

NEURAL ADAPTATION IN LOCAL REFLEX CONTROL OF LIMB MOVEMENTS

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Abstract: Neural adaptation, a change in the response of a neuron to repetitive stimulation, is a widespread property of neurons in many networks, including those controlling local reflex limb movements. The majority of previous studies have investigated the steady state properties of neurons rather than considering those of their adapting (transient) response. Bandlimited Gaussian White Noise, sinusoidal and walking stimulation signals have therefore, for the first time, been used to investigate neural adaptation in flexor and extensor motor neurons in the locusts local hind limb control system. Our results show that the adaptation rate of the response of two extensor and one flexor motor neuron are the same. We also show that the adaptation rate of the Fast Extensor Tibia motor neuron is affected by the properties of the stimulation signal.

1 INTRODUCTION

The adaptation of the response of individual or networks of neurons to constant stimulation is a widespread property of vertebrate and invertebrate nervous systems (Prescott and Sejnowski, 2008). It can be caused by a number of processes such as intrinsic cell mechanisms or extrinsic factors such as the mechanical properties of sensory receptors (French, 1986) and has many functions including gain control (Brenner et al., 2000).

Invertebrates provide the opportunity to gain physiological insight into a system which is simpler and more accessible than many vertebrate counterparts (Bassler, 1993). The current study concerns the resistance reflexes in the network of neurons which help to maintain postural stability in the hind leg of the locust. The sensory, inter and motor neurons in this local network are known to adapt their output amplitude or spike firing rate to repetitive stimulation (Field and Burrows, 1982; DiCaprio et al., 2002; Gamble and DiCaprio, 2003). An example of adaptation can be seen in the reflex response of the locusts Fast Extensor Tibia (FETi) motor neuron to GWN stimulation of its stretch receptor, the Femoro-tibial Chordotonal Organ (FeCO) (Figure 1). The FeCO

monitors the position of the tibia about the femur in the hind leg of a locust (Burrows, 1996).

Many previous studies (Newland and Kondoh, 1997; Field and Burrows, 1982; Gamble and DiCaprio, 2003; DiCaprio et al., 2002) focus on the steady state (SS)(Figure 1C) response of reflex limb control systems. These studies have used either sinusoidal type stimulation or Gaussian White Noise (GWN) with system identification modelling methods to characterise neuronal responses. As the adapting or transient (TR) response may be more important for reflex control we investigate the TR responses of the locusts motor neurons to GWN and functionally more relevant natural stimulation. The TR and SS responses are shown in Figure 1C between 4-8 s and 15-40 s respectively. Our aim is to determine if adaptation rate differs between motor neurons and if it is affected by the properties of the stimulation signal.

The motivation for this study is to gain deeper understanding of insect neurophysiology but this work may be of practical relevance for optimising the treatment of patients with neuromuscular dysfunction. It may also allow the features of such biological systems to be exploited to improve the design of engineering control systems used in robotic applications (bio-inspired design)(Bar-Cohen, 2006).

2 METHODS

Preparation of the adult male and female locusts, *Schistocerca gregaria* (Forskål) follows that used previously (Newland and Kondoh, 1997). To summarise, locusts were mounted ventral side uppermost in modelling clay, a hind leg was rotated through 90° and fixed anterior face uppermost. The angle between the femur and the abdomen, and the tibia and the femur, was set at 60°. The apodeme of the FeCO (Figure 1A) was exposed and clamped by forceps. The forceps were mounted on a shaker (Ling Altec 101, LDS Test and Measurement) and were moved by different stimulus signals. Two bandlimited GWN signals (27Hz and 50Hz cut off frequencies), sinusoidal (2.5 and 10Hz) and two “walking” signals were used in the current study. The 27Hz GWN signal was generated using a random binary generator (CG-742, NF Circuit Design Block) and bandlimited using a low pass filter (SR-4BL, NF Circuit Design Block). The 50Hz GWN signal and the sinusoidal and walking signals were generated in MATLAB. The “walking” signals were estimated from filmed recordings of the locusts obtained from a high speed camera (Redlake Imaging, Tring, UK) during walking. Apodeme position was converted to femoro-tibial angle using previous results (Field and Burrows, 1982). The GWN input was scaled so that ~99.7% of its values fell between 5 and 115°. Sinusoidal stimulus signals had amplitude values corresponding to a joint range between 16 and 102° and walking signals between 30 and 90°.

