Corticofugal inhibition compresses all types of rate-intensity functions of inferior collicular neurons in the big brown bat

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Abstract

Recent studies have shown that the auditory corticofugal system modulates and improves signal processing in the frequency, time and spatial domains. In this study, we examine corticofugal modulation of rate-intensity functions of inferior collicular (IC) neurons of the big brown bat, *Eptesicus fuscus*, by electrical stimulation in the primary auditory cortex (AC). Cortical electrical stimulation compressed all types of rate-intensity functions so as to increase the slope but decrease the dynamic range of IC neurons. Cortical electrical stimulation also shifts the responsive intensity of IC neurons to higher levels. These data indicate that corticofugal modulation also improves subcortical signal processing in intensity domain. The implication of these findings to bat echolocation is discussed. © 2000 Elsevier Science B.V. All rights reserved.

Theme: Sensory systems

Topic: Auditory systems: central physiology

Keywords: Bat; Corticofugal modulation; Inferior colliculus; Intensity-coding; Dynamic range

The processing of auditory information carried by complex sounds has been explained by neural interactions based on divergent and convergent projections within the ascending auditory system, but without considering the contribution of the descending (corticofugal) auditory system [19]. However, recent studies in bats have shown that the massive corticofugal system, which is topographically as well organized as the ascending system [1,2,8,9,17], extensively adjusts and improves subcortical auditory signal processing in the frequency, time and spatial domains [6,11,12,21–27]. These studies showed that the bat’s auditory cortex (AC) targets specific sites in the inferior colliculus (IC) with either transient, well-focused excitation or transient, broadly distributed inhibition depending on whether that site is tuned to the same frequency (same tonotopic value) or to a different frequency than the corresponding cortical site.

While corticofugal modulation decreases the auditory sensitivity of corticofugally-inhibited IC neurons [12,21,22], how this corticofugal inhibition may modulate the rate-intensity functions and thus the intensity sensitivity has not been examined. We addressed this question by studying corticofugal modulation of rate-intensity function of corticofugally-inhibited IC neurons in the big brown bat, *Eptesicus fuscus*, under free field stimulation conditions. We found that corticofugal modulation compressed all types of rate-intensity functions of IC neurons resulting in decreasing the dynamic range, increasing the sharpness of the monotonically linear portion of the rate-intensity function, and shifting the responsive intensity to higher levels. This modulation of rate-intensity functions may improve the analysis of echo intensity during the final phase of hunting.

Surgical procedures and the experimental set-up were basically the same as in a previous study [13]. Briefly, 1 or 2 days before the recording session, a 1.8-cm nail was glued onto the exposed skull of each of 11 Nembutal-
anesthetized (45–50 mg/kg b.w.) bats (b.w. 18–24 g). During recording, each bat was administered the neuro-leptanalgesic Innovar-Vet (0.08 mg/kg b.w. of fentanyl, 4 mg/kg b.w. of droperidol) and was tied to an aluminum plate inside a double-wall, sound-proof room (temperature 28–30°C). After fixing the head with a set screw, small holes were bored in the skull above the primary auditory cortex (AC) and the inferior colliculus (IC) for insertion of electrodes. An indifferent electrode (silver wire) was placed at the nearby temporal muscles.

Acoustic stimuli (4 ms with 0.5 ms rise-decay times at 2 pps) were generated with an oscillator (KH model 1200) and a homemade electronic switch. These stimuli were then amplified after passing through a decade attenuator (HP 350D) before they were fed to a small condenser loudspeaker (AKG model CK 50, 1.5 cm diameter, 1.2 g) that was placed 23.5 cm away from the bat. The loudspeaker was calibrated with a Brüel & Kjaer 1/4 inch (4135) microphone placed at the bat’s ear. The output was expressed in dB SPL in reference to 20 μPa root mean square.

During experiments, sound pulses were delivered from the loudspeaker placed at 40° contralateral to the recording site. A 3 M KCl glass micropipette electrode (diameter: 1 μm, impedance 5–10 MΩ) was used to isolate acoustically evoked IC neurons. The best frequency (BF) and minimum threshold (MT) of each isolated IC neuron were determined by systematically changing the frequency and intensity of sound pulses. At the MT, the neuron, on average, responded with 50% probability to BF pulses. A custom-made two tungsten-in-glass electrodes (tip: <10 μm, inter-tip distance: 30–50 μm) [12] was inserted into the AC at depths of 600–700 μm (the 5th layer of the AC) [14]. The responses of the IC neuron to BF sounds (at 10 dB above the MT) were then examined with electrical stimulation (4 ms train stimulus consisting of four monophasic pulses of 0.1 ms) in the AC (hereafter referred to as AC stimulation).

