

**Simultaneous coupling of phototaxis and electrotaxis in *Volvox algae***Yoshikatsu Hayashi<sup>1,\*</sup> and Ken Sugawara<sup>2</sup><sup>1</sup>*Brain Embodiment Laboratory, School of Systems Engineering, University of Reading, PO Box 225, Whiteknights, Reading RG6 6AY, United Kingdom*<sup>2</sup>*Department of Information Science, College of Liberal Arts, Tohoku Gakuin University, 2-1-1 Tenjinzawa, Izumi-ku, Sendai, Miyagi 981-3193, Japan*

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In nature, living creatures are affected by several stimuli simultaneously. The response of living creatures to stimuli is called taxis. In order to reveal the principles of taxis behavior in response to complex stimuli, we simultaneously applied photostimulation and electric stimulation perpendicularly to a *Volvox algae* solution. The probability distribution of the swimming direction showed that a large population of swimming cells moved in a direction that was the result of the composition of phototaxis and electrotaxis. More surprisingly, we uncovered the coupling of signs of taxis, i.e., coupling of phototaxis and electrotaxis induced positive electrotaxis, which did not emerge in the single stimulation experiments. We qualitatively explained the coupling of taxis based on the polarization of the swimming cells induced by the simultaneous photo- and electric stimulation.

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**I. INTRODUCTION**

The behavior of microorganisms has been always described under the influence of a single type of stimuli. However, normally in nature, the conditions are by far more complex than that; animals are affected by several stimuli simultaneously [1]. If an animal is exposed to two types of stimuli *a* and *b* simultaneously (Fig. 1), which type of stimulus does it select to response to? Or will it react in a new way, different from the usual reactions to either *a* or *b*? We will investigate these responses in living creatures by adopting evolutionarily primitive organisms as models. *Volvox algae* are a primitive multicellular organism evolved from a single-cell organism, *Cryptomonas*. The sign of phototaxis in *Volvox algae* is also affected by another environmental factor, temperature, being positive at room temperature (20 °C) and negative at lower temperature (16 °C) [4–6]. The cells of *Volvox algae* swim towards a light source or away from it. The direction of the algal phototaxis is reversed by environmental factors. Halldal found that the sign of phototaxis in *Platymonas* could be controlled by changing the concentrations of magnesium, calcium, and potassium ions in the medium [2,3].

From a cellular viewpoint, *Volvox algae* is a spherical multicellular alga (Fig. 2) with many features that recommend it as a model for the early development of photoreception in eukaryotes [7,8]. Individuals of this species contain only two distinct cell types, large reproductive cells and thousands of somatic cells that cannot divide. The somatic cells are arranged in a single layer at the surface of the transparent sphere, while the gonidia are located below the surface, where they have no direct contact with the external medium. All somatic cells are flagellated and possess eyes, and are responsible for guiding the colony to places of light conditions that are optimal for photosynthetic growth.

The orientation of the individual somatic cells within the spheroid, combined with the three-dimensional pattern in which their flagella beat, cause the spheroid to rotate in a

counterclockwise direction. The two flagella of each cell beat synchronously and in an almost precisely parallel fashion. The flagella of all cells beat towards the posterior of the spheroid and slightly to the right, causing the spheroid to rotate to the left as it moves forward [9,10]. Whether the cells accelerate or decelerate in response to on and off stimuli depends on environmental factors such as light intensity and its illumination history. Thus, colonial algae orient in light by a complex differential response of the cells at different sides of the colony [5]. When the colony shows positive phototaxis, the activity of the cilia exposed to light is less than that of the cilia in the shaded side of the spheroid, and the swimming cell can move towards the light source. In negative phototaxis, the photophobic responses of cilia are reversed.

