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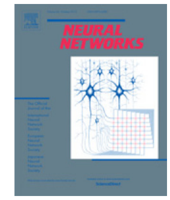

Improved system identification using artificial neural networks and analysis of individual differences in responses of an identified neuron

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ABSTRACT

Mathematical modelling is used routinely to understand the coding properties and dynamics of responses of neurons and neural networks. Here we analyse the effectiveness of Artificial Neural Networks (ANNs) as a modelling tool for motor neuron responses. We used ANNs to model the synaptic responses of an identified motor neuron, the fast extensor motor neuron, of the desert locust in response to displacement of a sensory organ, the femoral chordotonal organ, which monitors movements of the tibia relative to the femur of the leg. The aim of the study was threefold: first to determine the potential value of ANNs as tools to model and investigate neural networks, second to understand the generalisation properties of ANNs across individuals and to different input signals and third, to understand individual differences in responses of an identified neuron. A metaheuristic algorithm was developed to design the ANN architectures. The performance of the models generated by the ANNs was compared with those generated through previous mathematical models of the same neuron. The results suggest that ANNs are significantly better than LNL and Wiener models in predicting specific neural responses to Gaussian White Noise, but not significantly different when tested with sinusoidal inputs. They are also able to predict responses of the same neuron in different individuals irrespective of which animal was used to develop the model, although notable differences between some individuals were evident.

1. Introduction

Mathematical modelling has been used for many years to understand and describe biological systems, including their dynamics (Gamble & DiCaprio, 2003), the effects of experimental manipulation (Marder & Taylor, 2011), the impact of noise and variability (Sarkar, Christini, & Sobie, 2012) and how they change with ageing and disease (Horn, Ruppin, Usher, & Herrmann, 1993).

Linear and non-linear models, such as those derived by Wiener's method, have been widely used to quantify the behaviour of the nervous system (Kondoh, Okuma, & Newland, 1995; Marmarelis, 2004; Marmarelis & Naka, 1972). While these methods are powerful and provide quantitative descriptions of the linear dynamic transfer characteristics of a system (Marmarelis & Naka, 1973a) they can contain estimation errors due to background noise (Dewhirst, Angarita-Jaimes, Simpson, Allen, & Newland, 2012) and possibly overtraining of models (Tötterman & Toivonen, 2009). These estimation errors in turn produce erroneous predictions of the system's responses (Gamble & DiCaprio, 2003). Moreover, Wiener methods are not always applicable (Angarita-Jaimes et al., 2012) as the system expansion of the Wiener representation does not necessarily converge for all input functions (Palm & Poggio, 1977). In addition, such mathematical models have, in general, been fitted to the response to a stimulus of an individual (Dewhirst et al., 2012; DiCaprio, 2003; Marmarelis & Naka, 1972; Newland & Kondoh, 1997), without verifying if a particular model is a good representation of the population as a whole (Marder & Taylor, 2011). Using an average response to represent the population responses may be misleading due to different characteristics inherent to each individual (Goldman, Golowasch, Marder, & Abbott, 2001).

Recently, there has been an interest in modelling dynamic systems using Artificial Neural Networks (ANNs) since they have been found to model accurately many continuous functions (Haykin, 1999). In particular, they have been applied to chemical processes, plant identification and controller structures (Xing & Pham, 1995), and have been shown to have good predictive performance

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in simulations of non-linear dynamic systems (Hunt, Sbarbaro, Zbikowski, & Gawthrop, 1992), financial markets (White, 1988), classification (Suraweera & Ranasinghe, 2008) and pattern recognition (Bishop, 1995). The choice of ANNs to model so many different systems is, in part, due to their flexibility, adaptability and generalisation capabilities (Benardos & Vosniakos, 2007) and their easy application in software and hardware devices (Hunt et al., 1992; Twickel, Büschges, & Pasemann, 2011). They have been applied successfully as robot locomotion controllers (Beer, Chiel, Quinn, Espenschied, & Larsson, 1992; Chiel, Beer, Quinn, & Espenschied, 1992; Cruse et al., 1995) by imitating the nervous systems that produce motion in insects' legs. Taken together these characteristics make them a powerful tool for non-linear model description and control system implementation.

The nervous system of insects, such as the desert locust, is relatively simple compared to mammals and a number of the constituent neurons with specific function are identifiable in different animals (Burrows, 1996) making them ideal to test the potential of ANNs to model neuronal responses, to analyse their generalisation abilities from one animal to the next and to understand individual differences in identified neurons. Imposed movement of the tibia, relative to the femur of the locust results in a resistance reflex that opposes the applied movement. This reflex can aid during stance and walking, in situations such as tripping or under the influence of other external forces (Field & Matheson, 1998). The Fast Extensor Tibiae (FETi) motor neuron, which is activated during reflex movements, is identifiable in every animal and has been studied for many decades and various mathematical models have been developed to understand its dynamics (Dewhirst et al., 2012; Dewhirst, Simpson, Allen, & Newland, 2009; Newland & Kondoh, 1997). The linear and non-linear properties of the FETi responses are well known, however, computational limitations in parameter estimation and the noise and variability of individual recordings have yet to be understood in detail (Angarita-Jaimes et al., 2012; Dewhirst et al., 2012). These challenges provide the motivation to test and validate ANNs as an effective mathematical method to model and describe the neural response across individuals.

