hanced morphological differentiation, and increased the activities of CK and myokinase. The biologically active component appeared to be a protein, as evidenced by its lability to treatment with trypsin or protease and its stability to treatment with neuraminidase, phospholipase A_2, and concanavalin A. Polyacrylamide gel electrophoresis of the active fraction on 7.5 percent gels in tris-glycine buffer (*p*H 8.3) revealed five protein bands. The gels were negative to staining with periodic acid–Schiff reagent. In Fig. 1 and Tables 1 and 2, the term inactive peripheral nerve (PN) proteins refers to the pooled column proteins not contained in the fraction with K_{AV} = 0.54 to 0.56.
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24. Although the active PN proteins are most likely components of axons or axoplasm, it is possible that they might be derived from nonneuronal cells such as Schwann cells. Experiments are required to define the source of these proteins.
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Aural Representation in the Doppler-Shifted-CF Processing Area of the Auditory Cortex of the Mustache Bat

Abstract. *In the mustache bat (*Pteronotus parnellii rubiginosus*) the frequency and amplitude of an acoustic signal are represented in the coordinates parallel to the surface of the Doppler-shifted-CF (constant frequency) processing area of the primary auditory cortex. In this area all cortical neurons studied were excited by contralateral stimuli, and almost all of them were either excited or inhibited by ipsilateral stimuli. These are called E-E (ipsilateral and contralateral excitatory) and I-E (ipsilateral inhibitory and contralateral excitatory) neurons, respectively. The I-E neurons are directionally sensitive, while the E-E neurons are not. The E-E neurons are equally sensitive to echoes between 30° contralateral and 30° ipsilateral. Of the electrode penetrations orthogonal to the Doppler-shifted-CF processing area, 57 percent were characterized by either E-E or I-E neurons. Thus, there are at least two types of binaural columns: E-E columns, mainly located in a ventral part of the Doppler-shifted-CF processing area, where neurons are tuned to weak echoes; and I-E columns, mainly distributed in a dorsal part, where neurons are tuned to moderate to intense echoes. Therefore, neurons tuned to weaker echoes integrate or even multiply faint signals from both ears for effective detection of a distant small target, while neurons tuned to moderate to intense echoes are suited for processing directional information and are stimulated when a bat approaches a target at short range. The Doppler-shifted-CF processing area may be considered to consist of two functional subdivisions.*

The mustache bat, *Pteronotus parnellii rubiginosus*, emits orientation sounds which consist of a long constant-frequency (CF) component followed by a short frequency-modulated (FM) component. The long CF sound is an ideal signal for Doppler-shift measurement—that is, for the measurement of the relative velocity of a target—and it is also a good signal for target detection. The short FM sound, on the other hand, is suited for ranging, localization, and characterization of the target. In the orientation sound, the second harmonic is always predominant and its CF component is about 61 kHz (*1–4*). The mustache bat apparently uses this signal for detection of a moving target because it adjusts the frequency of the emitted CF component to receive a Doppler-shifted echo at a certain preferred frequency (61 to 62 kHz), to which the auditory system is sharply tuned. This interesting acoustic behavior is called Doppler-shift compensation (*2*).

Peripheral auditory neurons with a best frequency (BF) between 60 and 63 kHz show unusually sharp tuning (or threshold) curves. These sharply tuned neurons are apparently specialized for detection and frequency analysis of the CF component in echoes. The primary auditory cortex of this animal reflects this peripheral specialization by devoting a disproportionately large area to processing the CF component of Doppler-shifted echoes (Fig. 2A) (*5*). In this Doppler-shifted-CF processing area, the BF and best stimulus amplitude (BA) for the maximum excitation of a single neuron vary systematically with the location of the neuron in the cortical plane. The iso-BF contour lines are eccentric: neurons sensitive to 61 kHz are at the center and those sensitive to 62 or 63 kHz are at the circumference. The iso-BA contour lines are radial: neurons tuned to weaker sounds are in the ventral part and those tuned to intense sounds are in the dorsal part. These tonotopic and amplitopic representations are apparently related to those of the relative velocity and subtended angle (or cross-sectional area) of a target. The origin of the coordinates representing frequency and amplitude is off-center in the Doppler-shifted-CF processing area, so that both representations disproportionately express an acoustic signal of 61.5 to 62.0 kHz and 30 to 50 dB SPL (sound pressure level) over a larger cortical area (Fig. 2B) (*6*). These disproportionate tonotopic and amplitopic representations are apparently related to the predominant parameters of the acoustic signals used for echolocation.

