Journal of Computational Neuroscience manuscript No.
(will be inserted by the editor)

Predictive control of intersegmental tarsal movements in an insect

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Received: date / Accepted: date

Abstract In many animals intersegmental reflexes are important for postural and movement control making them ideal candidates for bio-inspired development design of treatment in neurological injuries such as drop foot and they can also be useful in robot design. Here we analyse an intersegmental reflex of the foot (tarsus) of the locust hind leg, which raises the tarsus when the tibia is flexed and depresses it when the tibia is extended. A novel method is described to measure and quantify the intersegmental responses of the tarsus to a stimulus to the femoro-tibial chordotonal organ. An Artificial Neural Network, the Time Delay Neural Network, was applied to understand the properties and dynamics of the reflex responses. The aim of this study was twofold: first to develop an accurate method to record and analyse the movement of an appendage and second, to apply methods to model the responses using Artificial Neural Networks. The results show that Artificial Neural Networks provide accurate predictions of tarsal movement when trained with an average reflex response to Gaussian White Noise stimulation compared to autoregressive models. Furthermore, the Artificial Neural Network model can predict the individual responses of each animal and responses to others inputs such as a sinusoid. A detailed understanding of such a reflex response could be included in the design of orthoses or functional electrical stimulation treatments to improve walking in patients with neurological disorders.

Keywords Reflex · Artificial Neural Network · Metaheuristic Algorithm · Evolutionary Programming · Particle Swarm Optimisation · Locust · Motor Control.

1 Introduction

The impairment of motor function in disease and ageing is an issue that costs health services enormous sums each year (Hanson et al. 2006). Individuals with neuromuscular disorders, such as proprioceptive deficits, show degradation in movement (Goble et al. 2009) where they are unable to sense the static or dynamic position of a joint, or limb segment (Gandevia et al. 2002). Individuals who survive a stroke may be left with foot drop making it difficult for them to raise the front of the foot (Stewart 2008), while patients who have suffered an amputation, need an improved understanding of neuromuscular control in healthy individuals to design better and optimised treatment, such as rehabilitation, or the use of prostheses and orthoses (He et al. 2001).

Analysing neuromuscular control in detail is therefore important to understand how the nervous system generates and controls movements in any situation (Webb et al. 2004). Furthermore, features of neuromuscular control can be exploited to improve the design of engineering control systems. The implementation of bio-

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inspired designs based on neuromuscular control has made important contributions in robotic engineering and autonomous systems (Delcomyn 2004), such as an improved gait and stability during walking in robotics (Dürr et al. 2004, Ijspeert 2008, Lewinger et al. 2011, Webb 2002).

Insects represent ideal models for studies of neuromuscular control since their nervous systems are relatively simple, the neurons involved in movement control are few and often identifiable and activity in many can be directly related to behaviour (Burrows 1996). Moreover, their limb design and neural control of movement are similar to humans (Pearson 1995, Ritzmann & Büschges 2007) having highly efficient control systems (Webb et al. 2004). Arthropods are highly adaptable and capable of moving over any type of terrain (Ritzmann & Büschges 2007). Such adaptability is currently needed in the autonomous control of walking robots, where irregular terrains and obstacle negotiation are still limited (Chen et al. 2011).

Here we develop methods to analyse and model control of an intersegmental reflex that consists of a movement of the tarsus around the tibio-tarsal joint in response to changes in the femoro-tibial joint angle (Burrows & Horridge 1974) that is thought to increase stability and affect postural control (Burrows 1996, Clarac et al. 1978). The movement is neurally mediated by the Femoral-Chordotonal Organ (FeCO) at the femoro-tibial joint of the hind leg (Burrows & Horridge 1974, Field & Burrows 1982). Similar reflexes to this one in the locust have evolved in other insects, such as the New Zealand Weta (Field & Rind 1981), in stick insects (Büschges & Gruhn 2007, Cruse et al. 1992) and in crustaceans (Clarac et al. 1978) suggesting an underlying control principle in arthropods related to stability and postural control that is also found in mammals (Halbertsma 1983, Pearson 1993).

The aim of the paper is to provide a generic model for the control of the tarsus and to assess the extent to which this is consistent between individuals. This paper describes novel methods to record and quantify reflex responses of the locust hind leg tarsus, and the application of a previously validated mathematical approach to model and predict biological responses using Artificial Neural Networks (ANNs) (Costalago Meruelo et al. 2016). It then asks whether individual responses or an average response from a group of animals should be used to model and study the system.

2 Methods

2.1 Experimental Methods

2.1.1 Video recordings

Adult male and female locusts (*Schistocerca gregaria Forskål*) were mounted in modelling clay ventral side up, with the left hind leg femur fixed at an angle of 30° to the abdomen and with the tibia free to move. All other legs, thorax, abdomen and head were fixed with modelling clay to prevent movement. The tibia was moved passively from 0° (fully flexed) to 180° (fully extended) and back to a fully flexed position in a series of passive steps performed using a micromanipulator, stopping every 10° for 5 s. The tibio-tarsal angle was recorded every 10° of femoro-tibial joint angle. This procedure was repeated five times for each individual, and the individual responses averaged to reduce the intra-subject variability. To determine whether the tarsal intersegmental reflex contained a mechanical component, or if it was purely neurally mediated, the same experiment was performed in each animal after nerve N5, containing the axons of motor neurons innervating tarsal muscles and sensory neurons was cut (Burrows 1996).