The aim of this work was threefold: first to develop a method to design ANNs to model FETi responses and to determine whether they provide an improved performance over previous mathematical models; second, to understand the generalisation properties of the ANNs across individuals and to different input signals, and third, to understand individual differences in an identified neuron between individuals. To address these issues the performance of the ANN models was measured by their ability to predict responses of an individual as well as different individuals and their responses to different input stimuli.

2. Materials and methods

2.1. Data recording and post-processing

Adult male and female desert locusts (*Schistocerca gregaria*, Forskål) were mounted ventral surface uppermost in modelling clay and fixed firmly with one hind leg rotated through 90° and the femur–tibia angle set to 60° with the anterior face up. The apodeme of the femoral chordotonal organ (FeCO) was exposed by cutting a small window in the cuticle of the distal femur and grasped with a pair of forceps attached to a shaker (Ling Altec 101, LDS Test and Measurement) (Fig. 1). The apodeme was cut distally to avoid movement of the tibia thus opening the reflex-control loop. The thoracic ganglia were then exposed by removing the cuticle of the ventral thorax and also the air sacs and small trachea around the ganglia. A wax covered silver platform was then placed under the meta- and mesothoracic ganglia and the connectives cut posterior to the metathoracic ganglion. The ganglionic sheath

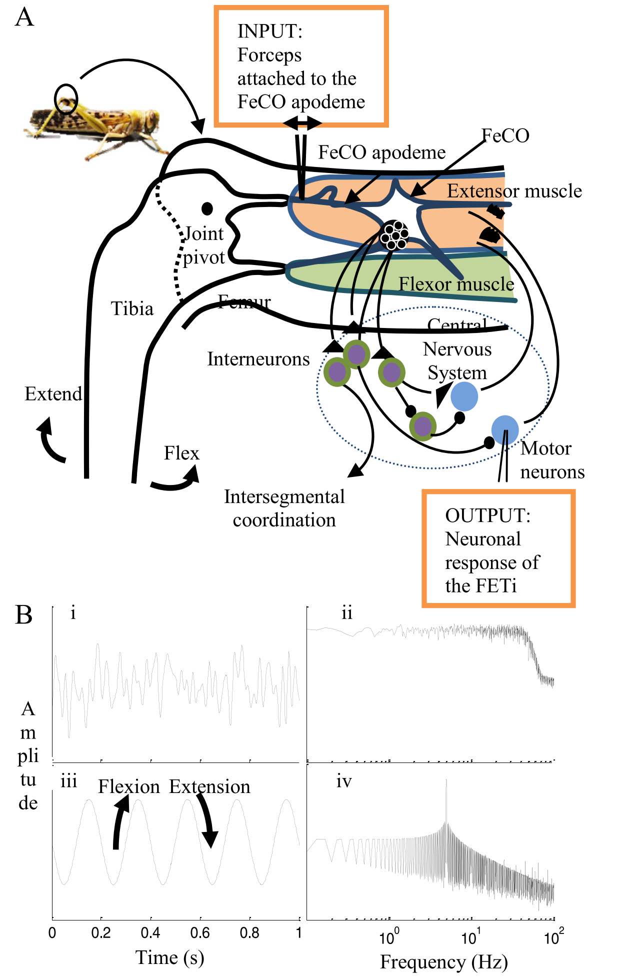

Fig. 1. (A) The components of the reflex control loop. The input was applied to the FeCO apodeme through a shaker and the output was the response of the FETi motor neuron. (B) The stimuli applied to the system included a band-limited Gaussian White Noise input shown in (i) the time domain and (ii) the frequency domain. A 5 Hz sinusoidal input was also applied and is shown in (iii) in time domain and (iv) in frequency domain.

was then softened by treating directly with protease (Sigma Type XIV) for 1 min (Newland & Kondoh, 1997). Intracellular recordings were made using glass microelectrodes, filled with 3M potassium acetate and with DC resistances of 50–80 MΩ, by driving an electrode through the sheath and into the soma of FETi. FETi receives monosynaptic and polysynaptic inputs from the femoral chordotonal organ (FeCO) that monitors movements of the tibia about the femur and which together underlie a simple resistance reflex that resists imposed movements of the hind leg (Field & Matheson, 1998).

The synaptic signals recorded in FETi were amplified and digitised with a sampling frequency of 10,000 Hz using a data acquisition board (USB 2527 data acquisition card, Measurement Computing, Norton, MA, USA) and stored for later analysis. They were then re-sampled at 500 Hz in Matlab® following a 3rd order low-pass anti-aliasing filter with a cut-off frequency of 250 Hz to remove residual high frequency noise (the spectrum of the recording is very low above 150 Hz). This re-sampling reduced the size of the files to process and, therefore, the computational time, without removing frequency components of interest. A high pass Butterworth filter of 3rd order and cut-off frequency of 0.2 Hz was applied to eliminate any slow time varying drift. A relatively small sample size of five was selected so that individual differences and similarities could be readily described, in addition to comparing