To investigate the cortical organization related to the localization of a potential target, we studied how sounds stimulating the left and right ears are represented in the Doppler-shifted-CF processing area, and how this aural representation is related to the tonotopic and amplitopic representations. As described below, we found that this area is organized in a very interesting way in terms of aural representation. That is, it consists of two functional subdivisions: one specialized for target detection by integrating excitatory signals from both ears, and the other for target localization by assembling excitatory signals from the contralateral ear and inhibitory ones from the ipsilateral ear.

The experiments were performed with 27 mustache bats, *P. parnellii rubiginosus* (body weight, 20 to 25 g) from Panama. A bat was anesthetized with sodium pentobarbital (30 mg per kilogram of body weight) and ether when necessary, and the flat head of a nail (1.8 cm long) was mounted on the posterodorsal surface of its skull with glue and cement. Then the bat was placed in a soundproof room heated to 33° to 34°C. To immobilize the bat's head, the shank of the nail was locked into a hollow metal rod with a setscrew. The skull covering the Doppler-shifted-CF processing area was removed. A tungsten wire electrode with a tip diameter of 5 to 15 μm was orthogonally inserted into the exposed cortical area to record action potentials from a single neuron or a cluster of a few neurons at depths between 200 and 1000 μm. To stimulate the left or the right ear

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semi-independently, an aluminum partition (60 × 60 cm²) covered with thin foam rubber was put along the median plane of the animal. The narrow space between the partition and the bat's head was filled with bone wax, which attenuated 60- to 63-kHz tone bursts stimulating the contralateral ear by 25 to 40 dB. Since each ear is most sensitive about 30° lateral, condenser loudspeakers 50 mm in diameter were placed 30° laterally on each side of the partition at a distance of 70 cm from the bat's ear. Tone bursts with rise and decay times of 0.5 msec and a duration of 4.5 or 50.0 msec were delivered at a rate of 2.0 per second from either loudspeaker, or from both successively or simultaneously. To study the directional sensitivity of single neurons in the horizontal plane, the partition was removed, and one of the loudspeakers was mounted on an acoustic perimeter 70 cm in radius. The tone bursts described above were delivered at a rate of 2.0 per second. The outputs of these loudspeakers were calibrated with a Brüel & Kjaer ¼-inch microphone placed at the bats' ears and the sound pressure was expressed in decibels referred to 0.0002 dyne/cm² root-mean-square. Responses of a single neuron or a neuron cluster to identical tone bursts were sampled 50 times and were expressed in the form of poststimulus time (PST) and cumulative histograms by a Nicolet computer (Fig. 1, A and B). Details of the instruments used for delivering acoustic stimuli and recording and processing neural responses to them are given elsewhere (*7, 8*).

In the Doppler-shifted-CF processing area, almost all neurons were excited by contralateral stimuli and were either excited or inhibited by ipsilateral stimuli, while a small number of neurons were monaural and responded only to contralateral stimuli. These three types of neurons are called E-E, I-E, and 0-E neurons, respectively. Figure 1A shows responses of an I-E neuron: inhibition of its background activity caused by ipsilateral stimuli and excitation by contralateral stimuli. When both ears were stimulated either simultaneously or successively, the excitation evoked by contralateral stimuli was reduced by ipsilateral stimuli (Fig. 1A, part 3). Figure 1B shows responses of an E-E neuron. Its excitation was usually greater to contralateral stimuli than to ipsilateral stimuli, but the BF, minimum threshold (MT; threshold at BF), and BA measured with contralateral stimuli were similar to those measured with ipsilateral stimuli. The stimulation of both the ears with sounds weaker than the BA evoked sum-