Recently, the role of the rotation of organisms in response to photostimuli has been revealed. The direct sensory motor coupling between the eyespot photoreceptor and the locomotor ciliary cells is combined in a single cell, *Zooplankton larvae*. When the axial rotation is very slow, the phototactic orientation does not occur. Axial rotation restores the ability to steer in a three-dimensional space, and is therefore essential for phototactic navigation [11]. In addition, in case of a multicell, the natural spinning frequency of the colony appears to be tuned to give the maximum photoresponse [12–14]. This type of sensory motor coupling might be important to consider their response to the complex stimulation.

On the other hand, electrotaxis, also known as galvanotaxis, has been known for eukaryotic ciliates such as *Paramecium* [1,15], *Chlamydomonas* [16], *Tetrahymena pyriformis* [17], and a multicellular organism, *Dicystostelium* [18,19]. Since electrotaxis is one of the most fundamental taxis, the electric stimulus was chosen as a counterpart to the photostimulus in our experiments.

As a response to a single stimulation, we first examined the phototactic and electrotactic signs of *Volvox algae* as a function of the intensity of the stimulation. Second, the photostimulation and electric stimulation were applied perpendicularly to the *Volvox algae* solution, and the response of the swimming cells was measured and discussed.

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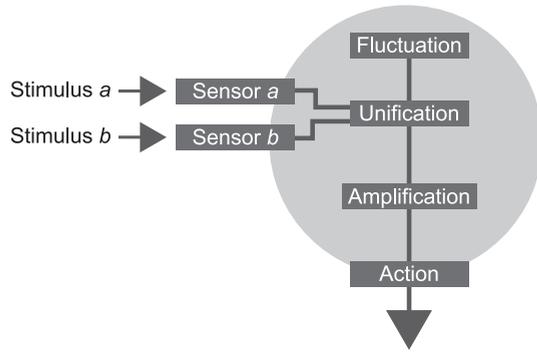


FIG. 1. Integration of sensory information for complex stimuli to produce one action. Internal fluctuations give rise to uniform distribution of swimming cells. Swimming cells orient to a certain direction when the sensors detect the external stimuli.

## II. MATERIALS AND METHODS

### A. Plants

*Volvox algae* were cultured for three weeks under 12 h of illumination at 2500 lux and 12 h of darkness. Their sizes vary from 0.3 mm to 1.0 mm in diameter. The temperature was kept constant at 23 °C. The cell suspension in the log phase of growth was used as the experimental material. A *Volvox algae* culture medium of 1 L contained 1 mg of  $\text{CaCO}_3$  and 50 mg of sterilized red soil. The swimming cells were collected by shedding white light and carefully extracting the concentrated part of the cell suspension with a micropipette [6]. This cell suspension was placed into an incubator in the dark for 2 h prior to the experiments.

### B. Analysis of the phototactic and electrotactic responses

The *Volvox algae* solution (3 mL;  $0.5 \text{ cells/mm}^3$ ) was placed in a 30-mm-square acrylic pool. We applied photostimulation and electric stimulation perpendicularly to each other, as shown in Fig. 3. The photostimulation was applied along the  $y$  axis using a white light emitting diode (LED), while the electric stimulation was applied along the  $x$  axis using aluminium plates placed on both sides of the acrylic pool. First, we performed the single stimulation experiment for both photostimulus and electrostimulus. For the complex stimulation experiments, the simultaneous stimulation of the photo- and electric fields was applied perpendicularly.

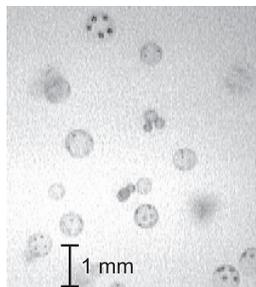


FIG. 2. Snapshot of the *Volvox algae* solution. Each multicellular organism has daughter algae below the layer of somatic cells.

