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Locust wing stretch receptor adaptation and recovery from adaptation

Aidas Alaburda*,

Rokas Buišas,

Robertas Guzulaitis,

Osvaldas Kaminskas,

Osvaldas Rukšėnas

*Department of Biochemistry
and Biophysics,
Faculty of Natural Sciences,
Vilnius University,
M. K. Čiurlionio 21/27,
LT-03101 Vilnius,
Lithuania*

Adaptation of action potential frequency is a common feature of neurons from various parts of the nervous system. Adaptation is thought to contribute to information coding, integration, input filtering and saving of metabolic resources. Despite intensive investigation, the kinetics of adaptation and recovery from adaptation are not fully described. The locust forewing stretch receptor (fSR) was used to investigate the kinetics of adaptation and recovery from adaptation in response to wing elevation. We have found that adaptation can be well described by a sum of two exponential decays with time constants 5.04 ± 0.6 s and 24.86 ± 2.45 s. The dependence of recovery on adaptation time was biphasic in 70% of the fSRs investigated. In these fSRs, the break point (10.54 ± 1.09 s) separates the initial linear phase from the following exponential one. These findings suggest that at least two mechanisms with different kinetics are involved in the adaptation of locust wing stretch receptor.

Key words: locust, forewing stretch receptor, adaptation, recovery from adaptation, action potential

INTRODUCTION

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 [1–4]. However, this encoding is not linear. When the wing is elevated and kept in a constant position, the frequency of action potentials decreases in time [2, 3]. This phenomenon is intrinsic to the wing stretch receptor and is called the adaptation of action potential frequency. Adaptation is a common feature of neurons from various parts of the nervous system [5–7]. Adaptation is thought to contribute to integration, input filtering and the saving of metabolic resources [8]. Multiple mechanisms may contribute to adaptation [6, 7, 9–13].

The adaptation of the locust wing receptor was described by a single exponential decay [2, 3]. However, a rapid sensory adaptation in the cockroach sensory neuron was described by a sum of two exponentially decaying processes [14]. A detailed analysis of the adaptation in hypoglossal motoneurons revealed that the initial linear phase of adaptation is followed by early and later phases described by a two exponential decays with substantially different time constants [7, 15].

The majority of adaptation mechanisms involve hyperpolarisation of the membrane [16–20]. When the stimulus for adaptation is removed, the mechanisms responsible for hyperpolarization inactivate not instantaneously but with some delay. This causes postadaptational inhibition [17, 19]. Therefore, adaptation and recovery from adaptation are tightly coupled. The recovery from adaptation can be used to describe adaptation [2, 3, 21–23].

The time of recovery from adaptation for the locust wing stretch receptor increases when the wing is elevated to a higher position [2], but it is not known how it depends on the duration of adaptation. In this study, we investigated the kinetics of adaptation and how recovery from adaptation depends on adaptation time.

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* Corresponding author. E-mail: aidas.alaburda@gf.vu.lt

METHODS

Animal preparation

The adult locust (*Locust migratoria*) was prepared for the experiment as described elsewhere [3]. In brief, a locust was decapitated, its legs were removed at the level of the coxae. Then the hind wings were cut, and guts were removed from the animal. The preparation was glued to the stand and installed in the test apparatus. The grounding silver wire was inserted into the abdomen. The forewing was fixed in an apparatus allowing measuring the angle of wing position.

Recording procedures

The signal from the forewing stretch receptor (fSR) located inside the locust trunk is recorded by the monopolar electrode as described by Robertson [3]. The extracellular recordings were performed with a DAM 80 amplifier (WPI, Sarasota, USA), gain 10 000, high pass filter 300 Hz, low pass filter 3 kHz. The data were digitized by Digidata 1 200 (Molecular Devices, Sunnyvale, USA) and stored in computer for analysis by means of Clampex (Molecular Devices, Sunnyvale, USA) software. All experiments were performed at room temperature (20–22 °C).

Data collection and analysis

The experiment started by keeping the wing in a horizontal position. The initial firing frequency of fSR was determined as a $1/\Delta t$ (Fig. 1). The wing was lifted (wing up in Fig. 1) to a 40° position and kept for an adaptation time. The adaptation time of increasing duration (2, 4, 6, 8, 10, 12, 15, 20, 30, 45, 60, 120, 180 s) was used during experimental trials. After adaptation time, the wing was returned to the initial horizontal position (wing down in Fig. 1).

