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Sensory fusion in *Physarum polycephalum* and implementing multi-sensory functional computation

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ABSTRACT

Surface electrical potential and observational growth recordings were made of a protoplasmic tube of the slime mould *Physarum polycephalum* in response to a multitude of stimuli with regards to sensory fusion or multisensory integration. Each stimulus was tested alone and in combination in order to evaluate for the first time the effect that multiple stimuli have on the frequency of streaming oscillation. White light caused a decrease in frequency whilst increasing the temperature and applying a food source in the form of oat flakes both increased the frequency. Simultaneously stimulating *P. polycephalum* with light and oat flake produced no net change in frequency, while combined light and heat stimuli showed an increase in frequency smaller than that observed for heat alone. When the two positive stimuli, oat flakes and heat, were combined, there was a net increase in frequency similar to the cumulative increases caused by the individual stimuli. Boolean logic gates were derived from the measured frequency change.

1. Introduction

1.1. Organism introduction

The myxomycete *Physarum polycephalum* is a single celled true slime mould which can grow to several centimetres in diameter, living on decaying wood and digesting organic matter such as bacteria and decomposing vegetation. The yellow cellular plasmodium consists of a multinuclear cytoplasm encompassed by a large single membrane, it's shape is determined by the local environment; combinations of nearby chemical sources, light, temperature and other factors affect the direction and shape which *P. polycephalum* grows (Carlilie, 1970; Durham and Ridgway, 1976; Knowles and Carlilie, 1978; Nakagaki et al., 2000, 2004). The organism has been shown to find food sources in mazes as well as being used for binary logic computation, shortest path estimation, solving geometric problems and approximating man-made transport networks (Adamatzky, 2010a, 2012; Latty and Beekman, 2009; Nakagaki et al., 2001; Nakagaki and Guy, 2008; Shirakawa and Gunji, 2010).

When attractants and repellents are in close proximity to *P. polycephalum*, the cell builds a spatial network of protoplasmic tubes. The cell's protoplasmic tube network connects to sources of attractants along the shortest path while avoiding repellent sources. Some attractants are indicators of potential food sources (Knowles and Carlile, 1978) however there are some chemicals that are chemoattractants but not food sources, instead they could be signalling chemicals from plants and insects in *P. polycephalum*'s natural environment (Costello and Adamatzky, 2013; Whiting et al., 2014). Alternatively these chemicals could act directly on the motor function or other key metabolic pathways within *P. polycephalum*. There are also chemicals which act as repellents, which the organism grows away from (Carlilie, 1970; Knowles and Carlile, 1978).

Exposing *P. polycephalum* to light invokes a negative response, causing the cell to migrate away from the source of light (Adamatzky, 2013a). *P. polycephalum* shows strong photoavoidance to white (Nakagaki et al., 1999; Wohlfarth-Bottermann and Block, 1981), ultra-violet (Nakagaki and Ueda, 1996) and blue light (Block and Wohlfarth-Bottermann, 1981). Light is also known to initiate the sporulation phase in the organism (Daniel and Rusch, 1962; Golderer et al., 2001; Kroneder, 1999; Takagi and Ueda, 2010), so *P. polycephalum* is capable of detecting different frequencies and intensity of light. Studies reported that warmer temperatures increased the frequency of shuttle streaming oscillations (Kamiya, 1959; Tauc, 1954). Durham and Ridgway observed migration of *P. polycephalum* towards a warmer portion of an agar substrate, with growth occurring along the temperature gradient from 20 to 34 °C (Durham and Ridgway, 1976). However, no electrical potential recordings had previously been made when heat was employed

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as a stimulus. *P. polycephalum* is evidently able to survive in a wide range of temperatures in the wild, indeed the authors have maintained cultures and observed growth from 2 °C to 35 °C. *P. polycephalum* is often incubated and experimented with at between 20 and 35 °C (Coggin and Pazun, 1996; Durham and Ridgway, 1976). Nakagaki demonstrated protoplasmic vein formation due to generation of regular oscillations when applying transient increases of 10 °C above room temperature (Nakagaki et al., 1996, 2000). Since these papers have noted the increase in oscillation frequency when *P. polycephalum* was warmed, it was decided that electrical recording of a protoplasmic tube should be performed and would constitute one stimulus while investigating sensory fusion of *P. polycephalum*.

It is not understood how *P. polycephalum* combines data from several opposing or additive stimuli. It is well documented that *P. polycephalum* responds to different environmental stimuli as described above, however there are several attractant and repellent stimuli present simultaneously within the natural environment, and how *P. polycephalum* computes, prioritises and acts when exposed to these various stimuli is totally unknown. The slime mould moves and grows by employing protoplasmic shuttle streaming, where waves of contraction and relaxation of the membrane forces cytoplasm to flow through protoplasmic tubes, extending the tip towards an attractant; it is thought that repellents inhibit this streaming. Time-lapse photography and video microscopy has shown the forward and backward flow of cytoplasm; the oscillation occurs with a period of between 50 and 200 s. This oscillation has also been measured electrically (Adamatzky and Jones, 2011; Whiting et al., 2014) and the frequency correlates approximately with that measured optically.