2.1.2 Shaker and laser recordings

In a second experiment, adult locusts were fixed in modelling clay ventral side up, with the femur fixed at 60° to the abdomen and with the tibia fixed at an angle of 60° to the femur, an angle which represents the middle of the linear range movement of the FeCO apodeme (Dewhirst et al. 2013).

The FeCO was exposed by removing a small piece of cuticle at the distal end of the femur, and the cavity perfused with locust saline. The FeCO apodeme (Kondoh et al. 1995) was grasped with a pair of fine forceps attached to a shaker (permanent magnet shaker LDS V101). The shaker was driven by a signal generated in Matlab®, which was amplified and converted to analogue via a digital-to-analogue converter (DAC) (USB 2527 data acquisition card (Measure Computing Norton, MA, USA). The movement of the tarsus was recorded with a Keyence laser displacement sensor (LK G3001V controller, LK G32 Head, Keyence) aimed at the last segment of the tarsus, the unguis.

The stimulus signals to estimate the model were designed and applied through Matlab®. Locusts walk at a step frequency of approximately 3 Hz (Burrows & Horridge 1974) and for this reason, Gaussian White Noise (GWN) was produced in the band-limited range between 0 - 5 Hz, and a 1 Hz sinusoidal input simulating walking was applied also, all with a duration of 40 seconds, during which the response was constant. The maximum peak-to-peak amplitude of the input signals was approximately 1 mm, which represents a femorotibial displacement of 90 (Dewhirst et al. 2013, Field & Burrows 1982). The signals were scaled so that approximately 99.7 % of their values fell within the femorotibial joint angle between 20° and 100° (0.9 mm of displacement of the FeCO apodeme). The frequency and phase response of the equipment was linear between 0 and 200 Hz.

GWN was chosen for system identification in line with common practice, since it covers a wide range of frequencies and amplitudes. A series of sine-waves would require much longer recordings, as for example at 0.1 Hz, 10 s are needed for just one cycle. The GWN created in MATLAB using its pseudo random number generator, randn, and then low pass filtered using a 5th order Butterworth filter with a cut-off frequency of 5 Hz, applied in the forward and reverse directions for zero phase shift. The recordings were performed five times for each animal and each stimulus which were later averaged to reduce the noise and intra-subject variability.

2.2 Mathematical Methods

2.2.1 Data Post-Processing

Recordings of tarsal movement from eight locusts were obtained at a sampling frequency of 10,000 Hz. The mean value was subtracted from the recordings to eliminate any effect of laser position. To eliminate low frequency noise and spontaneous movements not related to the applied stimulus, a third order high-pass Butterworth filter was applied with a cut-off frequency of 0.2 Hz. The data was then resampled to 500 Hz after applying an anti-alias filter (third order Butterworth with a cut-off frequency of 200 Hz), thereby reducing file size and processing time. Both Butterworth filters were applied in the forward and reverse directions to avoid introducing any phase delay. An average reflex response was calculated using the responses from the eight individuals to test whether the average was representative of the system or if individual responses provided better models.

2.2.2 Autoregressive Model

To provide a first assessment of the responses, an autoregressive model (AR) of the tarsal movements was developed. This model assumed that the tarsal response was a combination of current and past input samples. Considering the discrete form, the response of the system can be characterised as:

$$z(t) = \sum_{\tau=0}^{T-1} h(\tau)u(t-\tau) + v(t) \tag{1}$$

where $z(t)$ is the response, $h(\tau)$ is the transfer function of the system, $u(t-\tau)$ is the stimulus and $v(t)$ is the representation of all the noise in the system (internal and external). To calculate the parameters of $h(\tau)$ the least square method was used. The equation of the Minimum Mean Square Error cost function (Haykin 2004) is rearranged and it is assumed that the prediction is a linear function of the impulse response function. Combining the cost function with the system response, the least square estimate of the AR parameters can be obtained by:

$$\widehat{h} = (U^TU)^{(} - 1)U^Tz \tag{2}$$

where z is the output vector, U is the matrix of delayed input vectors (Ljung 1998) and $\widehat{h}$ the estimated model parameters. For a full derivation see (Dewhirst 2012).

To assess the performance of the mathematical models, the Normalised Mean Square Error (NMSE) (Equation 3) was used, when the model was trained with 2/3 of the data and tested with the 1/3 of data not used in training. This value gives an indication of the differences between the signals, where a 0% error represents no differences between the signals and a 100% represents a constant zero-valued response compared with the signal.

$$NMSE(\%) = 100 \cdot \frac{\sum_{i=1}^{N} y_i - {\widehat{y}_i}^2}{\sum_{i=1}^{N} {y_i}^2} \tag{3}$$