When responses of the IC neuron were not affected by AC stimulation, the neuron was abandoned. When responses of IC neurons were affected by AC stimulation, the interval between electrical and sound stimuli was adjusted (1–6 ms, mostly 1–3 ms) to produce at least 20% corticofugal effect in terms of number of impulses. At this interstimulus interval, the electrical current (5–50 μA, mostly 5–25 μA) that produced 30–50% corticofugal effect was chosen for subsequent experiments.

To study corticofugal modulation of intensity sensitivity of each IC neuron, the neuron’s number of impulses was recorded with BF sounds delivered at 10 dB increments above the MT before, during and after AC stimulation. A rate-intensity function was then obtained by plotting the number of impulses against the stimulus intensity for each stimulation condition. The effect of corticofugal modulation on the neuron’s intensity sensitivity was then examined by comparing the width and shift in dynamic range as well as the slope of the monotonically linear portion of the rate-intensity function obtained before and during AC stimulation.

Recorded action potentials were amplified with conventional techniques and sent to a computer (Gateway 2000, Fig. 1. Three different types of rate-intensity functions obtained from IC neurons of the big brown bat, Eptesicus fuscus. (A) Monotonic: a neuron’s number of impulses increased monotonically with stimulus intensity. (B) Saturated: a neuron’s number of impulses increased with stimulus intensity to a maximum and did not change more than 25% thereafter (indicated by 25% horizontal dashed line). (C) Non-monotonic: a neuron’s number of impulses increased with stimulus intensity to a maximum and decreased more than 25% thereafter. The dynamic range (DR) of each rate-intensity function was determined according to the intensity range corresponding to the number of impulses that was 10% below the maximum and 10% above the minimum (indicated by dotted lines). The slope (%/dB) of the rate-intensity function was obtained by dividing the change in the number of impulses in percent within the DR by the DR (e.g. between filled arrow heads in A). The best frequency (BF, kHz), minimum threshold (MT, dB SPL), recording depth (μm) and latency (ms) of these three neurons were 59.6, 30, 1399, 14 (A); 32.0, 22, 826, 11 (B); 47.1, 30, 1019, 12 (C).
We examined corticofugal modulation of intensity sensitivity of IC neurons by measuring the variations in the width and shift in the dynamic range, as well as the slope of each neuron’s rate-intensity function resulting from AC stimulation. The dynamic range of each rate-intensity function was determined according to the intensity range corresponding to the number of impulses that was 10% below the maximum and 10% above the minimum (Fig. 1A–C, DR). The slope of the rate-intensity function was obtained by dividing the percent change in the number of impulses within the dynamic range by the dynamic range and expressed in %/dB (e.g. Fig. 1A between filled arrow heads). The slope is an indication of a neuron’s sensitivity to variation in stimulus intensity. Thus a large (sharp) slope represents a high sensitivity to variation in stimulus intensity.

Fig. 2A–1, B–1, C–1 show the PST histograms of three representative IC neurons that were obtained with BF sounds delivered at 10 dB above the MT of each neuron.
before (a), during (b), and after (c) AC stimulation. The number of impulses of all three neurons greatly decreased during AC stimulation but recovered instantly after AC stimulation. Fig. 2A-2, B-2, C-2 show their rate-intensity functions that were obtained before (filled circles), during (unfilled circles) and after (dashed) AC stimulation. In all three neurons, the rate-intensity functions obtained before and after AC stimulation were essentially congruent (Fig. 2A-2, B-2, C-2, a vs. c). However, the rate-intensity functions obtained before and during AC stimulation were different, and the difference was larger at low sound intensities than at high sound intensities (Fig. 2A-2, B-2, C-2, a vs. b). This observation indicates that the dynamic range and slope of the rate-intensity function obtained before and during AC stimulation were different. This observation also indicates that corticofugal inhibition was more effective at low than at high sound intensities, similar to previous studies [6,12]. We calculated the effectiveness of corticofugal inhibition in percent by dividing the difference in the number of impulses due to AC stimulation by the number of impulses obtained before AC stimulation. This calculation showed that percent inhibition reduced sharply with sound intensity within 20–30 dB above the MT before reaching a plateau level at still higher intensities (Fig. 2A-3, B-3, C-3).

Table 1 shows that the average dynamic range (top row) of all three types of rate-intensity functions significantly decreased and the slope (middle row) significantly increased, during AC stimulation (paired t-test, P<0.005).

These data also show that IC neurons with non-monotonic rate-intensity functions had the smallest dynamic range and largest slope while neurons with monotonic rate-intensity functions had the largest dynamic range and smallest slope. The dynamic range and slope of the neurons with saturated rate-intensity functions had intermediate values. Repeated measure one-way ANOVA indicated that the dynamic range and slope of these three types of IC neurons were significantly different whether obtained before or during AC stimulation (P<0.005).