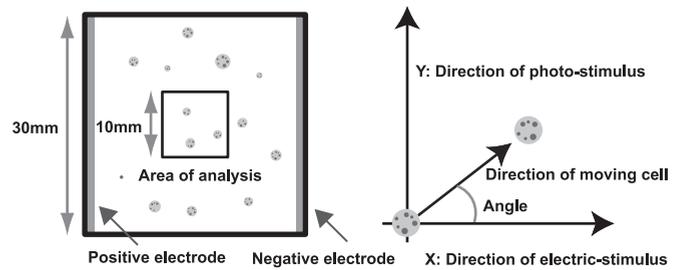


FIG. 3. Experimental apparatus. The *Volvox algae* solution was placed in a 30-mm-square acrylic pool. The photostimulus was applied along the  $y$  axis using a white LED, while the electric stimulus was applied along the  $x$  axis using aluminium plates on both sides of the pool with the negative electrode on the right side.

To determine the characteristic behavior of the swimming cells in response to stimulation, we calculated their average velocities, i.e., the position of the cell on the onset of the stimulus was marked as the starting point, the position of the cell 5 s later was marked as the end point (Fig. 3), and the distance and the angle for the given coordinates were calculated between these two points. The swimming directions were calculated in the polar coordinates with the bin of  $30^\circ$ , and the probability distributions were obtained for each condition.

The velocities of the swimming cells were calculated and categorized into four bins:  $-45^\circ \leq \text{Region 1} < 45^\circ$ ,  $45^\circ \leq \text{Region 2} < 135^\circ$ ,  $135^\circ \leq \text{Region 3} < 225^\circ$ , and  $225^\circ \leq \text{Region 4} < 315^\circ$ . In each bin, the average velocities and standard deviations were calculated and presented as a function of the external stimulation's intensity.

The strength of the photostimulus and electric stimulus was set as follows:

(1) The intensity of light was set to 78, 152, and 244 lux at the center of the pool.

(2) The intensity of the electric field was set to 0.07, 0.13, 0.2, and 0.27 V/mm.

In each experimental condition, about 180 swimming cells in total were investigated.

## III. RESPONSE TO SINGLE STIMULATION

As a response to a single stimulation, we first examined the phototactic and electrotactic signs of *Volvox algae* as a function of intensities of photostimulus and electric stimulus.

### A. Analysis of swimming directions

When the 78-lux light was applied to the *Volvox algae* solution, most of the swimming cells moved towards the light source, as shown in Fig. 4(a). As the light intensity increased from 78 to 152 lux, the population of the swimming cells was divided into two distributions. About half of the swimming cells showed positive phototaxis, and about 30% showed negative phototaxis. Furthermore, when the light intensity was increased to 244 lux, about half of the population showed negative phototaxis.

*Volvox algae* also undergo electrotaxis. When the intensity of the electric stimulus was set to 0.07 V/mm, the probability distribution of the swimming cells' directions slightly shifted

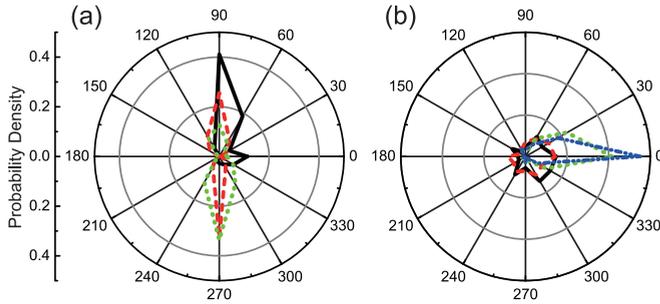


FIG. 4. (Color online) Probability density of the swimming directions (degrees) in the single stimulation experiment. (a) The light intensity was set to 78 (solid line), 152 (dashed line), and 244 lux (dotted line). (b) The electric field was set to 0.07 (solid line), 0.13 (dashed line), 0.2 (dotted line), and 0.27 V/mm (dashed dotted line).

towards the angle of 0 [Fig. 4(b)], i.e., a small population of the swimming cells showed negative electrotaxis. As the intensity of the electric field increased to 0.27 V/mm, about half of the population showed negative electrotaxis. As the intensity of the electric field increased further, the distribution of the swimming directions became sharper along the direction parallel to the electric field.