2.2.3 Artificial Neural Networks

To further model the intersegmental reflex responses of the tarsus a dynamical artificial neural network, a Time Delay Neural Network (TDNN) (Waibel et al. 1989), was used. This network also used delayed versions of the input to estimate the output, turning the static Feed-Forward Network into a dynamic network (Haykin 2004). Using this, we assumed the reflex responses to be a combination of current and past input samples. The network was formed by an input node, an output node and a number of hidden layers with hidden nodes. The activation function for each hidden node was a sigmoid. The output node had a linear function, so all the non-linear calculations were performed inside the network. The training algorithm for the network was the Levenberg-Marquadt back propagation algorithm, which has higher accuracy and faster convergence time than classical back-propagation algorithms (Bishop et al. 1995). The number of delayed samples used in the input was set to 100 samples, which was based on preliminary work (optimisation of decrease in NMSE as the delay increases for a set architecture). The architecture of the network was optimised using the recorded data with a metaheuristic algorithm, where the number of layers and neurons for the each of the responses recorded is obtained. The full description of the methodology for the network design and training is shown elsewhere (Costalago Meruelo et al. 2016).

3 Results

3.1 Intersegmental Reflex Responses

3.1.1 Static Intersegmental Reflex Responses

Movement of the tibia to different fixed femoro-tibial angles led to tarsal positions dependent on femoro-tibial angle (Fig. 1). The average response of eight animals showed that the tibio-tarsal angle strongly depended on the femoro-tibial joint angle. As the tibia was extended, the tarsus was depressed and as the tibia was flexed the tarsus was levated, thereby maintaining a constant position relative to the abdomen (Burrows & Horridge 1974). A Spearman's rank correlation coefficient of the average response between the tibio-tarsal angle and the femoro-tibial angle was calculated and the results (r = 1.00, $p < 0.001$) for both extension and flexion of the tibia, confirmed that changes in the femoro-tibial joint angle and changes in the tibio-tarsal joint angle were correlated. Correlations for extension in individual animals were always equal to 1.0 and, for flexion, were between 0.98 and 1.0 (except in one animal where it dropped to 0.92).

Analysis using regression showed that the relationship between the femoro-tibial joint angle and the tibio-tarsal joint angle is non-linear. Although the responses differed slightly between flexion and extension of the tibia, both could be represented, in part, through linear regression. During extension of the tibia, the tarsus was depressed following a linear regression with a slope of $\beta = 0.32$ (R2 = 0.98, $p < 0.001$), suggesting an almost linear response below femoro-tibial angles of 150°. During flexion of the tibia, the tarsus was elevated following a linear regression with slope of $\beta = 0.29$ (R2 = 0.85, $p < 0.001$). In this case, the tarsal response did not follow a straight line as in tibial flexion, indicating higher levels of non-linearity during flexion than during extension of the tibia.

The movements of the tarsus were not simply dependent on femoro-tibial joint angle, but also the direction from which an angle was approached. During extension, the tibio-tarsal angle increased gradually until the leg was fully extended, increasing faster near the fully extended tibial positions (above 150°). During flexion the tibio-tarsal angle initially decreased slowly (small changes in tibio-tarsal angle to changes in femoro-tibial angle), but then more steeply after the tibia reached 60°, and even more steeply for angles lower than 30°. To establish whether the reflex was purely neuronal or whether it contained a mechanical component, the experiment was repeated in each animal with nerve N5 severed. The results show that when nerve N5 was cut little movement of the tarsus was evident, however a Pearson's correlation test showed that there was a significant small movement of the tarsus to changes in femoro-tibial angle (r = 0.37, p = 0.02). These changes, however, were significantly different (using a T test) from the large changes observed when nerve N5 was intact (p = 0.001). These results indicate that the tarsal intersegmental reflex control system was mainly neuronal, with only a possible small mechanical coupling component.

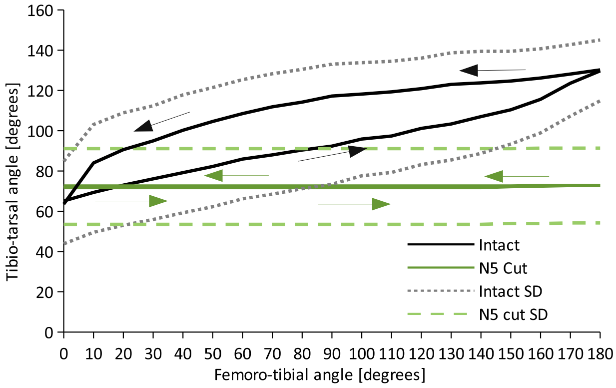

Fig. 1 Average tarsal response to movement of the tibia about the femoro-tibial joint. Responses are shown for the intact leg and when nerve N5 was cut. The arrows represent the direction of travel of the femoro-tibial angle. There was a significant difference between the two responses (N5 intact and cut). Tarsal depression corresponds to an increase in the tibio-tarsal angle, while tarsal extension to a decrease in angle. A hysteresis effect can be seen in the intact leg, and with the nerve cut, very little of the response remained.

3.1.2 Laser Recordings of the Intersegmental Reflex Responses

In response to a 1 Hz sinusoidal stimulus applied to the FeCO, the movements of the tarsus followed approximately the positive gradient of the sinusoid, although not so well the negative gradient (Fig. 2A). This indicates that stretches of the FeCO apodeme, equivalent to a flexion of the tibia, evoked a levation of the tarsus, whereas relaxation of the apodeme, equivalent to tibial extension, evoked tarsal depression. These responses showed that tarsal depression (upward deflection of the trace) was smoother than tarsal levation (downward deflection of the trace), reflecting the activity of the underlying motor neuron activity, which also resulted in spontaneous movements before the stimulus to the FeCO was applied.