Fig. 3A-1, B-1, C-1 show the intensity level that corresponds to the dynamic range of all three types of rate-intensity functions obtained before (filled circles) and during (unfilled circles) AC stimulation. It is clear that the dynamic range of all three types of rate-intensity functions became smaller and shifted to higher intensity levels during AC stimulation. This shifting of the dynamic range mainly took place at the low end of the dynamic range. To highlight the change in the dynamic range of IC neurons as a result of AC stimulation, we connected the midpoints of all dynamic ranges of IC neurons determined before and during AC stimulation and produced a middle dynamic range curve for each stimulation condition. As shown in Fig. 3A-2, B-2, C-2, the middle dynamic range curves of all three types of rate-intensity functions shifted from low to high intensity levels during AC stimulation.

Table 1 indicates that AC stimulation shifted significantly the middle dynamic range intensity (i.e. the intensity that corresponds to middle dynamic range) of all IC neurons.

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Table 1

<table>
<thead>
<tr>
<th>Type</th>
<th>n</th>
<th>Monotonic</th>
<th>Saturated</th>
<th>Non-monotonic</th>
<th>P (ANOVA)</th>
</tr>
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<tbody>
<tr>
<td>DR (dB)</td>
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<td>Range</td>
<td>Mean±S.D.</td>
<td>Mean±S.D.</td>
<td>P (paired t-test)</td>
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<td>AS</td>
<td>8</td>
<td>25.0–41.0</td>
<td>33.9±6.1(a)</td>
<td>24.0±7.0(d)</td>
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<td>AS+ES</td>
<td>12</td>
<td>16.0–40.0</td>
<td>26.1±6.9(b)</td>
<td>19.3±7.5(e)</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>15.0–28.0</td>
<td>20.3±4.8(c)</td>
<td>12.2±4.5(f)</td>
<td>0.0016</td>
</tr>
<tr>
<td>Slope (%/dB)</td>
<td></td>
<td>Range</td>
<td>Mean±S.D.</td>
<td>Mean±S.D.</td>
<td>P (paired t-test)</td>
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<tr>
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<td>1.32–2.37</td>
<td>1.66±0.38(g)</td>
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<td>AS+ES</td>
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<td>1.50–4.50</td>
<td>2.54±0.78(h)</td>
<td>3.36±0.78(k)</td>
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<td></td>
<td></td>
<td>2.11–4.70</td>
<td>3.19±0.94(i)</td>
<td>4.72±1.23(l)</td>
<td>&lt;0.0001</td>
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<tr>
<td>Middle DR intensity (dB)</td>
<td></td>
<td>Range</td>
<td>Mean±S.D.</td>
<td>Mean±S.D.</td>
<td>P (paired t-test)</td>
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<tr>
<td>AS</td>
<td>8</td>
<td>54.5–82.5</td>
<td>68.2±9.9</td>
<td>75.9±10.1</td>
<td>&lt;0.0001</td>
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<tr>
<td>AS+ES</td>
<td>12</td>
<td>39.5–80.0</td>
<td>61.9±14.2</td>
<td>67.7±13.4</td>
<td>&lt;0.0001</td>
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<tr>
<td></td>
<td></td>
<td>34.5–76.0</td>
<td>57.0±12.5</td>
<td>62.6±11.6</td>
<td>0.0748</td>
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</table>

*Paired t-test shows that AC stimulation significantly decreased the DR but increased the slope and middle DR intensity of all three types of rate-intensity functions (P<0.0001–0.0007). Repeated measures one-way ANOVA shows significant difference in the DR and slope among three types of rate-intensity functions obtained before and during AC stimulation (P<0.0001–0.0016). A Student–Newman–Keuls multiple comparison post test shows significant difference between (a) and (b) (P<0.01); (a) and (c) (P<0.001); (b) and (c) (P<0.05); (d) and (f) (P<0.01); (e) and (f) (P<0.05); (g) and (h) (P<0.01); (g) and (i) (P<0.01); (h) and (l) (P<0.05); (j) and (k) (P<0.05); (j) and (l) (P<0.001); (k) and (l) (P<0.01). P, significance level; n, number of neurons; AS, acoustic stimulus; AS+ES, acoustic stimulus plus electrical stimulation in the AC (see text for description of different types of rate-intensity functions).
Fig. 3. (A-1, B-1, C-1) Distribution of the dynamic ranges of three types of IC neurons (A-1, monotonic; B-1, saturated; C-1, non-monotonic) determined before (filled circles) and during (unfilled circles) AC stimulation. Note that the change in dynamic range was larger at the low than at high intensity end. (A-2, B-2, C-2) The middle dynamic range intensity of all three types of IC neurons obtained before (filled circles) and during (unfilled circles) AC stimulation. These curves are generated by connecting the midpoints of the dynamic ranges of all IC neurons shown in A-1, B-1 and C-1. Note that these curves shift from left to right during AC stimulation.

neurons to higher intensity levels (Table 1, bottom row, paired t-test, \(P<0.005\)). However, AC stimulation did not produce a significant difference in the shift of the middle dynamic range intensity among IC neurons with different types of rate-intensity functions (repeated measure one-way ANOVA, \(P>0.01\)).