1.2. Known stimuli in Physarum polycephalum

Basic carbohydrates are the most tested chemotactic substances, with glucose, galactose and manose being the strongest attractants of those investigated in the literature (Carlilie, 1970; Kincaid and Mansour, 1978b; Knowles and Carlile, 1978). Often a culture of *P. polycephalum* is fed with oat flakes, which are approximately 70% carbohydrate. It has also been demonstrated that Agar itself is a chemo-attractant, with 8% concentrations of agar gel producing stronger responses than oat flakes by way of increased frequency (Whiting et al., 2014). Non-food sources also have chemotactic properties with enzyme cyclic 3′,5′-AMP phosphodiesterase inhibitors among the compounds tested (Kincaid and Mansour, 1979), additionally volatile organic chemicals showed chemotactic properties (Costello and Adamatzky, 2013; Whiting et al., 2014). While all the studies of attractant and repellent stimuli on *P. polycehpalum* have been performed individually, there is no study detailing the effect on the growth or frequency of streaming in the organism while changing multiple variables, but there is presumably a basic hierarchy of stimuli, which controls *P. polycephalum*'s behaviour. This study documents the effects of combinations of multiple stimuli on the oscillation frequency and spatial growth of *P. polycephalum*.

1.3. Multisensory integration

It is well known that other organisms combine several senses; every organism which can sense its environment must perform some kind of sensory fusion, to understand its surroundings and plot resultant behaviour. Multisensory integration, or sensory fusion, in animals more developed than sponges is performed by a nervous system (Calvert et al., 2004), while simple or unicellular organisms have nervous system homologs of intra- and inter- cellular communication pathways (Sakarya et al., 2007). Prokaryotes have a system of biochemical processes which govern behaviour; stimuli driven protein transmitter and receptor driven responses (Bourret, 2006), often having multi-component levels (Bren and Eisenbach, 2000) allowing for competitive or inhibitive binding on receptor sites which, when responding to multiple stimuli, is akin to multisensory integration (Clarke and Voigt, 2011). Eukaryotic fungi have also demonstrated multi component stimuli response signalling pathways through genome analysis (Catlett et al., 2003). It is likely that *P. polycephalum* uses multi-component pathways to perform multisensory integration; chemotaxis, phototaxis thermotaxis and other stimuli are combined to change parameters of protoplasmic streaming which ultimately governs the direction of movement and life cycle stages.

1.4. Logic gates

Boolean logic is a field of mathematics which describes binary arithmetic, calculating truth values for logic inputs; a logic gate is the physical manifestation of a Boolean operation. Boolean logic is fundamental to computer science as electronic logic gates form the basis of digital operations in computers. The logic operations AND, OR and NOT are the basic operations of Boolean logic; combinations of these basic functions can produced derived gates such as XOR or more complex multi-gate logic. Modern digital logic gates are made up of discrete electronic components such as transistors and resistors, which can be miniaturised and operate at fractions of a second. Organism based logic gates have also been attempted, scientists have implemented a Boolean NOR gate in *Escherichia coli* using fluorescence expression (Tamsir et al., 2011). It has been shown that bacteria inherently calculate Boolean logic during DNA transcription (Bonnet et al., 2013). Yeast too, show AND-gate like control of DNA promoters (Teo and Chang, 2014); even mammalian cells have multi-input logic control of gene regulation which has been adapted into Bio-Logic gates (Kramer et al., 2004). *P. polycephalum* is also capable of computing Boolean logic AND, OR and NOT gates (Tsuda et al., 2004) based on growth along agar channels towards attractants. Other papers have added to this field with cascaded *P. polycephalum* gates (Adamatzky, 2010b; Jones and Adamatzky, 2010; Schumann and Adamatzky, 2011) producing more complex combinational logic such as a one-bit adder. This paper aims to investigate sensory fusion in *P. polycephalum* and implement various computational functions.

2. Method

2.1. Electrical measurement of Physarum polycephalum

P. polycephalum was grown in accordance with the common agar culture method, described in detail in a previous paper (Whiting et al., 2014). For experimentation the protoplasmic tube was grown on a customised 9 cm petri dish, similar to the setup we showed previously (Adamatzky, 2013a; Whiting et al., 2014) with two 50 mm long strips of 10 mm wide electrically conductive aluminium tape (Farnell, UK) aligned in a petri-dish with a 10 mm gap in the middle; 1 ml 2% non-nutrient agar drops were placed on the tape tips as demonstrated in Fig. 1 to form hemisphere electrodes.

A *P. polycephlum* inoculated oat flake was placed on the ground electrode and a bare oat flake was placed on the recording electrode; over the course of several hours to days a protoplasmic tube would grow across the gap to digest the bare oat flake, when this had occurred the Petri dish was ready for recording. Electrical measurement of *P. polycephalum* was performed on the tube between the two agar electrodes by connecting the ends of the conductive tape to a PicoLog ADC-24 high resolution analogue-to-digital data logger (Pico Technology, UK); this was connected via USB to a laptop installed with PicoLog Recorder software to record the data.