In response to a 5 Hz band-limited GWN (Fig. 2B), tarsal movement did not follow the higher frequency inputs, smoothing the response. Movements of the tarsi from 8 different individuals to a 1 Hz stimulus applied to the FeCO showed that they have similar responses but with varying amplitudes. There was also an observable delay between the input to the FeCO and the movement of the tarsus of 0.1 s, resulting from known neural conduction times and synaptic delays (Burrows 1996, Endo et al. 2015).

3.2 Autoregressive Model of the Intersegmental Responses

The linear model of the average tarsal intersegmental response was calculated using the autoregressive model (AR) model described in Section 2.2.2. The parameters of the model were calculated using the first of the three 5 Hz band-limited GWN responses, averaged across the eight individuals (which in turn are the average of three recordings). One model for each individual response was calculated, as well as a model for the average response.

As an example for the average response and a typical movement, the responses from Animal 5, are shown in Figure 2. The performance of the models for these responses, when the parameters were calculated for Animal 5 and the average response across all individuals, are shown in Figure 3. The best performing model was the AR model calculated for Animal 8, with a NMSE of 29.3 % for the GWN input, when tested on unseen data. When the models were tested with 1 Hz inputs, the best performing model, however, was the one estimated with GWN responses from Animal 1, which was the second worst at predicting GWN inputs. These results are shown in Figure 5 in the next Section along with the results from the Artificial Neural Networks for comparison. The AR model calculated with the average response across all individuals was able to predict the average response better than any other individual model, with a NMSE = 27.2 %, when tested with unseen data. The performance of this model with the average tarsal response to 1 Hz sinusoid was also better than with any of the individual responses, with a NMSE = 4.6 %.

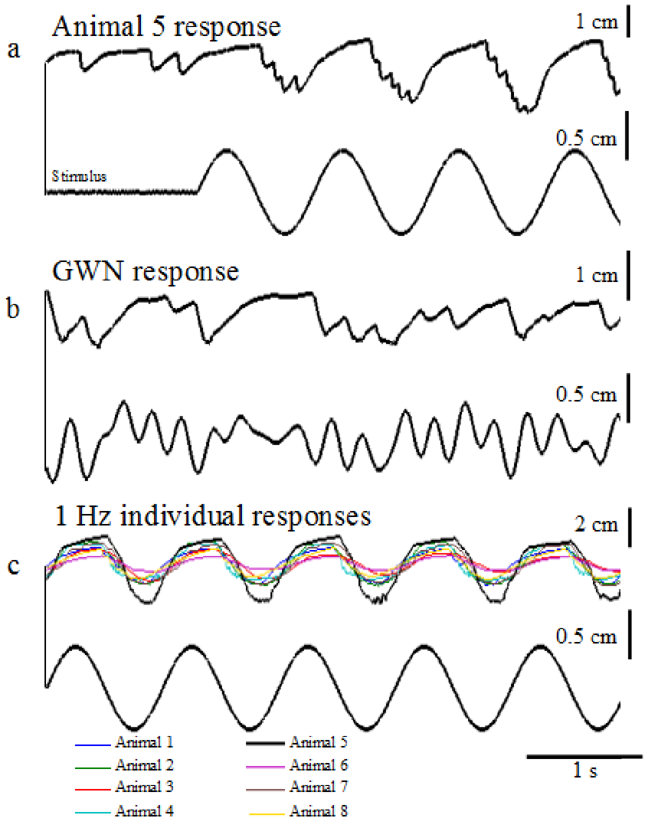

Fig. 2 Intersegmental tarsal movements evoked by displacement of the FeCO. a) Movements of the tarsus of animal 5 to a 1 Hz sinusoidal stimulus. b) Movements of the tarsus of Animal 5 to a 5 Hz band-limited GWN stimulus. c) Movements of the tarsi of all eight individuals to a 1 Hz sinusoidal stimulus. An upward deflection of the tarsal movement traces represents tarsal depression.

3.3 Artificial Neural Networks

3.3.1 Metaheuristic Algorithm TDNN Architecture

Using the responses from the eight animals and the average response across all individuals to band-limited GWN, a metaheuristic algorithm (Costalago Meruelo et al. 2016) was run until the optimal architectures for each response were obtained (Table 1), with a total of 9 models, 8 from the animals and one from the average. While the algorithm was set to a maximum of five layers and 32 nodes per layer, the algorithm only produced architectures with one or two layers. The algorithm was set to run over 50 iterations or generations, however, the ANN architectures converged and the best or optimal network obtained after the 35th generation for all the individual responses, including the average response. We therefore assumed it had reached the maximum fitness within 35 generations.

