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Embodied models of delayed neural responses: Spatiotemporal categorization and predictive motor control in brain based devices

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ABSTRACT

In order to respond appropriately to environmental stimuli, organisms must integrate over time spatiotemporal signals that reflect object motion and self-movement. One possible mechanism to achieve this spatiotemporal transformation is to delay or lag neural responses. This paper reviews our recent modeling work testing the sufficiency of delayed responses in the nervous system in two different behavioral tasks: (1) Categorizing spatiotemporal tactile cues with thalamic "lag" cells and downstream coincidence detectors, and (2) Predictive motor control was achieved by the cerebellum through a delayed eligibility trace rule at cerebellar synapses. Since the timing of these neural signals must closely match real-world dynamics, we tested these ideas using the brain based device (BBD) approach in which a simulated nervous system is embodied in a robotic device. In both tasks, biologically inspired neural simulations with delayed neural responses were critical for successful behavior by the device.

1. Introduction

In order to respond to real world stimuli at the appropriate time, the nervous system must transform stimuli in space and time or hold a signal for a time period before responding behaviorally. For example, consider a rodent that sweeps its whiskers along an object to determine its shape. How are the sensory impulses combined across time and across multiple whiskers to categorize the object? In another instance, when a rabbit receives a puff of air in the eye, which is paired with a stimulus predicting the occurrence of the air puff, it learns over time to close its eyelid precisely in time to protect the eye from the noxious stimulus. After the noxious stimulus arrives, how is the predictive stimulus maintained long enough to allow associative learning to take place?

Nervous systems integrate signals over durations ranging from microseconds (e.g. delay lines in the owl auditory system, (Carr & Konishi, 1990)) to seconds (e.g. persistent firing during working memory tasks, (Funahashi, Bruce, & Goldman-Rakic, 1989; Fuster & Alexander, 1971)). A mechanism for integrating signals over time is provided by lag cells, found in the visual thalamus of the cat, which respond to a visual stimulus with a characteristic delay that varies from cell to cell (Saul & Humphrey, 1992). This type of cell can function in a similar manner to delay lines, and has been proposed to provide a mechanism for direction selectivity in simple cells in the visual cortex of the cat (Jagadeesh, Wheat, Kontsevich, Tyler, & Ferseter, 1997).

Additional mechanisms for maintaining a signal over time have been found at the synapse. For example, long term depression of parallel fiber synapses onto Purkinje cells is maximal when parallel fibers are stimulated within a time window from 125 to 250 ms prior to climbing fiber activation (Chen & Thompson, 1995). A candidate "eligibility trace" mechanism is embodied in a nonlinear calcium response in these synapses which is maximal when the parallel fiber input precedes climbing fiber activation from 50 to 200 ms (Wang, Denk, & Hausser, 2000).

To test models of delayed neural responses, we used an approach employing brain based devices (BBDs), in which a simulated nervous system is embodied in a robotic device, to test mechanisms of delayed neuronal responses during behavior (Almassy, Edelman, & Sporns, 1998; Edelman et al., 1992; Krichmar & Edelman, 2002, 2005; Krichmar, Nitz, Gally, & Edelman, 2005; Seth, McKinstry, Edelman, & Krichmar, 2004a, 2004b). The BBD approach forces the modeler to consider how the timescale of neural mechanisms matches the timescale of behavior. Physical embodiment is critical for understanding issues of timing in the real world. Virtual sensory input and simulated motor output are designed by the modeler and can inadvertently bias a neural simulation. However, when embedding a nervous system simulation in a behaving device, the device's behavioral response must match its sensorimotor signals. Moreover, physical embodiment in such a device emphasizes many of the challenging aspects of discrimination in the real world: noisy sensors, movement variation, and complexity of a real-world environment.

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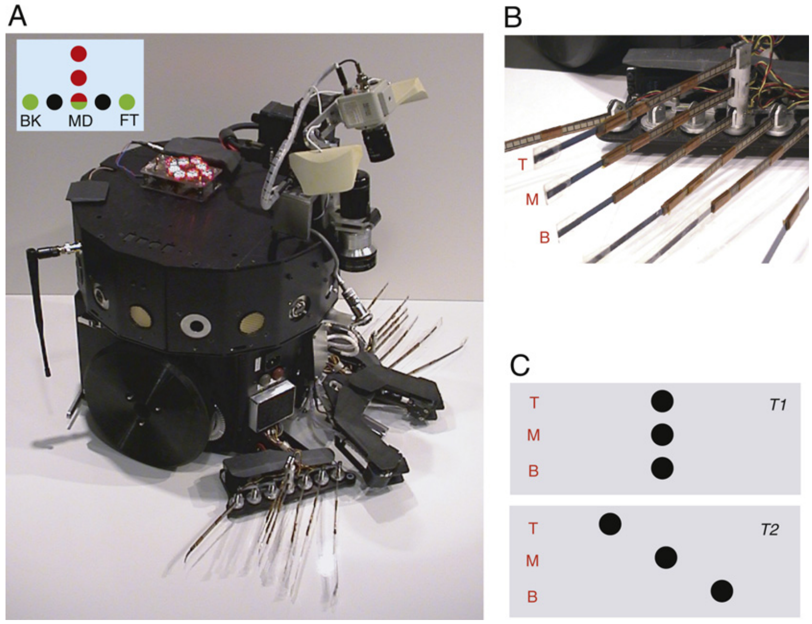

