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Adaptation of locust wing stretch receptor firing in dynamic mode

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Locust wing stretch receptor is known to exhibit firing frequency adaptation when the forewing is lifted to a constant position. However, during flight, the wing periodically moves and the receptor's response properties are in this dynamic mode unknown. We recorded extracellularly the response from the *Locusta migratoria* forewing stretch receptor while the wing was periodically lifted and found that the adaptation of the stretch receptor is expressed in a dynamic mode as well; however, this adaptation is weaker than in the static mode.

Key words: sensory systems, adaptation, information coding, locust

INTRODUCTION

Sensory systems are part of the brain, providing information about animal's environment and internal status. These systems not only convert information into the nerve code, but also perform some forms of information processing. For instance, some sensory organs respond to constant stimuli by decreasing the response; this is called adaptation. Adaptation of action potential frequency is an example of sensory information processing.

Sensory organs may differ by modalities or between species, however, they share a lot of common features of signal transduction and information processing. As an example, locust wing stretch receptor is a convenient object for investigating the principles of information coding in sensory systems. Locusts are cheap to buy, simple to handle, easy to record the action potentials from the wing stretch receptor in different wing positions [1].

In locusts, the stretch receptor sensory organ consists of the cell body and a dendritic arbor of a single neuron embedded within a strand of connective tissue that spans the base of the wing to an internal diaphragm. The main function of the locust wing receptor is to control the frequency of wing movement, compensate the influence of external disturbances and coordinate the action of different muscle groups [2]. The locust wing stretch receptor encodes the wing position by a series of action potentials – the higher wing is lifted, the higher frequency of action potentials [1]. However, this encoding is not linear: the longer a wing stays in the same position, the lower is the frequency of action potentials due to adaptation [1]. This characterization of the wing stretch receptor was obtained in a static mode when the wing was kept in a constant position for one minute or more. But in natural conditions, when a locust is flying, wings are periodically moving up and down at approximately 23 Hz [3]. Therefore, we decided to investigate whether the adaptation of locust wing stretch receptor happens in a dynamic mode when a wing is moving up and down.

Here we present data when stretch receptor action potentials are recorded while a wing is periodically moving up and down.

MATERIALS AND METHODS

The locust was prepared for the experiment as described by Robertson [1]. Shortly, the legs are removed at the level of the coxae. Then the locust is decapitated and the guts are removed. The preparation is glued to the stand and installed in the test apparatus. The grounding silver wire is inserted into the abdomen. The wing is fixed in an apparatus allowing measuring the angle of wing position (Fig. 1). The wing was released from the clamp and attached to the wing lifter

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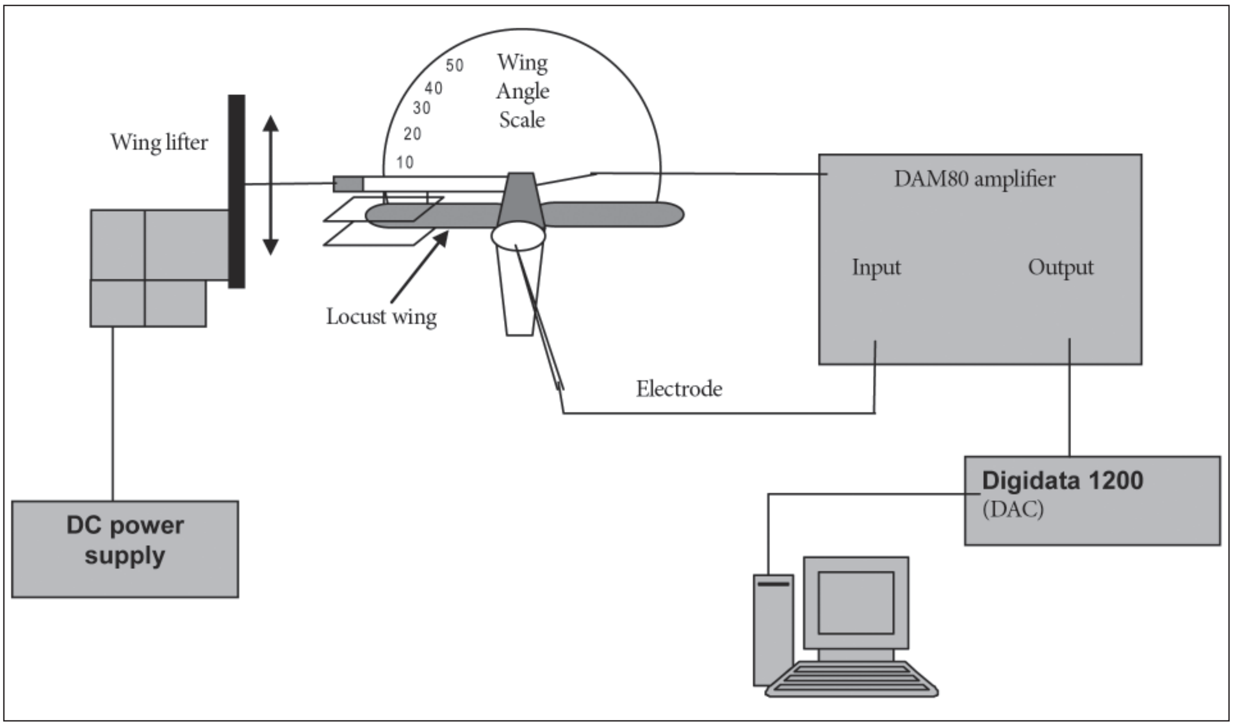