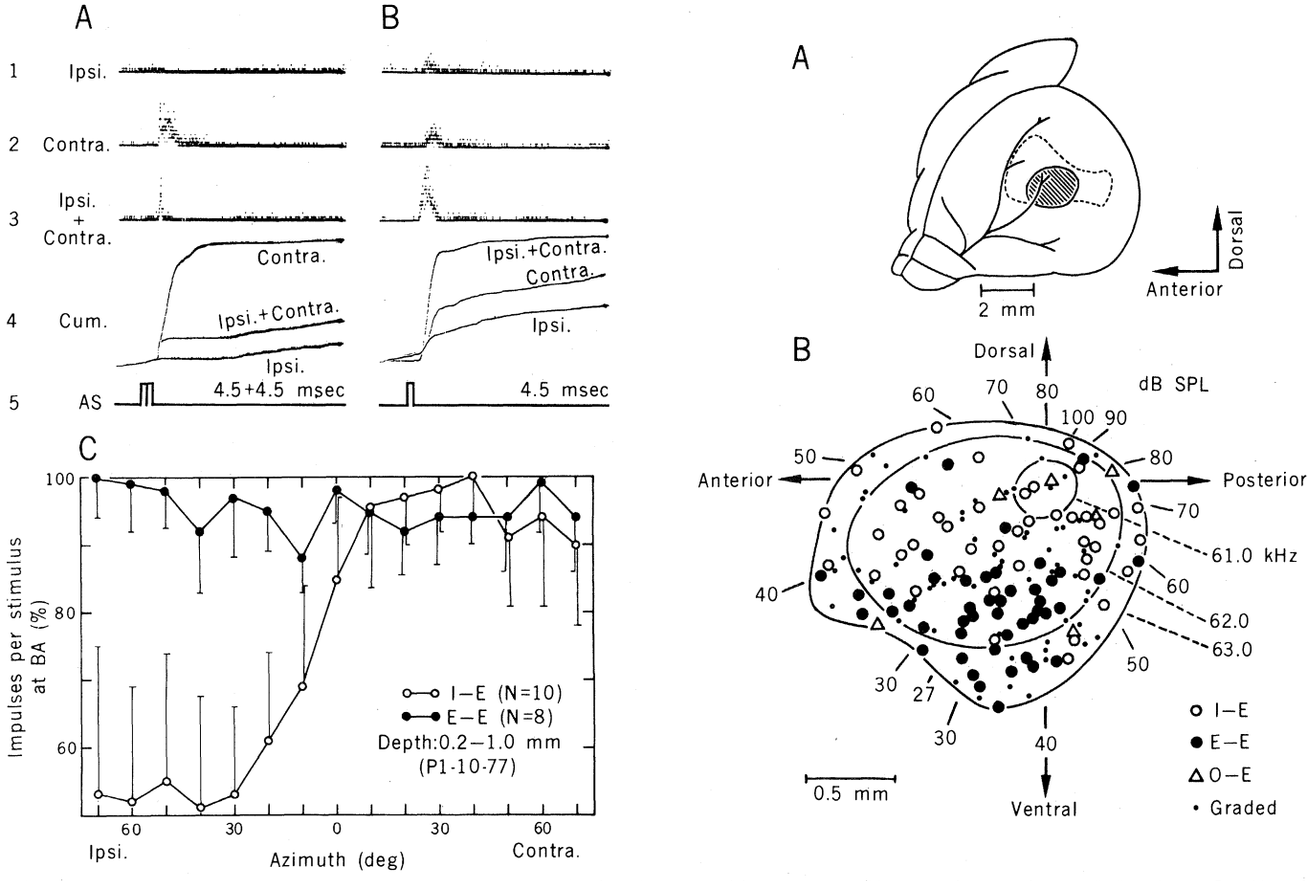

Fig. 1 (left). Responses of (A) I-E and (B) E-E neurons and (C) directional sensitivity curves of neurons in an I-E or an E-E column. In (A) and (B), each histogram represents the sum of responses of a single neuron to an identical tone burst or identical tone bursts delivered 50 times. The bin width of the histogram is 0.2 msec. Parts 1 to 3 are PST histograms of responses; part 4 shows cumulative (*Cum.*) histograms of the responses above; and part 5 shows the envelopes of full-wave-rectified acoustic stimuli (*AS*). The responses are for an ipsilateral stimulus alone (*Ipsi.*); a contralateral stimulus alone (*Contra.*); or (A) successive or (B) simultaneous delivery of the ipsilateral and contralateral stimuli (*Ipsi. + Contra.*). The ipsilateral and contralateral stimuli are, respectively, (A) 64.59 kHz, 68 dB SPL and 64.46 kHz, 38 dB SPL and (B) 62.27 kH, 28 dB SPL and 62.27 kHz, 43 dB SPL. (C) Impulses per stimulus at the BA as a function of azimuth. Each circle and vertical line represent the mean and standard deviation. The number of clusters of neurons studied between 0.2 and 1.0 mm in depth is 10 in the I-E column (○) and 8 in the E-E column (●). Fig. 2 (right). (A) Dorsolateral view of the left cerebrum. The primary auditory cortex and the Doppler-shifted-CF processing area are, respectively, the area surrounded by the dashed line and the shaded part in it. (B) Distributions of the four types of columns in the Doppler-shifted-CF processing area. Note the segregation of I-E (○) and E-E columns (●) in the dorsal and ventral parts, respectively. The distributions of the 0-E (△) and graded (•) columns are also shown. The data are pooled from six mustache bats. The iso-BF contours are shown by eccentric lines and three digits, the iso-BA contours by radial lines and two digits.

mation or even facilitation of the responses (Fig. 1B, part 3). In a 0-E neuron, the BF, MT, BA, and impulse-count function measured for stimulation of both ears were identical to those for a contralateral stimulus alone.