The locust wing was lifted and returned to the initial position (0°) by hand. The position of the wing was changed in less than one second.

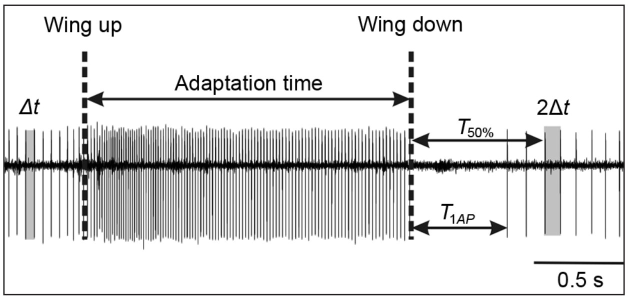

Fig. 1. Elevation (40°) of the forewing (wing up) causes an immediate increase in the frequency of firing the fSR. The initial high frequency adapts over time (adaptation time). Then the wing is moved down to initial position (wing down). T_{1AP} – time of the first action potential appearance after the wing is down. $T_{50\%}$ – time of recovery to a 50% of the initial frequency after the wing is moved down. Δt – time interval between two action potentials when the wing is in horizontal position

The parameters of recovery from adaptation – T_{1AP} (time between wing down and the first action potential) and $T_{50\%}$ (time between wing down and recovery to 50% of the initial frequency) – were measured (Fig. 1). The locust wing was kept in a horizontal position between trials for at least 10 minutes for a full recovery from adaptation. The reciprocal interspike interval was used as an instant frequency of fSR.

The kinetics of fSR action potential frequency adaptation was estimated by fitting with two exponential decays $f(t) = f_0 + A_1{*}\exp(-t/\tau_1) + A_2{*}\exp(-t/\tau_2)$, where $f(t)$ is the action potential frequency at t, t is a time from the onset of adaptation, τ_1 and τ_2 are the time constants of adaptation, f_0, A_1 and A_2 are the fitting parameters. The fitting was done with the Origin (OriginLab, Northampton, USA). The experimental trials with the adaptation time exceeding the slower time constant of adaptation at least three times (120 s) were used for evaluating the adaptation kinetics.

Using a sliding linear regression, the break point was determined from the curve describing the dependence of the recovery parameters (T_{1AP} and $T_{50\%}$) on adaptation time. The linear regression was fitted through the first three and the next three points, and the difference of steepness between the two lines was calculated. Then this procedure was repeated by moving the start of linear regression by one data point and repeating this up to the end of data. The point with the maximal difference in the steepness of linear regressions was taken as a break point. It should be noted that due to the method used, only break points occurring after more than 6 s could be detected. Recovery from adaptation up to the break point was fitted by a straight line: $T_{1AP} = B_1 + B_2{*}t$, and $T_{50\%} = C_1 + C_2{*}t$, where t is the adaptation time, B_1, B_2, C_1 and C_2 are the fitting parameters. Recovery from adaptation after the break point was fitted by an exponential law: $T_{1AP} = D_1 + D_2{*}\exp(-t/\tau_{1AP})$ and $T_{50\%} = E_1 + E_2{*}\exp(-t/\tau_{50\%})$, where τ_{1AP} is the time constant describing the recovery of T_{1AP}, $\tau_{50\%}$ is the time constant describing the recovery of $T_{50\%}$, t is the time from the break point, D_1, D_2, E_1 and E_2 are the fitting parameters.

The data were analyzed statistically by using a two-population (independent or paired) t-test (OriginLab, Northampton, USA). The difference was accepted as significant at $p < 0.05$. The data are presented as the mean ±SE (standard error).

RESULTS

Adaptation of locust forewing stretch receptor

The frequency of fSR action potentials increases when the wing is lifted to a 40° position (wing up in Fig. 1). The maximal frequency after wing elevation was 156 ± 10 Hz (n = 20). When the wing was kept in the elevated position, the fre-