Fig. 1. A. Darwin IX with its left and right whisker arrays. The arrangement of a whisker array is shown in the inset. Each array has 7 whiskers arranged in a row of 5 and a column of 3. Whiskers used for wall following are marked in white (FT, MD, BK). Whiskers that provide input to the neural simulation are marked in black. Note that one whisker (white/black) is used for both purposes. B. Detail of a whisker array: The top (T), middle (M), and bottom (B) whiskers in the column are labeled; these whiskers provide input to the neural simulation. C. Schematic of textures T1 and T2. Each texture consists of pegs embedded in a wall; pegs are aligned in rows corresponding to the whiskers in a column. Pegs in the top row deflect the top whisker (T), and similarly for pegs in the middle row (M) and the bottom row (B).

By using a real-world environment, not only is the risk of biases reduced, but the experimenter is also freed from the burden of constructing a highly complex simulated environment.

This paper describes recent work testing biologically inspired mechanisms of delayed neural responses that facilitate categorization of spatiotemporal tactile cues and predictive cerebellar motor control using the BBD approach. We find that a population of lag-cell-like neuronal units that respond to artificial whisker deflections in a moving device is sufficient to support texture discrimination of whisker–barrel responses lasting approximately one second. In a task where the device's own movement causes visual optic flow, we show that a delayed eligibility trace mechanism at simulated Purkinje cell and deep cerebellar nuclei cell synapses allows for an association in which the visual cue predicts a future collision.

2. Spatiotemporal pattern discrimination in Darwin IX

Haptic sensory information provided by mystacial vibrissae (whiskers) of the rat allows the animal to discriminate among different textures in its environment (Harvey, Bermejo, & Zeigler, 2001; Prigg, Goldreich, Carvell, & Simons, 2002). This requires the integration of sensory input from the whiskers across time and space, providing an excellent model system for exploring spatiotemporal pattern categorization. To explore how haptic data may be integrated into perceptual categories, we equipped a BBD, Darwin IX, with artificial whiskers and a simulated nervous system based on the neuroanatomy of the rat somatosensory system.

In our experiments with Darwin IX, the device autonomously explored a walled environment containing two distinct textures each consisting of various patterns of pegs embedded in the walls. It became conditioned to avoid one of the textures by association of this texture with an innately aversive stimulus (i.e. a change in reflectivity of the environment's flooring). This aversive stimulus was used in an experimental paradigm analogous to fear-conditioning with a 'foot-shock' at particular locations in the environment. Similar to a rodent in such a conditioning paradigm, Darwin IX demonstrated its aversive behavior by stopping ("freezing") and then moving away from noxious stimuli.

We tested the idea that a diverse population of neuronal units with varying sensory response delays could bridge the temporal gaps brought about by moving a tactile sensor across a spatial pattern. Such a scheme has been found in the visual system of the cat (Saul & Humphrey, 1992) and may be a mechanism for direction selectivity in the primary visual cortex (Jagadeesh et al., 1997). Delayed neuronal responses, which have been found in the perirhinal cortex of the rat, can be as long as four seconds from stimulus onset (Beggs, Moyer, McGann, & Brown, 2000).

2.1. Darwin IX: Construction and experimental paradigm

Darwin IX is based on a mobile robotic platform (Nomadic Technologies) augmented by a whisker array on each side (Fig. 1A). Each array consists of seven whiskers arranged in a single column of three and single row of five where one of the whiskers was both the row and column (see Fig. 1A, inset). The whisker column supplied input to the simulated nervous system, while whisker row supported innate avoidance and wall-following behaviors. The whiskers are made of two polyamide strips, placed back to back, that emit a signal proportional to the bending of the strip (Abrams, Gentile Entertainment).

Darwin IX's default behavior was to move forward in a straight line at a speed of ~8 cm/s. Darwin IX also had an innate wall-following capability based on signals from the first, third, and fifth whiskers in the whisker row. The innate wall-following behavior was programmed with a simple feedback controller that maintained these three whiskers within a desired range (see Seth et al. (2004b) for details).

Darwin IX had an innate freezing/avoidance response which was triggered upon detection of a simulated foot-shock by a downward pointing infra-red sensor that measured changes in reflectivity of floor surface. Construction paper, which was the same color as the floor but more reflective, was placed upon the floor in locations to trigger an innate aversive response. This