To explore the functional differences among I-E, E-E, and 0-E neurons for sound localization, their MT's, BA's, and number of impulses per stimulus at the BA were measured as a function of azimuth by placing one of the condenser loudspeakers at different azimuth angles without the partition. In I-E neurons the best azimuth in terms of the MT, BA, and number of impulses per stimulus at the BA ranged between 20° and 40° contralateral. Their MT's and BA's became remarkably higher when the sound source was moved from 20° contralateral to 20° ipsilateral. The number of impulses per stimulus at the BA changed drastically between these two azimuth angles (Fig. 1C). The I/E neurons were more directionally sensitive than monaural (0-E) neurons. In E-E neurons, on the other hand, the directional sensitivity curve in terms of the MT, BA, and number of impulses per stimulus at the BA was somewhat flat (Fig. 1C). They were much less directional than monaural neurons. Since the E-E neurons were equally sensitive to sounds delivered at any angle between 30° ipsilateral and 30° contralateral, they are poorly suited for coding target localization but are suited for target detection.

In the Doppler-shifted-CF processing area, neurons in an orthogonal electrode penetration are characterized by nearly identical BF's and BA's regardless of depth (*6*). Therefore we investigated whether each penetration was further characterized with one of the three types of neurons. It was found that 57 percent of the orthogonal penetrations were characterized by either I-E or E-E neurons. For instance, when an I-E neuron was recorded at a superficial depth, all other neurons at subsequent depths were also I-E. When the electrode was placed in another location and an E-E neuron was recorded near the surface, all other neurons at increasing depths were also E-E. In 4 percent of the orthogonal penetrations, all neurons were monaural (0-E) regardless of depth. Therefore, there are at least three types of aural representation columns: I-E, E-E, and 0-E. In the remaining 39 percent, aural representation gradually varied with the depth of neurons, from I-E to 0-E and to E-E, or vice versa. Monaural neurons were always recorded at depths of 500 to 600 μm in these penetrations. Such a change in aural representation with depth cannot be explained by assuming that our so-called orthogonal penetrations in fact traversed three different types of columns, because (i) no monaural neurons were found in the I-E and E-E columns studied and (ii) the percentage of the 0-E columns was very small. Thus, there seems to be a fourth type of column: a "graded" column (*9*). In each of these four types of columns, the BF's, MT's, and BA's of neurons for contralateral stimuli were nearly identical.