Fig. 1. Experimental setup for recording activity of locust wing stretch receptor

during wing movement experiments (Fig. 1). The wing was moving at a 10 Hz frequency.

The signal from wing stretch receptor inside the locust trunk is recorded by a monopolar electrode guided by a micromanipulator.

The extracellular recordings were performed with a DAM 80 amplifier (WPI, Sarasota, USA) (gain 10000, high pass filter 300 Hz, low pass filter 3 kHz). Data were digitized by Digidata 1200 (Molecular Devices, Sunnyvale, USA) and by means of Clampex (Molecular Devices, Sunnyvale, USA) software stored in computer for analysis.

All experiments were performed at room temperature (20–22 °C).

The action potentials were automatically detected by the *Pick Peeks* function from the Origin (OriginLab, Northampton, USA) software. The inverted interspike interval was used as an instant action potential frequency. During periodic wing movement, the stretch receptor responded by bursts of action potentials. Only interspike intervals inside bursts were used for analysis.

The differences between action potential frequency in different experimental conditions were checked for significance by the paired t test. The frequencies were significantly different at $p < 0.05$.

RESULTS

We compared the response of the locust wing stretch receptor in static and dynamic modes. As expected, the locust wing stretch receptor responded by a series of action potentials of a decreasing frequency when the wing was lifted to a 30-degree position (Fig. 2, lower trace, triangles) [1].

The adaptation of wing stretch receptor action potential frequency was observed in all animals tested (n = 26).

However, it was not known whether the adaptation of action potential frequency takes place in the physiological conditions when the wing is moving up and down periodically. To test this, we recorded action potentials from the wing stretch receptor when a wing was periodically moved up and down at a 10 Hz frequency (Fig. 2, upper trace, circles n = 6).

The locust wing stretch receptor responded by a series of bursts of action potentials when a wing was periodically moved up and down. As described before [5, 2, 10], one burst corresponded to one cycle of a wing movement. The action potential frequency (see methods) decreased during testing (Fig. 2, upper trace, circles), but less than when the wing was lifted and kept at the same position (Fig. 2, lower trace, triangles). These qualitative observations were quantified by comparing the action potential frequencies when a wing was kept at a 30-degree position and periodically moved to the same position 5, 10, 15, 20, 25, 30, 35 seconds after starting stimulation (Fig. 3). We can see that at all times tested (Fig. 3, n = 6) the frequency of locust wing stretch receptor action potentials is significantly higher when wing is periodically moved (Fig. 3, white bars) as compared to the wing kept in a constantly elevated position (Fig. 3, grey bars).