A small window was cut in the ventral thorax to gain access to the meso- and meta- thoracic ganglia. The ganglia were supported by a wax coated silver platform which also served as the reference electrode. Glass micro-electrodes, filled with potassium acetate, were driven into the soma of the motor neurons (Figure 1A). Intracellular recordings were made from the posterior intermediate flexor tibiae (PIFITi) and the slow and fast extensor tibiae (SETi and FETi) motor neurons with the use of an Axoclamp 2A amplifier (Axon Instruments). Signals were digitised ($f_s = 10\text{kHz}$) using the USB 2527 data acquisition board (Measurement Computing, Norton, MA, USA) and stored on a computer hard-drive for further analysis. An example of the response of the FETi motor neuron to 50Hz GWN stimulation of the FeCO is shown in Figure 1C. As only synaptic inputs were recorded in the motor neurons we quantify adaptation by calculating the power in 1 s long non overlapping blocks of data. The responses recorded from the PIFITi, SETi and FETi motor neurons to 27Hz bandlimited GWN stimulation were used to investigate whether adaptation rate varied between motor neu-

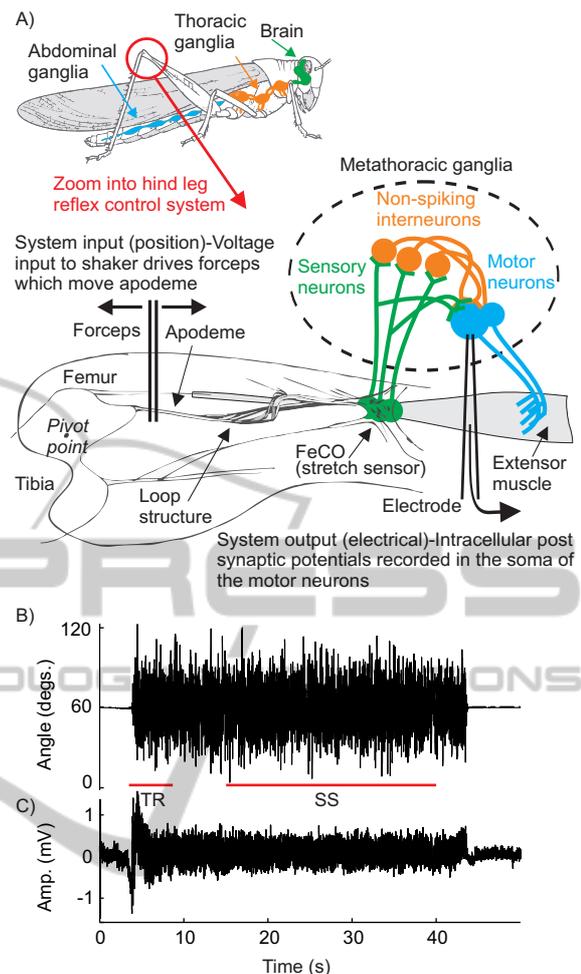


Figure 1: The locusts nervous system (A) and an example intracellular recording from the FETi motor neuron showing how it adapts its response to 50Hz bandlimited GWN stimulation of the FeCO (B,C). The GWN input signal applied to the FeCO is shown in (B). An example of the intracellular post synaptic response of a FETi motor neuron to this stimulus is shown in (C). Its transient (TR), adapting response can be seen in (C) between ~ 4 and 8 s. Its steady state response (SS) can be seen between ~ 15 and 40 s. Signals were preprocessed to remove slow time varying drifts using a high pass filter with a cut off frequency of 0.5Hz.