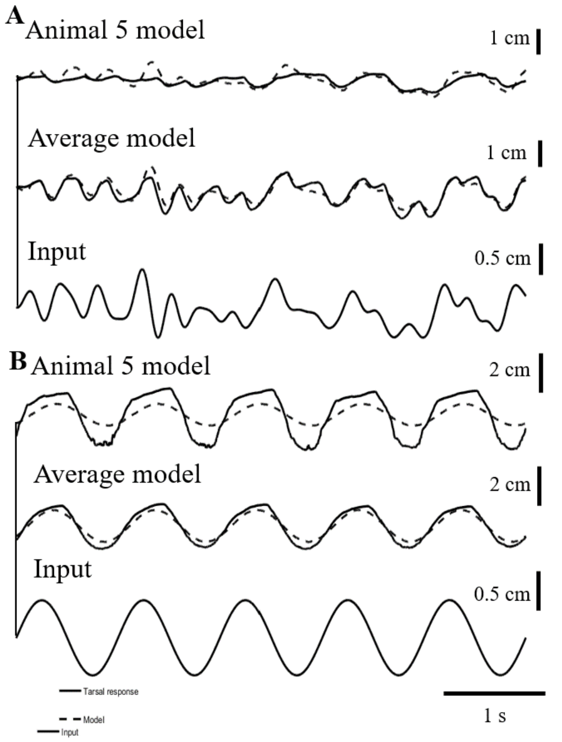

Fig. 3 Autoregressive Model predictions of unseen 5 Hz band-limited GWN and 1 Hz sinusoidal inputs (dotted lines show the model while the black line the response). A) Prediction of the model for Animal 5 to 5 Hz GWN on top, prediction of the model for the average tarsal response with 5 Hz band-limited GWN in the middle and 5 Hz band-limited GWN input in the bottom. B) Prediction of the AR for Animal 5 to a 1 Hz input on top, prediction of the AR for the average response to a 1 Hz input in the middle and 1 Hz sinusoidal input to the FeCO. The parameters of the model were calculated using a 5 Hz band-limited GWN tarsal response and tested with unseen data.

Table 1 Number of nodes per layer for the TDNN designed using the metaheuristic algorithm.

	Layer 1	Layer 2
Average response	4	-
Animal 1	3	-
Animal 2	5	-
Animal 3	5	1
Animal 4	2	1
Animal 5	3	1
Animal 6	3	-
Animal 7	4	-
Animal 8	3	-

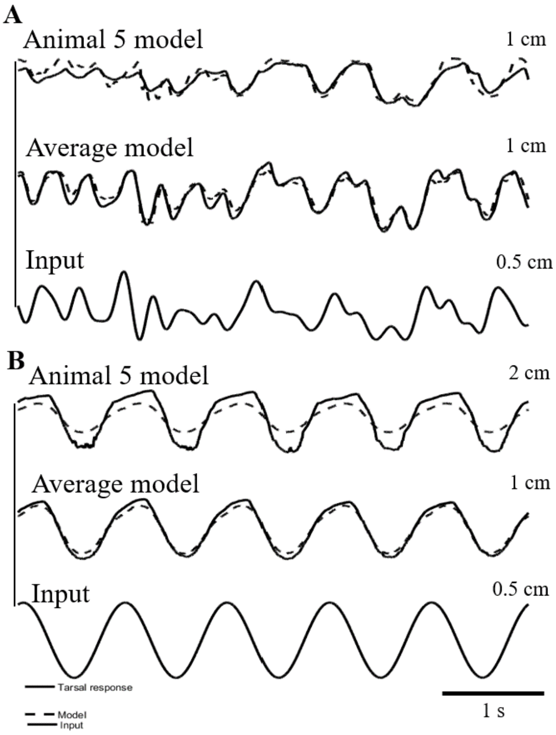

Fig. 4 TDNN predictions of unseen 5 Hz band-limited GWN and 1 Hz sinusoidal inputs (dotted line represents the model and black line the response). A) Prediction of the model for Animal 5 to 5 Hz GWN in the top, prediction of the model for the average tarsal response with 5 Hz band-limited GWN in the middle and 5 Hz band-limited GWN input. B) Prediction of the TDNN for Animal 5 to a 1 Hz input in the top, prediction of the TDNN for the average response to a 1 Hz input in the middle and 1Hz sinusoidal input. The parameters of the model were calculated using a 5 Hz band-limited GWN tarsal response and tested with unseen data.

3.3.2 TDNN models of the Intersegmental Responses

The TDNN models optimised for the individual and the average responses were tested using unseen GWN data and a sinusoidal input, none of which were used in the training of the algorithm. The models were able to approximate the response of the 5 Hz GWN and follow its trajectory, both in the case of the TDNN trained with recordings from Animal 5 and with the average response calculated across all animals (Fig. 4).

For a 1 Hz stimulus applied to the FeCO, it was clear that the model trained with Animal 5 was not able to predict the high amplitude movements of the tarsal responses in Animal 5, although the model trained with the average response could predict the average response to 1 Hz (Fig. 4B).