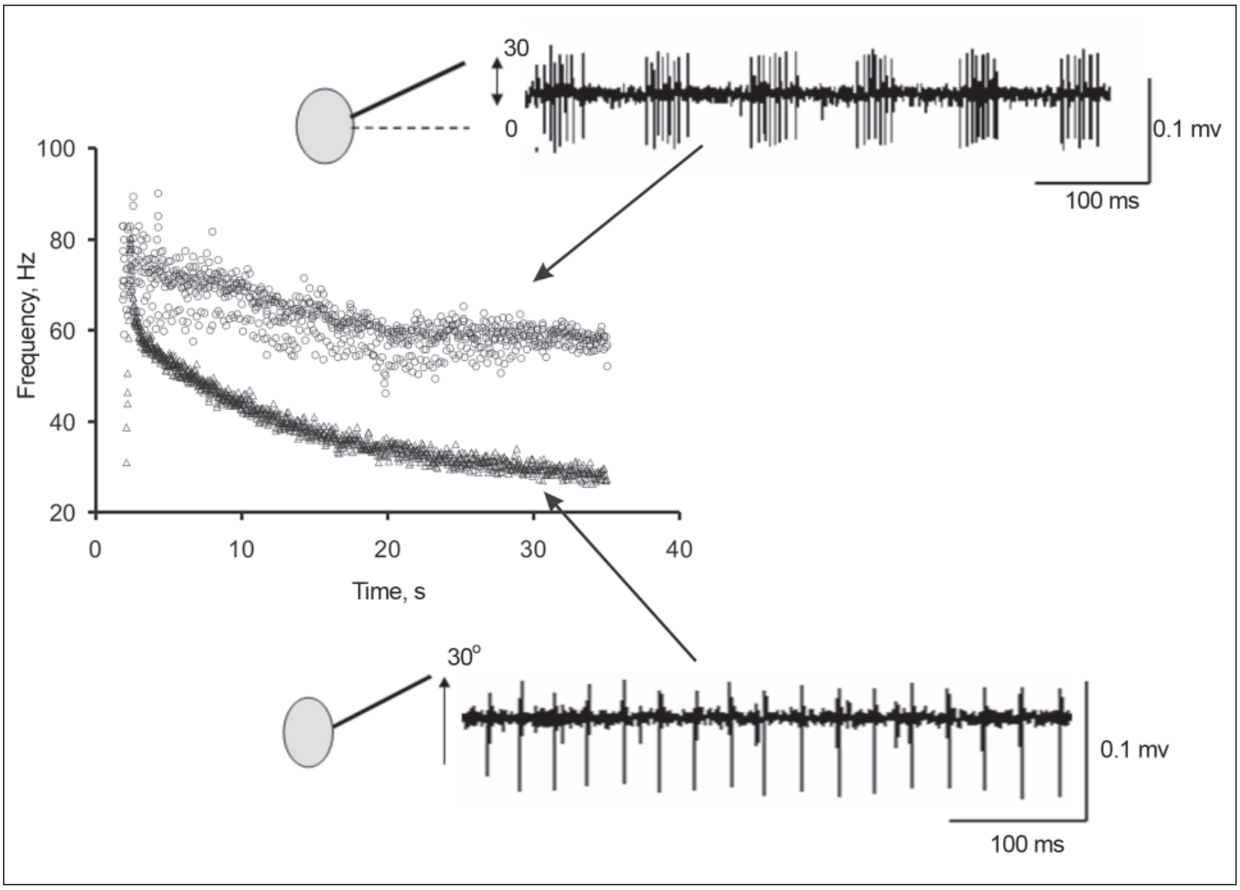

Fig. 2. Frequency of stretch receptor action potentials when wing is lifted to the constant position at 30 degrees (lower trace, triangles) and is periodically moved from 0 to 30 degree position (upper trace, circles). Both traces are from the same locust.