In order to determine if corticofugal modulation produced differential effects on the intensity sensitivity of these three groups of IC neurons, we compared the percent changes in dynamic range, slope and the middle dynamic range intensity as a result of AC stimulation. As shown in Table 2, AC stimulation did not produce any significant difference in the changes in dynamic range, slope and middle dynamic range intensity among these three different groups of IC neurons (repeated measures one-way ANOVA, \(P>0.01\)).

We show that IC neurons can be classified into three types according to their rate-intensity functions (Fig. 1). Although IC neurons differed in how number of impulses increased at high stimulus intensities, they all monotonically increased the number of impulses within the dynamic range (Fig. 1). Therefore, we used changes in the dynamic range and slope of the monotonic portion of the rate-intensity function under AC stimulation conditions to determine the effect of corticofugal modulation on intensity sensitivity of IC neurons. We have shown that AC
Table 2

<table>
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<tr>
<th>Type</th>
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<th>Saturated</th>
<th>Non-monotonic</th>
<th>P</th>
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<td>DR (dB)</td>
<td>Range</td>
<td>12.2–43.3</td>
<td>2.5–44.0</td>
<td>5.9–66.7</td>
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<td></td>
<td>Mean±S.D.</td>
<td>29.6±12.3</td>
<td>26.5±13.5</td>
<td>39.9±19.4</td>
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<tr>
<td>Slope (%/dB)</td>
<td>Range</td>
<td>12.2–51.7</td>
<td>1.0–71.6</td>
<td>4.0–91.7</td>
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<td></td>
<td>Mean±S.D.</td>
<td>35.5±17.2</td>
<td>35.9±23.2</td>
<td>52.1±31.7</td>
</tr>
<tr>
<td>Middle DR intensity (dB)</td>
<td>Range</td>
<td>7.1–18.3</td>
<td>3.6–20.5</td>
<td>3.9–20.7</td>
</tr>
<tr>
<td></td>
<td>Mean±S.D.</td>
<td>11.5±3.4</td>
<td>10.2±5.3</td>
<td>10.9±5.3</td>
</tr>
</tbody>
</table>

*Repeated measures one-way ANOVA reveals no significant difference in these changes among three different types of rate-intensity functions (P = 0.1245–0.8411). P, significance level; n, number of neurons.

stimulation significantly increased the slope (Fig. 2) and decreased the dynamic range (Fig. 3A-1, B-1, C-1) in all corticofugally-inhibited IC neurons (Table 1, top and middle rows).

AC stimulation significantly shifted the dynamic range (Fig. 3A-1, B-1, C-1) and the middle dynamic range intensity (Fig. 3A-2, B-2, C-2) to higher intensity levels (Table 1, bottom row). The observed shift in dynamic range was larger at the low than at the high intensity end (Fig. 3A-1, B-1, C-1). This asymmetrical shift in the dynamic range occurred because AC stimulation produced a more pronounced effect at the low than at the high intensity levels (Fig. 2A-3, B-3, C-3).

We observed significant differences among the three types of IC neurons in dynamic range and slope whether obtained before or during AC stimulation (Table 1, top and bottom rows). These observations indicate that there is a trade-off in the intensity coding properties of IC neurons. For example, non-monotonic IC neurons had significantly smaller dynamic ranges and larger dynamic range slopes than the other two types of IC neurons (Table 1). These data suggest that non-monotonic IC neurons are most sensitive to intensity changes over a smaller range of intensity than the other two types of IC neurons. In spite of these differences, AC stimulation did not produce any significantly differential or selective effects on intensity coding among these three types of IC neurons (Table 2).

As described earlier, previous studies have shown that the corticofugal system extensively adjusts and improves subcortical auditory signal processing in the frequency, time and spatial domains [6,11,12,21–27]. We have now demonstrated that corticofugal modulation also improves subcortical signal processing in the intensity domain by increasing the sensitivity to intensity change over a smaller intensity range at higher sound intensity levels (Figs. 1–3; Table 1).

During hunting, bats emit sounds and analyze the returning echoes to extract information about the targets [3]. As the bats approach the targets, the returning echoes become stronger. To have optimal reception of echoes, bats reduce the pulse intensity to compensate for increasing echo intensity [4,5,10,16]. In addition, bats contract their middle ear muscles during pulse emission [7,20] to attenuate self-stimulation and increase the threshold for target detection and discrimination [4,5,15,18]. We propose that bats may additionally utilize corticofugal inhibition to improve the analysis of echo intensity by increasing sensitivity to change of echo intensity over a smaller intensity range at higher echo intensity levels.

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