The TDNN models had lower NMSE than the AR models for every individual, including the average response (Fig. 5). These NMSE values were calculated for TDNN

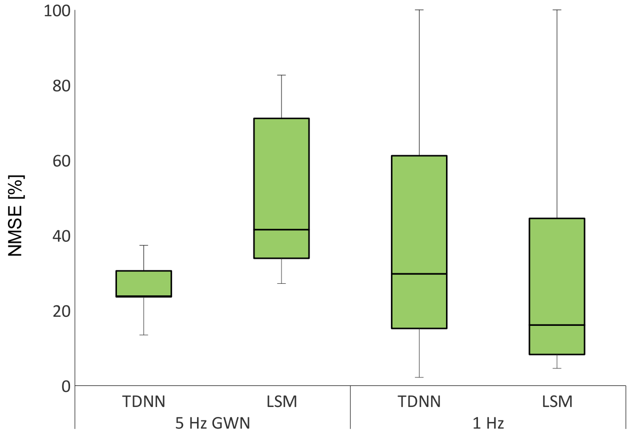

Fig. 5 Boxplots of the NMSE of the individual models when tested with unseen GWN and 1 Hz sinusoidal inputs from the same individual as training, but not the same response as used in the training.

models trained with a specific individual (or the average response across all individuals) and tested with unseen data from the same individual (or the average response). With a mean value of 25.3 % for the NMSE, the TDNN produced a better model than the AR, with 50.6 %.

To corroborate whether the TDNNs were better at predicting the tarsal responses, a paired samples t-test was applied, chosen for the normality of the data (Shapiro-Wilk Test, p = 0.881 for the TDNN models and p = 0.098 for the AR models), despite the small sample size (9 samples in total, considering models for the 8 individuals and the average response across them). The results showed that the TDNN had a statistically significantly lower NMSE (25.3 ± 7.1 %, mean standard deviation) than the AR models (50.6 ± 22.1 %), with t(16) = -3.924 and $p < 0.01$. This indicated that the TDNN were statistically significantly better at predicting the tarsal intersegmental responses. This result was confirmed with a non-parametric Mann-Whitney U-test ($p < 0.01$).

To show the generalisation of such models (Fig. 6) also shows the prediction of these networks with both GWN a sinusoidal stimulus input, with models estimated in one animal (identified on the x-axis) tested on all other animals (identified by different markers). Table 2 shows that the performance of the TDNN models appeared slightly worse than the performance of the AR (59.4 ± 74.4 % for the TDNN and 47.8 ± 62.9 % for the AR).

To determine whether the difference between the NMSEs of the AR and the TDNN, when tested with a 1 Hz stimulus and the response from the same animal as used in training, was statistically significant, a Mann-Whitney U test was applied to the data, since both models produce non-normal data (Shapiro-Wilk Test has a $p = 0.00 < 0.05$ for both the TDNN models and the AR models, indicating that the data from both models was non-normal). The results from the test indicated that the performance of both models was not significantly different (U = 34.0, p = 0.61).

Therefore, the TDNN models are statistically better at predicting the responses to 5 Hz band-limited GWN than the AR models, however they were not statistically different to them when predicting responses to a 1 Hz sinusoid.

3.3.3 Generalisation of TDNNs to different individual responses

To analyse generalisation in more detail, the models trained with 5 Hz band-limited GWN were then tested with the responses from all individuals and the average of these (Fig. 6). Here, the term generalisation refers to the ability of the model to predict the tarsal reflex responses in different individuals that were not used in the training process. In Figure 5, each box-plot represents the NMSE of a specific model, trained with either the average response or the responses from individual animals (1-8). The NMSE was calculated when these models were applied to all the responses, represented by the different markers.

Results show that the models could predict well the responses from some individuals. The model from the average response was the best performing model, while that of Animal 3 was the worst performing model. However, there were some responses that were poorly predicted by the models, such as the model of the average response that could not predict the GWN responses of Animal 5. The average response across all animals, however, was predicted by all the individual models (see black dots in Figure 5).

All individual models had a prediction error higher than 100 % when tested with Animal 5, with the exception of the model trained with Animal 5, and the model trained with Animal 1. The model trained with Animal 1 was able to predict all the responses from any individual, better than the model trained with the average response calculated across individuals, with the exception of the tests on recordings from Animal 3 and 8.

The median of the performances from each of the models is shown in Figure 7. The table shows the median value of all the NMSE when the TDNN was tested with GWN and with a 1 Hz sinusoidal stimulus. Overall, the TDNN had a mean NMSE performance of 86.8 % when tested with 5 Hz GWN and 64.7 % when tested with 1 Hz. It should be noted that there are many outliers in the distribution (NMSE values higher than 100 %,