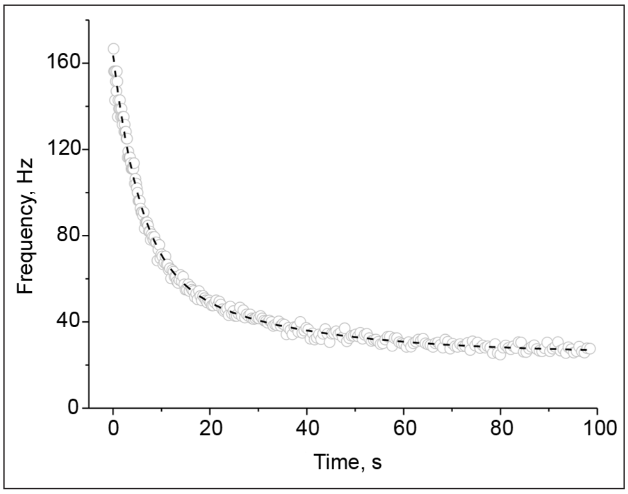

Fig. 2. An example of decay of action potential frequency over time when the wing was lifted up to a 40° position. Circles represent the instantaneous frequency of fSR, dotted line – fitting with two exponential decays

quency of fSR action potentials decreased over time. Five out of 20 fSRs stopped generating AP within 120 s of elevation. The remaining 15 fSRs reached the final frequency of AP generation (calculated within 120–130 seconds) 16 ± 2 Hz (n = 15). An example of fSR frequency decay in time is displayed in Fig. 2 (circles).

This process can be fitted by two exponential decays (dotted line in Fig. 2).

The average time constant of the faster exponential decay was $\tau_1 = 5.04 \pm 0.6$ s, and the slower one was $\tau_2 = 24.86 \pm 2.45$ s (n = 20). These results indicate that at least two mechanisms with different kinetic properties are involved in the adaptation of locust fSR. The second mechanism is about five times slower than the first one.

Recovery from adaptation of locust forewing stretch receptor

Next we tested how recovery from adaptation depends on adaptation time. Two parameters – T_{1AP} and $T_{50\%}$ (see Methods) – were used to describe recovery from adaptation.

The dependence of T_{1AP} on adaptation time displayed biphasic behaviour in 14 out of the 20 fSRs tested. An example of this dependence is shown in Fig. 3A (circles). The break point (Fig. 3A) separated the early linear part from the later exponential one in the dependence of T_{1AP} on adaptation time. The average of the straight line parameter was $B_2 = 0.14 \pm 0.02$ (n = 14). The second part was well fitted by a single exponential law with the average time constant $\tau_{1AP} = 30.10 \pm 4.47$ s (n = 14). The break point was at 18.00 ± 1.66 s (n = 14). The dependence of T_{1AP} on adaptation time in the rest six fSRs was well fitted by a single exponent with the average time constant 24.57 ± 5.85 s (n = 6). This value was not significantly different ($p > 0.05$) from the average value of the time constant calculated for fSRs displaying a biphasic behavior.

The same 14 fSRs (out of 20) that displayed the biphasic dependence of T_{1AP} on adaptation time displayed a biphasic recovery of $T_{50\%}$ from adaptation time as well. An example of biphasic dependence of $T_{50\%}$ on adaptation time is shown in Fig. 3B (circles). The break point (Fig. 3B) separated the linear early part from the later one. The early part was well described by a straight line with the average parameter $C_2 = 0.56 \pm 0.09$ (n = 14), and the later part was fitted by a single exponential law with the average time constant $\tau_{50\%} = 40.92 \pm 15.07$ s (n = 14). The average of the break point was at 10.54 ± 1.09 s (n = 14). The dependence of $T_{50\%}$ on adaptation time in the rest six fSRs was well fitted by a single exponential law with the