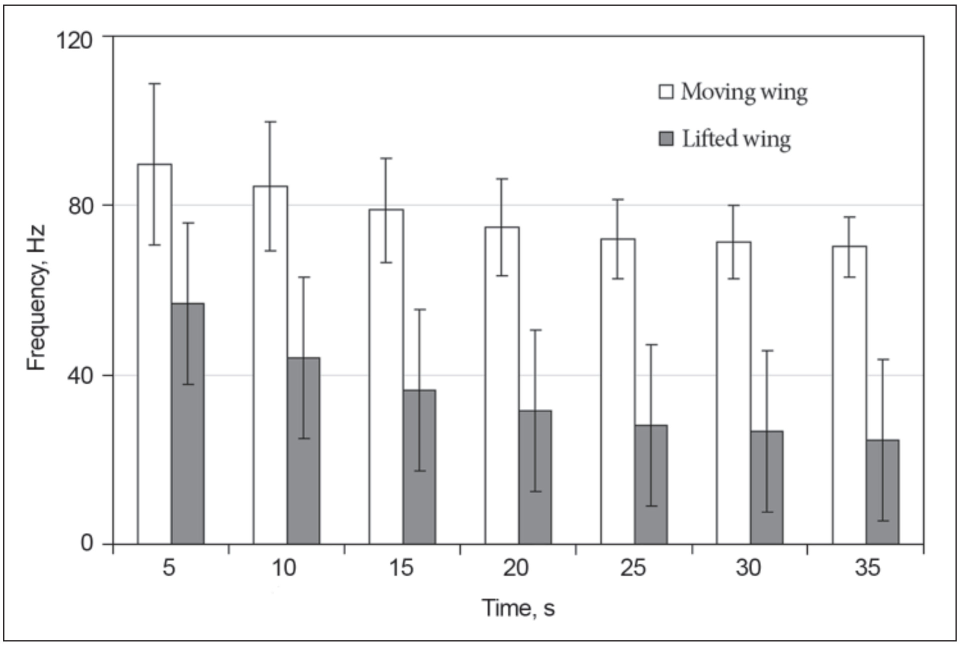

Fig. 3. Averaged frequency of stretch receptor action potentials when wing is lifted to the constant position at 30 degrees (white bars) and is periodically moved from 0 to 30 degree position (grey bars) at different time moments after stimulus starts

DISCUSSION

The locust wing stretch receptor encodes the position of a wing by a series of action potentials – the higher the wing, the higher the frequency of action potentials [1, 2, 4, 5]. However, this encoding is not linear.

When the wing is elevated and kept in a constant position, the frequency of the action potentials decreases in time [1, 4]. This phenomenon is intrinsic to the wing stretch receptor and called adaptation of action potential frequency. Adaptation is a common feature of neurons from various parts of the nervous system [6–8]. Adaptation is thought to contribute to integration, input filtering and saving metabolic resources [9]. Multiple mechanisms may contribute to the adaptation [6].

The frequency adaptation of locust wing stretch receptor action potentials in a static mode when a wing is lifted to a constant position was known before [1, 4]. In this investigation, we show that, apart from the static mode, adaptation occurs also in the dynamic mode when a wing is periodically lifted up and down. However, adaptation in the dynamic mode is significantly weaker than in the static one.

The adaptation process in the stretch receptor starts from the moment a wing is lifted [1, 4], which corresponds to stimulus onset in other types of neurons [4, 6]. The recovery from adaptation is not instantaneous; it takes some time [11]. When a wing is periodically moved up and down, adaptation and recovery from adaptation occur at the same time. We think that adaptation is weaker in dynamic conditions for two reasons: because a wing spends less time in an elevated position (and therefore needs less time for adaptation) and because of recovery periods when a wing is in a lowered position.

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SKĖRIO SPARNO VYRIO TEMPIMO RECEPTORIAUS ATSAKO ADAPTACIJA ESANT DINAMINIAM REŽIMUI

Santrauka

Yra žinoma, kad sparno vyrio tempimo receptoriaus signalas adaptuojasi, kai sparno padėtis yra stabili. Skrendant sparnas periodiškai juda, todėl svarbu sužinoti tempimo receptoriaus būklę tuo metu. Ekstraląsteliniu įrašymo metodu užregistravome signalą iš tempimo receptoriaus periodiškai judindami sparną. Nustatėme, kad sparnui judant veikimo potencialų dažnio adaptacija yra silpnesnė nei tuomet, kai sparnas yra pakeltas.

Raktažodžiai: sensorinės sistemos, adaptacija, informacijos kodavimas, skėriai