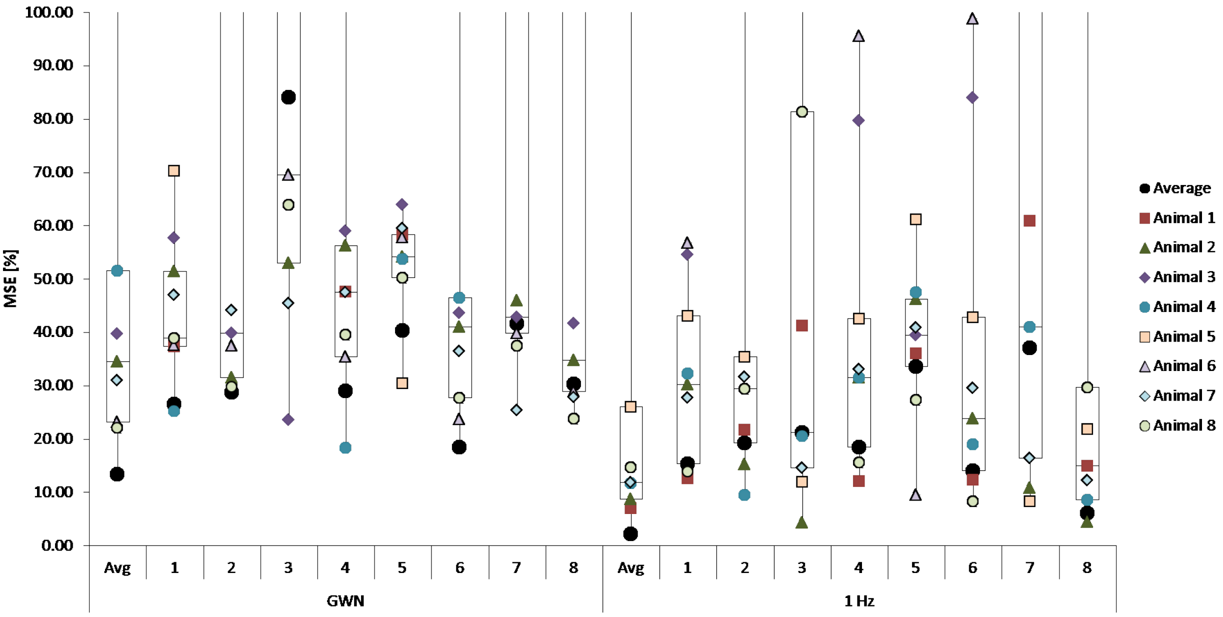

Fig. 6 Performances represented by the NMSE for all the TDNN models tested with either 5 Hz band-limited GWN or a 1 Hz sinusoid. Each of the box-plots represents the performance of a TDNN trained with one of the responses, either the average tarsal response or one of the eight individual responses (as indicated on the axis). The networks were trained with 5 Hz band-limited GWN responses. The markers of the box-plots represent the NMSE. For ease of visualization, values above 100 % are not shown, since they indicate failure of the model to predict the response (a constant zero-valued response would provide a NMSE of 100%) and precise values above 100% thus add little additional insight. These extreme values were however included in the non-parametric statistical analysis

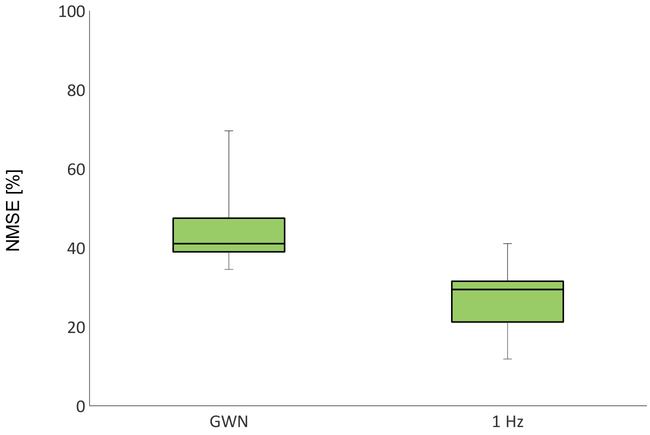

Fig. 7 Boxplots of the median of the NMSE values for each of the nine TDNN models. The NMSE value presented for each model was the median of the NMSE values calculated with that model and averaged across all the individuals, including the average response.

reason why the median is shown instead of the mean), which bias estimates of mean values.

Figure 7 shows that the model trained with the responses from Animal 1 had lower performance error than any other model, while the model trained with the responses from Animal 3 has the highest errors, although this may only be true due to the NMSE values of the TDNN tested with Animal 5, which caused outliers. The model trained with recordings from Animal 5 could predict all the individual responses with a low performance not much higher than the best performing model, considering that its responses could not be predicted by any other model.

To estimate whether the performances of the models were significantly different (i.e. the animal used for training data, or average response, had a significant impact on the performance of the model), a Friedman test was chosen. This test was chosen because it analysed the differences in three or more groups of dependant variables (i.e. repeated tests from different animals within the same network). The test was applied to the NMSE values obtained with GWN and 1 Hz separately. The test also gives some insight into the importance of the animal chosen to design the model, or whether the average across individuals could be used as a representation of the system.

The Friedman test was also chosen because of the non-normality of most of the data (the Shaphiro-Wilk tests have $p < 0.05$ for Animal 2, 3, 6, 7 and 8, and $p < 0.001$ for the overall data). Results indicated that the NMSE values were significantly different (-2(8) = 21.9, p = 0.01) when the networks were tested with a 5 Hz band-limited GWN and when they were tested with 1 Hz sinusoid (2(8) = 15.3, p = 0.05). These statistical tests indicate that the training data used to design the networks affects significantly the performance of the model when predicting data from different individuals.