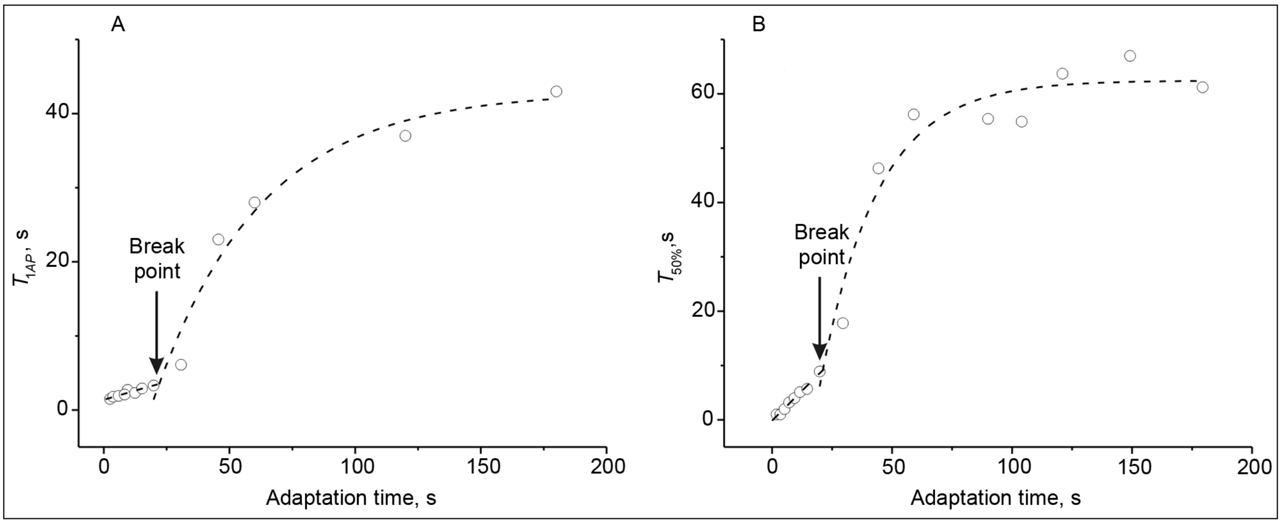

Fig. 3. Examples of biphasic dependence of T_{1AP} (A) and $T_{50\%}$ (B) on adaptation time. In both panels, circles represent experimental data. Dotted line up to the break point represents the linear fitting, and after the break point it shows the fitting with the single exponential law

average time constant 30.10 ± 6.68 s (n = 6). This value was not significantly different ($p > 0.05$) from the average value of the time constant calculated for fSRs displaying a biphasic behaviour.

The biphasic dependence of recovery from adaptation on adaptation time indicates that recovery from adaptation qualitatively depends on the moment the adaptation was stopped and the recovery started. If adaptation had been stopped before the break point, recovery from adaptation was fast. However, if the adaptation time exceeded the break point, the duration of recovery increased dramatically. We have shown that the adaptation of fSR action potentials can be described by two exponential decays with different time constants: τ_1 and τ_2. We have tested how the break point in recovery from adaptation is related to both phases of fSR adaptation, characterized by time constants τ_1 and τ_2. The value of the break point in the dependence of T_{1AP} on adaptation time corresponds to 3.91 ± 0.72 τ_1 and 0.92 ± 0.17 τ_2 (n = 14), and the break point in the dependence of $T_{50\%}$ on adaptation corresponds to 3.07 ± 1.29 τ_1 and 0.52 ± 0.08 τ_2 (n = 14).

DISCUSSION

General remarks

Traditionally, adaptation of the locust wing stretch receptor is described by a single exponential decay [2, 3]. Here, we have found that adaptation process in locust fSR can be described more precisely by two exponential decays. These findings indicate that at least two processes with different kinetics are responsible for adaptation: one process is aproximately five times faster than the other one. Two phases of adaptation are described in the cockroach sensory neuron and in other types of neurons [7, 14, 15].

Recovery from adaptation can also be used for investigatng the adaptation mechanisms [2, 3, 21, 22]. The investigation of recovery from adaptation in locust fSR has demonstrated that recovery time increases with increasing the wing elevation amplitude [2]. In this study, we investigated how recovery from adaptation depends on adaptation time. We found that in 70% of fSRs the dependence of recovery on adaptation time was biphasic: the break point separated the early linear phase from the later exponential one. If the locust wing was elevated for a short time (less than the break point), the recovery from adaptation was very fast. However, if the elevation time exceeded the break point, the time of recovery from adaptation dramatically increasesd. More than three τ_1 of adaptation and less than one τ_2 of adaptation pass before the break point for fSR with biphasic recovery. This indicates that the faster adaptation process is almost finished at the break point, while the slower one is still going on for biphasic fSR.