rons. The effect on adaptation rate was investigated when the FETi was stimulated with 50Hz bandlimited GWN, sinusoidal and walking stimulation signals. The change in neural power over time was modelled using the exponential equation $y(t) = A + Be^{(-t/\tau)}$ where t represents time and $y(t)$ represents the neurons neural power normalised by its base line power (BLP). BLP was calculated from a 1 s window taken from each recording before stimulation was applied. The final SS power is represented by A , and $A + B$ is the peak power amplitude. Adaptation rate was quantified by the time constant τ which represents the time

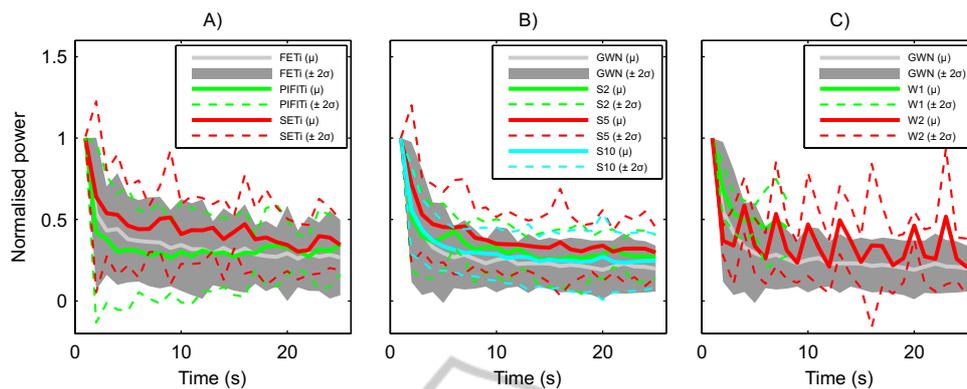


Figure 2: Adaptation of the different motor neurons to the same 27Hz bandlimited GWN stimulation signal (A) and adaptation of the response of the FETi motor neuron to different stimulus signals (B,C). (A) shows the mean and ± 2 std of power in the response of PIFITi ($n=6$), SETi ($n=6$) and FETi ($n=14$) motor neurons. (B,C) show how the power (mean and ± 2 std) in the response recorded from the FETi motor neuron varies when different stimulation signal types are applied. GWN, S2, S5 and S10 represent the 50Hz bandlimited GWN, 2Hz, 5Hz and 10Hz sinusoidal stimulation signals respectively. W1 and W2 are the two walking stimulation signals. Five recordings for each stimulus signal type were made from FETi in different animals.

taken for the BLP normalised neural power to fall by 63.2% of B . The Nelder Mead (simplex) (Nelder and Mead, 1965) iterative search method was used to estimate the time constant τ .

3 RESULTS

To investigate whether adaptation rate varies in different motor neurons we calculated and plotted the mean power and ± 2 standard deviations in the response of one flexor motor neuron (PIFITi)($n=6$) and two distinct physiological types of extensor motor neuron, fast (FETi), and slow (SETi)($n=14$ and 6) (Figure 2A). Each recording was made from a different animal. To aid comparison, power values were normalised by the value calculated from the first window. TR and SS sections of responses were defined using mean power levels (Figure 2A) and visual analysis of the signals. Thus the TR response was defined as the response which occurred within the first 3 s after stimulus onset (Figure 2A). The SS response was defined as the response which occurred after 10 s of stimulus onset (Figure 2A). The power of all three motor neuron types falls to approximately 40% of their initial values within the TR section (Figure 2A). The median difference of the mean of the power in the TR and SS sections is significantly different from zero (Wilcoxon signed-rank test, $p < 0.05$) for each motor neuron type. Signal power remains relatively constant in the SS section (Figure 2A, B and C). The rate of adaptation of the response of the PIFITi, SETi and FETi motor neurons to 27Hz bandlimited GWN appears to be similar (Figure 2A, B). There was no significant difference between the time constant values for the

different motor neurons ($p=0.48$, Kruskal Wallice).