### B. Analysis of swimming velocities

The average velocities of the swimming cells showed that the velocity decreased when swimming towards or away from the light source [Fig. 5(a)]. The velocity of the swimming cells depends on the frequency of the cilia. When the rotation of the cilia is suppressed on the sphere in response to the light stimulus, it is natural to think that the lower activity of the cilia leads to a lower speed of the whole colony. In addition, Fig. 5(a) does not show the significant difference on increasing the light intensity, i.e., the velocities of the swimming cells were independent of light intensity.

On the other hand, the electric field suppresses the motion perpendicular to the field [Fig. 5(b)]. As the intensity of the electric field increased, the average velocity increased towards the anode and decreased towards the cathode. Here, we assessed the dependence of velocity on the strength of

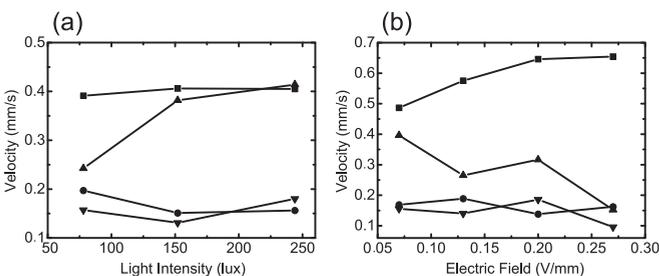


FIG. 5. Average velocities of the swimming cells as a function of (a) light intensity and (b) electric field. The square represents the average velocity in Region 1 [average standard deviation is (a) 0.14 and (b) 0.60]; the circle represents the average velocity in Region 2 [(a) 0.10 and (b) 0.14]; the triangle represents the average velocity in Region 3 [(a) 0.14 and (b) 0.18], and the inverted triangle represents the average velocity in Region 4 [(a) 0.12 and (b) 0.12].

the electric field to investigate if the *Volvox algae* solution should be regarded as a charged colloid solution. With the typical velocity of the swimming cell being  $v = 0.5$  mm/s (Fig. 5), the characteristic length  $L = 0.5$  mm and viscosity of water  $\eta = 10^{-3}$  Pa s, the Reynolds number is estimated as  $Re < 1.0$ . In this range of the Reynolds number, the Stokes law  $F = 6\pi\eta Lv$  can be applied; therefore, the terminal velocity of the charged colloid  $v$  is given by

$$v = \frac{qE}{6\pi\eta L}, \quad (1)$$

where  $q$  is the net charge of the swimming cell and  $E$  is the intensity of the electric field. If the electrotaxis of *Volvox algae* is represented by electrophoresis, Eq. (1) suggests that the estimate of the number of ions should be  $10^8$ . This is a highly unrealistic value since the cells should be neutral, indicating that electrotaxis cannot be explained by electrophoresis.

## IV. RESPONSE TO COMPLEX STIMULATION

If an animal is exposed to two types of stimuli  $a$  and  $b$  simultaneously, which type does the animal select to respond to or does it make a compromise? To answer these questions, we simultaneously applied photostimulation and electric stimulation perpendicularly to each other.

### A. Analysis of swimming directions

*0.07 V/mm electric field.* The electric field (0.07 V/mm) was applied simultaneously with weak (78 lux) or strong (152 lux) photostimulation. A large population of swimming cells moved toward the light source and some slightly moved towards the direction of the first quadrant when the light intensity was 78 and 152 lux [Fig. 6(a)]. At this light intensity, the single stimulation experiment showed negative phototaxis (Fig. 4). However, a significant population did not show negative phototaxis, indicating that the electric field might have suppressed the negative phototaxis.

*0.13 V/mm electric field.* When a weak (78 lux) photostimulation was applied, a significant population of swimming cells moved towards the first quadrant [Fig. 6(b)], which was the direction of the composition of the two stimulation vectors (photo- and electric stimulation). The light intensity of 152 lux still could produce the negative phototaxis because it was suppressed by the electric field.