Possible mechanisms of adaptation

Biophysically, adaptation means a gradual hyperpolarisation of the membrane during sustained constant stimuli [16–20]. Multiple ion currents may contribute to hyperpolarisation of membrane [6, 7, 9–13]. Different types of neurons may employ different mechanisms for adaptation. For example, the m-current and the Ca^{2+}-dependent K^+ current play an important role in the adaptation of rat CA1 pyramidal neurons [6], while in mouse spinal motoneurons, a block of these currents does not affect adaptation [11]. Instead, in this type of neurons, inactivation of fast Na^+ channels is crucial for adaptation [11]. What could be the mechanisms responsible for two phases of adaptation in locust wing stretch receptor? The methods used in this project do not provide a direct answer. By analogy with the mechanisms causing adaptation in cockroach mechanoreceptor neuron [14], we suggest that a slow inactivation of fast Na^+ channels could be responsible for the faster phase of adaptation of the locust wing stretch receptor. The mean time constant of ~5 s for this phase of adaptation is slower than the one reported in the cockroach mechanoreceptor neuron [14]; however, a wide range of inactivation time constants of Na^+ channels has been reported in different types of excitable cells [14, 24]. The slower phase of locust wing stretch receptor adaptation could be due to the electrogenic activity of the Na^+–K^+ pump as reported in the cockroach mechanoreceptor neuron [25]. After a prolonged generation of the action potentials, the intracellular concentration of Na^+ concentration may increase, and the Na^+–K^+ pump will start generating a net outward current while restoring the ion equilibrium. The biphasic recovery from adaptation of the locust wing stretch receptor favours this hypothesis: if the adaptation exceeds a certain duration, the intracellular concentration of Na^+ may increase, and the Na^+–K^+ pump will start generating a net outward current causing membrane hyperpolarization. However, the contribution of the electrogenic activity of the Na^+–K^+ pump to adaptation was not proven in spider mechanoreceptor neurons [23] and hypoglossal motoneurons [7]. The results we have obtained do not allow excluding some other mechanism contributing to adaptation in the locust wing stretch receptor.

Two phases of recovery from adaptation

The early linear phase of recovery from adaptation was missing in 30% of the fSRs. Does it mean that there are systematic differences between fSRs or that there are other explanations? Firstly, all fSRs expressed two phases of adaptation with different time constants. However, the time constant of faster adaptation in biphasic fSRs (5.86 ± 0.65 s, n = 14) was significantly longer than in the others (3.11 ± 0.94 s, n = 6). Therefore, the early linear phase of recovery from adaptation was not found in part of fSRs because it was too short to be detected by the experimental procedures used:

just break points longer than 6 s could be detected (see Methods). Secondly, there were no significant differences between time constants characterizing the later exponential phase in biphasic fSR and exponential recovery in the other fSRs. This implies that there are no systematic differences among the fSRs.

CONCLUDING REMARKS

We have found that the adaptation of the locust forewing stretch receptor can be described more precisely by the sum of two exponential decays. The dependence of recovery on adaptation time was biphasic in 70% of fSRs. In these fSRs, the break point separates the initial linear phase from the following exponential one. These findings suggest that at least two mechanisms with different kinetics are involved in the adaptation of the locust wing stretch receptor.

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Aidas Alaburda, Rokas Buišas, Robertas Guzulaitis,
Osvaldas Kaminskas, Osvaldas Rukšėnas

SKĖRIO SPARNO VYRIO RECEPTORIAUS ADAPTACIJA IR SAVYBIŲ ATSIKŪRIMAS PO ADAPTACIJOS

Santrauka

Veikimo potencialų dažnio adaptacija yra gerai žinoma įvairių smegenų sričių neuronų savybė. Manoma, kad adaptacija svarbi koduojant bei integruojant informaciją, filtruojant įėjimus bei taupant metabolinius resursus. Nepaisant to, kad šis reiškinys seniai tyrinėjamas, adaptacijos bei kitimo po adaptacijos charakteristikos laike nėra visiškai aprašytos.

Šiame darbe nagrinėjant adaptacijos savybes kaip modelinę sistemą naudojome skėrio sparno vyrio tempimo receptoriaus atsakus į sparno pakėlimą. Nustatėme, kad adaptacija gerai aprašoma dviejų eksponenčių su laiko konstantomis 5,04 ± 0,6 s ir 24,86 ± 2,45 s suma. 70 % atvejų tirtų tempimo receptorių savybių kitimas po adaptacijos buvo bifazis, juose lūžio taškas (10,54 ± 1,09 s) skyrė pradinę tiesinę nuo vėlesnės eksponentinės dalies. Gauti rezultatai rodo, kad mažiausiai du skirtingi mechanizmai su skirtingomis kinetinėmis savybėmis turi įtakos skėrio sparno vyrio tempimo receptoriaus adaptacijai.

Raktažodžiai: skėrys, sparno vyrio tempimo receptorius, adaptacija, veikimo potencialas