To investigate if stimulus signal properties affect adaptation rate we calculated the mean power and ± 2 standard deviations of the responses of the FETi motor neuron to bandlimited 50Hz GWN, sinusoidal (2, 5 and 10Hz) and two walking input signals (Figure 2B and C). For each stimulus type results were obtained from recordings made in 5 different animals. Visual analysis of the results suggests that adaptation rate is similar for the different stimulation signals (Figure 2B and C). However, we found a significant difference between the time constant values ($p=0.01$, Kruskal Wallice); a post hoc (Dunn-Sidak) test revealed a difference between the walk 2 and the 5Hz sinusoidal stimulation signal.

The effect that stimulation signal type had on adaptation was probed further by investigating how adaptation rate varied with transient response power (TRP). Both TRP and the time constant of the exponential function fitted to the power values were normalised by the base line power. In general the scatter plots of time constant against TRP normalised by BLP (Figure 3) show no correlation between variables (Spearman rank correlation). The result when 10Hz sinusoidal stimulation is applied suggests that the variables are correlated but not at the 95% significance level ($r=0.9$, $p=0.08$)(Figure 3 S10).

4 DISCUSSION

The aim was to investigate whether adaptation rate differs between motor neuron types and if it is affected by the properties of the stimulation signal. Adaptation rate was quantified by the time constant of

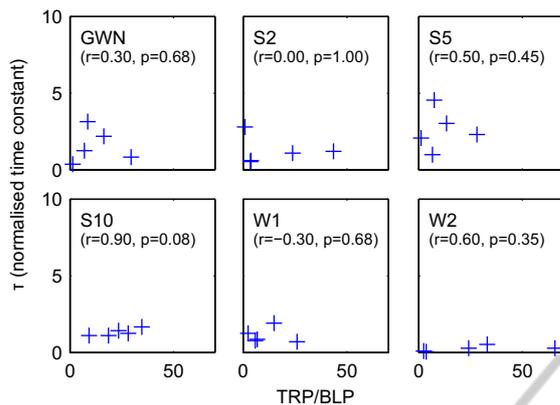


Figure 3: Relationship between the rate of adaptation, measured by the time constant of an exponential function fitted to the power values, and the transient response power (TRP). Both values are normalised by the base line power (BLP) which is calculated from a 1s window taken from the recording before stimulation is applied. GWN, S2, S5 and S10 represent the 50Hz bandlimited GWN, 2Hz, 5Hz and 10Hz sinusoidal stimulation signals respectively. W1 and W2 are the walking signals. Five recordings for each stimulus signal type were made from FETi in different animals. Correlation is tested using Spearman rank correlation. We found no correlation between TRP and the time constant.

an exponential function fitted to the response power of the motor neurons. We have shown that the adaptation rate of the response of two extensor (SETi and FETi) and one flexor (PIFITi) motor neuron to 27Hz bandlimited GWN stimulation of the FeCO is the same. Our results are contrary to those found in the study by Field and Burrows (1982). They found that the PIFITi motor neuron showed little difference in its response after 10 s of stimulation, whereas we found a drop in power of approximately 40% after 3 s. Field and Burrows (1982) also found that the fast and slow flexor motor neurons exhibited different rates of adaptation whilst we found that the fast and slow extensor motor neurons exhibited the same rate of adaptation. It should be noted that they stimulated the FeCO using repetitive triangular movements with a frequency of 5Hz and femoral tibial joint angles between 40° and 80°. This is very different from the 27Hz bandlimited GWN used in the current study and their excursion of $\pm 20^\circ$ does not cover the full range of movement that occurs during walking or kicking. Our results could also occur because the extensor and flexor neurons may share common inputs, a property well known to occur in vertebrate studies (Luca and Erim, 2002).

We have also shown that the adaptation rate of the FETi motor neuron can be affected by the properties of the stimulation signal, as has been found in other work (Fraser et al., 2006). We have used correlation analysis to show that FETi response power decreases to its steady state level within the same amount of

time regardless of its transient response power (both BLP normalised). Further experiments and analysis are required to understand how this adaptation affects the function of the reflex response.

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