*0.2 V/mm electric field.* When a weak (78-lux) photostimulus was applied, a significant population of swimming cells moved towards the first quadrant well aligned to the electric field [Fig. 6(c)]. Once again, we observed the response of the swimming cells in the composition of the two stimulation vectors (photo- and electric stimulation). On the other hand, a significant population of the cells moved towards the third quadrant when the light intensity was set to 152 lux.

*0.27 V/mm electric field.* Figure 6(d) shows the response of the swimming cells to the complex stimulation when the strength of the electric field was set to 0.27 V/mm. In case of the weak light intensity (78 lux), the swimming cells clearly

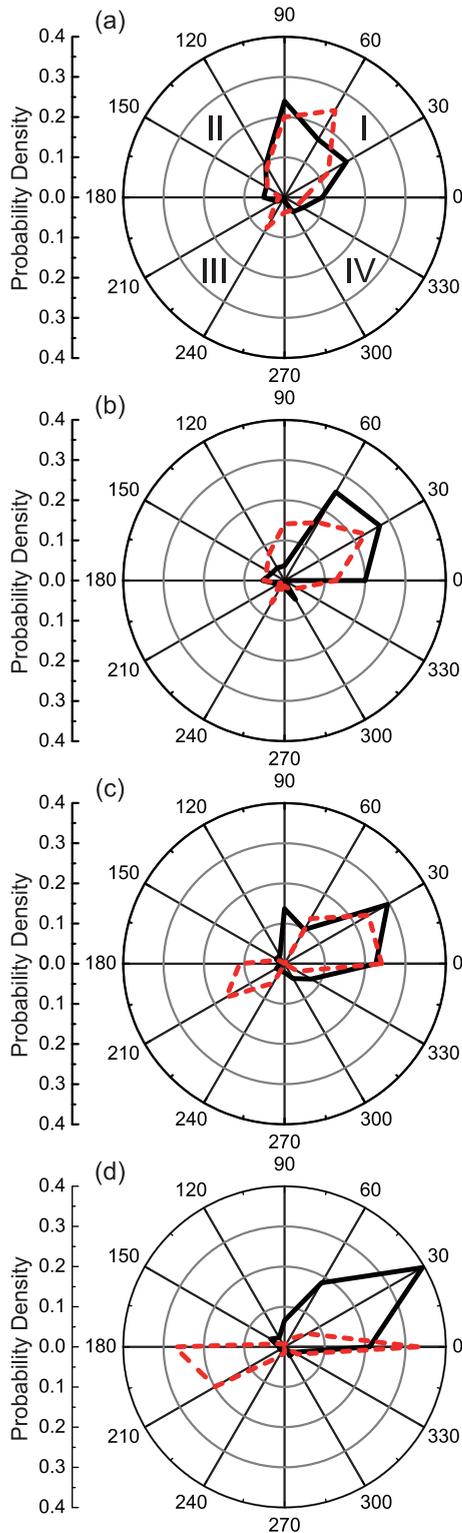


FIG. 6. (Color online) Probability density of the swimming directions (degrees) in the simultaneous stimulation experiments. The light intensity was set to 78 (solid line) and 152 lux (dotted line). The electric field was set to (a) 0.07, (b) 0.13, (c) 0.2, and (d) 0.27 V/mm. The definition of the quadrants is presented in (a).

showed the composition of both phototaxis and electrotaxis. When the light intensity was set to 152 lux, we observed that

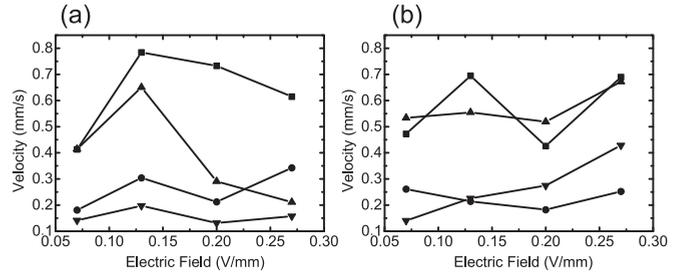


FIG. 7. Average velocities of the swimming cells as a function of electric field. The light intensity was set to (a) 78 and (b) 152 lux. The square represents the average velocity in Region 1 [average standard deviation is (a) 0.41 and (b) 0.31]; the circle represents the average velocity in Region 2 [(a) 0.20 and (b) 0.12]; the triangle represents the average velocity in Region 3 [(a) 0.20 and (b) 0.29] and the inverted triangle represents the average velocity in Region 4 [(a) 0.08 and (b) 0.17].

