher when $R_1$ is smaller.

In Fig. 8, we simulate the decisions of bacteria under one realization of randomly-distributed bacterium locations and random releasing times of molecules at all bacteria. We plot the spatial distribution of cooperators in this realization. The number of cooperators around the population center is higher. We note that this observation is also consistent with that in Fig. 3(a).
Fig. 8. The spatial distribution of cooperators under one realization of randomly-distributed locations of bacteria and random release times of molecules at all bacteria in a simulation with \( R_0 = 50 \mu m \) and \( \lambda = 1.2 \times 10^{-1}/\mu m^2 \).

VI. CONCLUSIONS AND FUTURE WORK

In this work, we analytically modeled a QS-based communication system of a microbial population in a 2D environment. Microorganisms were randomly distributed on a circle with a constant density where each one releases molecules at random times and with a fixed emission rate. To analyze the observations and responsive behaviors at bacteria, we first analytically derived the asymptotic channel response at a circular RX due to continuous emission of molecules at 1) one point TX and 2) randomly-distributed point TXs on a circle in a 2D environment. From this analysis, the number of molecules observed at each randomly-distributed bacterium was analyzed and the expected density of cooperative bacteria over a spatial random point process was analytically derived. Our analytical results were validated using a particle-based simulation method. Interesting future work includes: 1) Experimental validation of our current analytical results and 2) Applying game theory to our current model with elaborated payoffs and strategies.

APPENDIX

PROOF OF THEOREM 1

Applying \(|b| = 0\) to (6), we first write \( \mathcal{N}_{self} \) as

\[
\mathcal{N}_{self} = \int_{\tau=0}^{\infty} \int_{r=0}^{R_0} \int_{\theta=0}^{2\pi} q \exp \left( -\frac{r^2}{4D\tau} - k\tau \right) \frac{d\theta}{2(2\pi)} \frac{d\tau}{2\pi} dr.
\]

We then apply [16, Eq. 2.33.12] given by

\[
\int x^n \exp(-\beta x^n) dx = - (\gamma - 1)! \frac{\exp(-\beta x^n)}{n} \times \sum_{k=0}^{\gamma-1} \frac{x^{n+k}}{k! \beta^{\gamma-k}}, \quad \gamma = m + 1 \quad n,
\]

to (22) and use some basic integral manipulations to rewrite (22) as

\[
\mathcal{N}_{self} = \int_{\tau=0}^{\infty} q \exp(-k\tau) \left( 1 - \exp \left( -\frac{R_0^2}{4D\tau} \right) \right) d\tau. \quad (24)
\]

We finally apply \( \int_{0}^{\infty} \exp(-px) dx = 1/p \) [16, Eq. 3.310], and [16, Eq. 3.324.1] given by

\[
\int_{0}^{\infty} \exp \left( \frac{-\beta x}{x} - \gamma x \right) dx = \frac{\beta}{\gamma} K_1\left( \sqrt{\beta\gamma} \right), \quad (25)
\]
to (24) to arrive at (7).

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