4 Discussion

4.1 Tarsal intersegmental responses

Using new approaches we have developed extensive and quantitative analysis of an intersegmental reflex in which movement of the tarsus about the tibio-tarsal joint was mediated by changes in the position of the tibia about the femoro-tibial joint. As the leg was flexed, the apodeme of the FeCO was stretched and the tarsus levated, and when the leg was extended, the apodeme was relaxed and the tarsus depressed. We then modelled the reflex movements of the tarsus using both Autoregressive and Artificial Neural Networks and showed that the models produced by the ANNs provided better predictions of the intersegmental responses. Finally, we then analysed the variability in responses of reflex movements between animals and asked how good the models from individual animals were in predicting the tarsal reflex movements in different animals.

4.2 Artificial Neural Networks for system identification in biological systems

Costalago Meruelo et al. (2016) described a novel method to model and predict neural responses using ANNs and to explore and understand such responses with a high degree of accuracy. The method used to design the ANN architecture, a combination of Evolutionary Algorithms and Particle Swarm Optimization (Eiben & Smith 2003, John 1992, Kennedy & Eberhart 1995), optimised the architecture of the network to individual and averaged responses. The design of the optimal architecture was necessary to reduce computational time, improve prediction accuracy, reduce over-fitting and improve generalization capabilities (Angeline et al. 1994, Yao 1999, Suraweera & Ranasinghe 2008). The same method used here, produced small networks with up to two hidden layers and a small number of nodes in each layer to model tarsal movements, although the networks were smaller for tarsal responses than for neural responses (Costalago Meruelo et al. 2016). The small size is thought to be better at generalising and in reducing over-fitting (Sietsma & Dow 1991, Suraweera & Ranasinghe 2008). Larger networks may produce a lower error in the training data, but are less able to predict the responses to a novel stimulus. We have shown here that the ANNs were able to outperform significantly previously used mathematical methods such as the AR. For example, using ANNs the prediction error was reduced by approximately 10 % compared to the LNL methods (Dewhirst et al. 2013) and by 25 % compared to Wiener methods (Newland & Kondoh 1997*a*,*b*). It should be pointed out, however, that such comparisons must be considered with caution, since it is not just the model structure or its type that affects the results, but also the size or number of model parameters that can impact the fit and ability to generalise. For tarsal intersegmental responses ANNs had approximately half the mean square error of the linear models suggesting than ANNs were better than linear models commonly used in biological systems (Marmarelis 2004).

4.3 Individual variability in the tarsal intersegmental reflex responses

Angarita-Jaimes et al. (2012) showed that the NMSE errors of models of motor neurons could not be ascribed only to modelling errors or background noise, but may also be due to individual differences of the same neuron between animals. Similarly, Schneidman et al. (2000), showed that in information rates in the visual system of flies that the common underlying response across individuals contributes about 70 % of the information recorded in the response, whereas the remaining 30 % comes from individual differences in the insect such as initial state, or inadvertent excitation of sensory neurons. We show that a common response underlies the control of limb movements across individual locusts, since all models could predict some, but not all, of the responses from other locusts, independently of the locust used for training. Nevertheless, the ability of each model to predict the responses from each of the locusts differed considerably. These inter-subject variations indicate the dangers of building models of biological systems based on results from one or just a few animals, and this risk will undoubtedly increases when larger models that may include the whole leg is made by combining the results of a series of experiments from different animals. These differences in the prediction errors can partly be explained by differences across animal responses, as a result of spontaneous activity found in central interneurons and motor neurons (Büschges et al. 1994, Field & Burrows 1982), differences in parameters (Marder & Taylor 2011) and electrical and cellular noise (Faisal et al. 2008). In our study averaging the signals before system identification represents a step forward to reduce noise in the data. Averaging across individual differences, however, has the potential to lead to a model that does not represent any individual animal well, although this does not seem to be the case in our study.

4.4 Wider implications

Our results show clearly that our models derived from real biological data can predict the movements of the tarsus based on information about the movement of the tibia around the knee joint. Such predictive control could be used in the design of prostheses and orthoses for gait deficiencies could benefit greatly by adding a reflex response. Powered or active prosthesis that aid movement have already improved gait (Shultz et al. 2016), however their development has been slow over the last few years because of limitations in technology (Au & Herr 2008). Bioinspired systems could provide the next step in their development providing more natural movement. Functional Electrical Stimulation (Rushton 1997) could benefit from reflex modelling, improving the natural voluntary movements for which reflexes are necessary. Including feedback responses from the environment in the form of flexibility and easiness into foot movement would be advantageous as current systems lack this adaptability due to being based on pre-programmed patterns (Jiménez-Fabián & Verlinden 2012). Furthermore, robotics, autonomous systems and control already use direct applications of principles from biological systems (Beer et al. 1997). In robotics, some of the most successful legged robots are based upon arthropods (Ritzmann et al. 2004), however, their design has raised issues related to the level of autonomy, stability and coordination (Bares 1999). Local reflexes, such as those seen in insects have been shown to successfully improve robot locomotion (Espenschied et al. 1993, 1996) when implemented, since insects have the ability to deal with uneven terrain, a characteristic that robots aim to emulate (Chen et al. 2011, Cruse et al. 1998, Delcomyn & Nelson 2000, Kovač et al. 2008, Lewinger et al. 2011).

Acknowledgements Alicia Costalago Meruelo was supported by an EPRSC grant (EP/G03690X/1) from The Institute of Sound and Vibration Research and the Institute for Complex Systems Simulations at the University of Southampton.

Ethical approval: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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