the swimming cells moved towards the positive electrode, i.e., positive electrotaxis.

**B. Analysis of swimming velocities**

The average velocities of the swimming cells are shown in Fig. 7. The average velocity as a function of electric field showed a nonlinear curve profile; however, the complex stimulation might not affect the average velocities significantly except for the suppression of the velocity along the y axis as shown in the case of single stimulation experiments.

**V. DISCUSSION**

When the single stimulation was applied, we observed that *Volvox algae* changed the sign of the phototaxis as the light intensity increased, and that the swimming cells showed only negative electrotaxis in the present range of the electric field strength.

When the complex stimulation was applied, the swimming direction of the cells seemed to be composed of phototaxis and electrotaxis. The experimental evidence also suggests that the coupling of the two taxis should induce the positive electrotaxis, which has not been demonstrated in the single stimulation experiments.

In colonies, all somatic cells possess eyes and cilia, which means that the colony has thousands of individual visual motor systems. As the colony rotates, each cell passes through the illuminated side to the shaded side repeatedly. In the positive phototaxis, stop response was observed on the illuminated side of the colony and flagellar acceleration occurred on the shaded side, while in the negative phototaxis, these photophobic responses were reversed [5]. The experiments on the ionic environment led to the hypothesis that the sign of phototaxis is determined by membrane polarization and depolarization, changing the sign of phototaxis from positive to negative [6].

Electrotaxis can be caused by the polarization of cells, i.e., the electrostatic field hyperpolarizes the membrane potential on the anode side and depolarizes the membrane potential on the cathode side, resulting in the change of the rotational direction of cilia. The organisms orient themselves parallel to

the direction of the electric field and move towards the anode in the case of single cells [15,17]. The slime mould *Dictyostelium* shows robust electric-field-guided migration and offers a good model to study electrotaxis. Using this genetically tractable organism, Shanley *et al.* have investigated the role of  $\text{Ca}^{2+}$  signaling in electrotaxis, and reported that electric fields induce a significant and sustained  $\text{Ca}^{2+}$  elevation [18].

Regarding the complex stimulation experiments, Ekelund *et al.* reported that *Chlamydomonas* respond both phototactically and galvanotactically [16]. If an electric field and a light stimulus are applied simultaneously, the electrostatic field perpendicular to the phototactic direction inhibits phototaxis. From the control engineering viewpoint, Kim *et al.* demonstrated that *T. pyriformis* is controllable using both galvanotaxis and phototaxis [17] (although independently applied). However, the mechanism of phototaxis and electrotaxis coupling is not known.

The electric signal transmission involved in the light reception was studied in *Chlamydomonas*, where the light reception caused a change in the electrostatic profile, causing depolarization across the single cell [20]. The signal transmission from the photoreceptor produces the membrane polarization or depolarization, which leads to the change in the rotational speed of cilia through ionic sensitive channels. To summarize above, the photo- and electric responses are coupled at the level of membrane potential.

The distribution of the ions inside cells is directly related to the membrane potential, so, it is reasonable to consider the coupling of taxis in terms of polarization of cells. The polarization of cells, as in the case of electrotaxis, can be regarded as the dipole formation of the cell as a net charge distribution [15,17]. In the case of phototaxis, the ciliary motion is switched off for the illuminated side and on for the shadowed side for positive phototaxis, and the response of the ciliary motion is reversed for the negative phototaxis. The fact that the phototactic response depends on the strength of the ionic solution [6] indicates that the phototactic response is mediated by the polarization of the membrane. Thus, the ciliary motion is regulated by the degree of polarization of membrane potential [20], so, in the multicellular organism, the net charge distribution across the whole colony can be regarded as dipole formation. Therefore, we assume that the phototaxis should be also actuated by the induced dipole moment.

In order to discuss the characteristic behavior in each experimental condition, we will consider how the electric field affects the dipole formed by the photostimulation, and explain the coupling of the taxis in terms of the polarization as a whole colony when the electric field is applied simultaneously. Regarding the stability of the rotational and translational motion [11], the rotational axis of the whole colony is also taken into account.

In the present experimental setup, the positive phototaxis is actuated by the ion distribution polarized along the  $y$  axis with the positive charge towards the source of light and the negative charge away from the source of light. The rotational axis should be parallel to the  $y$  axis, since the direction of the dipole vector should correspond to the rotational axis to stabilize the translational motion.

When the electric field was perpendicularly applied to this induced dipole along the  $y$  axis, the rotational axis pointing at

the positive direction along the  $y$  axis was oriented clockwise towards the direction of the electric field along the  $x$  axis. This induced dipole interacting with the external field would explain

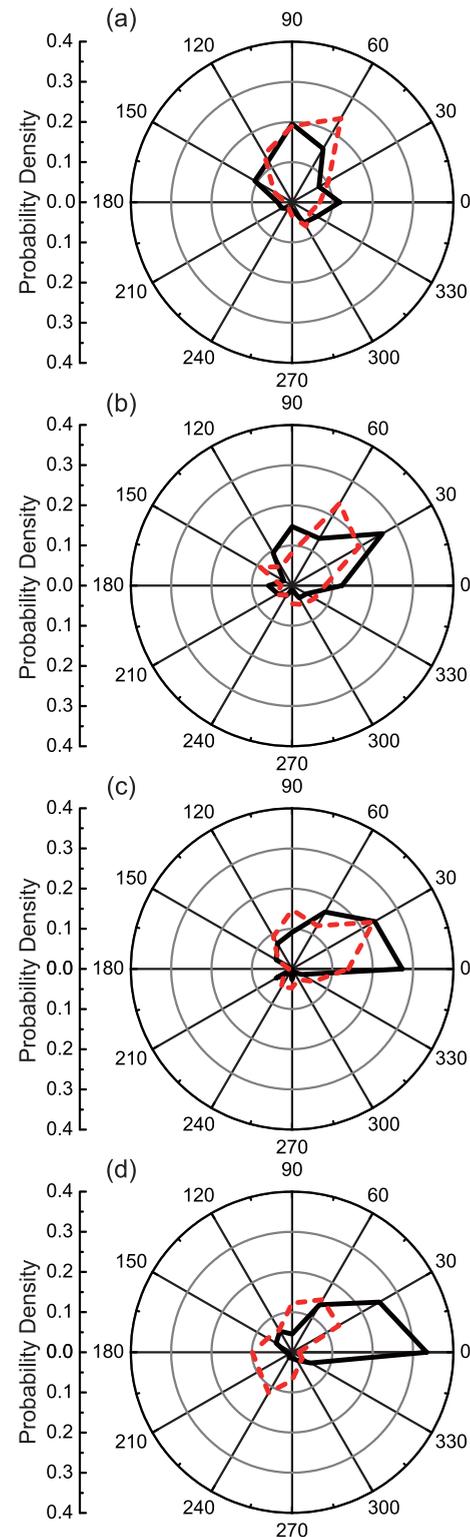


FIG. 8. (Color online) Probability density of swimming directions (degrees) in the complex stimulation condition. The light intensity was set to 78 (solid line) and 152 lux (dotted line). The electric field was set to (a) 0.07, (b) 0.13, (c) 0.2, and (d) 0.27 V/mm.

the population of the swimming cells in the first quadrant as shown in Figs. 6(a) and 6(b). However, this middle range electric field suppresses the negative phototaxis [Figs. 6(a) and 6(b)].

When the electric field is strengthened further, we hypothesize that the simultaneous application of the strong electric field and the strong photostimulation in a perpendicular manner should induce the quadrupole along the  $x$  axis.

If the rotational axis does not correspond to the direction of the induced electric field of the quadrupole, the rotational motion of the whole colony destabilizes the translational motion of swimming cells for two reasons: (1) The whole colony experiences the tangential force with respect to the rotational axis in forward and inverse directions for the rotational motion due to the electric interactions of the internal charge distribution with the external electric field; (2) membrane potential in each cell becomes hyperpolarized or depolarized, accelerating or decelerating the rotational motion, respectively, as the whole colony rotates around. Therefore, the stable translational motion can be realized when the rotational axis corresponds to the direction of the induced quadrupole along the  $x$  axis. The induced quadrupole of the whole colony is symmetric with respect to the  $y$  axis, so, the swimming cells move toward the positive and negative directions along the  $x$  axis, explaining the population of the swimming cells as shown in Fig. 6(d) when the electric field is strong.

Even though our hypothesis of dipole and quadrupole formation would explain the essential point of the coupling of taxis, (1) composition of phototaxis and electrotaxis in the case of weak electric field, and (2) positive electrotaxis in the case of strong photo- and electric stimulation, the formation of the dipole and quadrupole should be verified experimentally in the future study. We suggest that a possible test could be intracellular recording of membrane potential (see, for example, [21]). The swimming cells can be deciliated by incubation in a standard solution of ethanol, and the complex stimulation can be applied to the immobilized cells. It would be possible to measure the membrane potential by electrodes across the cells to investigate the distribution of charges. It is worth mentioning that we cannot exclude the possibility that the rotational motion of the whole colony might be coupled to the dynamics of polarization.

## VI. CONCLUSION

In case of the single stimulation, we observed that *Volvox algae* changed the sign of the phototaxis as the light intensity increased, and that the swimming cells showed only negative electrotaxis in the present range of electric field strength. In the case of the complex stimulation, the swimming direction seemed to be composed of both phototaxis and electrotaxis.

The experimental evidence suggests that the coupling of phototaxis and electrotaxis should induce positive electrotaxis, which has not been demonstrated in the single stimulation.

Responding to a set of external stimulation, all sensory information is transmitted to the membrane potential which leads to the change in the rotational speed of the cilia, actuating the rotational and translational motion of the whole colony. So, it is reasonable to consider the distribution of the ions inside the cells which is directly related to the membrane potential.

We hypothesize that the phototaxis should be actuated by the dipole moment and that the simultaneous application of the strong electric field and the strong photostimulation in the perpendicular manner should induce the quadrupole. Our hypothesis led us to qualitatively explain the coupling of taxis, incorporating the polarization as a whole colony and the dynamical stability of the rotational/translational motion: (1) Photo-induced dipole interacting with the weak electric field for the composition of phototaxis and electrotaxis; (2) quadrupole formation for positive electrotaxis which has not been demonstrated in the single stimulation.

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## APPENDIX: TIME-LAG STIMULATION CONDITION

If an animal is first exposed to one type of stimulus and then to another, can it still respond to the second stimulus? To answer this question, the swimming cells were exposed to photostimulation for 20 s, and then an electric stimulation was applied in addition to the photostimulation. The trajectories of the swimming cells were recorded for 5 s from the moment when the electric stimulation was applied.

The distribution of the swimming directions (Fig. 8) showed (1) composition of phototaxis and electrotaxis was observed in the case of the weak electric field and (2) the positive electrotaxis was observed in the case of the strong photo- and electric stimulation. Thus, it is confirmed that the swimming cells can respond to the second stimulus, i.e., the coupling of photo- and electrotaxis was also observed in the time-lag stimulation condition. The difference could be that the probability distribution of the swimming directions was broader in the time-lag stimulation condition than that in the simultaneous stimulation condition.

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