Finally, the tangential distributions of these four types of columns were studied in relation to the tonotopic and amplitopic representations. To obtain enough data from a single bat to explore the distributions, it was essential to identify the type of column within a short time. We did this by examining the characteristics of two clusters of a few neurons at 250 and 750 μm in each orthogonal penetration. The BF's, MT's, and BA's of these neuron clusters for contralateral stimuli were also measured. In each of six bats used, 21 to 35 penetrations were within the Doppler-shifted-CF processing area.

As reported previously (*6*), two types of amplitopic representations were found. In five of six bats studied, high BA's were represented dorsally and low BA's ventrally, with intermediate BA's between them (V-type). In the remaining bat, the BA's increased in a counterclockwise direction with a discontinuity at the anteroventral part (N-type). In both types, the amplitopic representation in the posterior half was the same, so that all the data from the five bats showing the V-type amplitopic representation were pooled together with the data from the posterior half of the Doppler-shifted-CF processing area showing the N-type amplitopic representation in order to show the distribution of the four types of columns in relation to iso-BF and iso-BA contours (Fig. 2B).

The distributions indicate that the I-E and E-E columns segregate in an interesting pattern: the I-E columns are mainly located dorsally and the E-E columns ventrally. The graded columns, however, are scattered. The number of 0-E columns found was so small that their distribution remains to be further studied. In the dorsal area, where I-E columns were mainly found, neurons were tuned to moderate to intense sounds. In the ventral area, where E-E columns were mainly located, neurons were tuned to weak sounds. It is clear that the aural representation is correlated with the amplitopic (BA) representation. The aural representation in the anterior half of the Doppler-shifted-CF processing area showing the N-type amplitopic representation remains to be studied.

One important functional significance of these aural and amplitopic representations in the Doppler-shifted-CF processing area is that neurons tuned to weak echoes are equally sensitive to echoes in any direction from 30° contralateral to 30° ipsilateral, and integrate or even sometimes multiply faint signals originating from both ears for effective detection of a target. When the mustache bat flies toward a target, the echo intensity from it becomes stronger. Then neurons tuned to moderate to intense echoes are excited. They are suited for processing directional information. The Doppler-shifted-CF processing area thus not only has coordinates of frequency versus amplitude, it also consists of functional subdivisions suited for target detection or target localization (*10*).

As described above, the clear functional organization of the primary auditory cortex of the mustache bat is apparently related to its specialization for processing sonar signals. As a mammal, however, the mustache bat may also share some common features of the functional organization of the primary auditory cortex with other mammals. In fact, the tonotopic representation of the mustache bat shows a certain common feature, although it is specialized (*5*). The amplitopic and aural representations in relation to the tonotopic representation have not yet been explored in any species other than the mustache bat. The primary auditory cortices of cats and dogs are similar to each other in the tonotopic representation. The iso-BF contour lines run dorsoventrally (*11, 12*). In both these species, the energy of communication sounds is not highly concentrated at a particular frequency. If one thus assumes that their primary auditory cortices are organized in a similar way, the data for cats and dogs may be combined for comparison with those for the mustache bat.

In the cat's primary auditory cortex, summation and suppression columns have been found (*13*), which are comparable to E-E and I-E columns in the mustache bat. The suppression columns occupy a rostrocaudal strip sandwiched between two strips of summation columns. In the dog's primary auditory cortex, neurons located dorsally are more sensitive than those located ventrally. This difference in sensitivity is, however, only for ipsilateral stimuli (*11*). The data for dogs are curious in terms of the amplitopic representation because the main excitatory input does not come

from the ipsilateral ear, but from the contralateral ear (*6*). In any case, the data for cats and dogs suggest that the neurons most sensitive to acoustic signals are E-E, as found in the mustache bat. However, the functional significance of the aural representation found in cats and the sensitivity representation found in dogs is not yet clear. In the mustache bat, orientation sounds consist of two distinct components, which are used for the extraction of certain information about a target, and the auditory cortex is apparently organized for effective processing of such information. Since the auditory system has evolved together with the vocalization system that generates the acoustic signals used by the species, the functional organization of the auditory system should be studied in terms of receiving and processing acoustic signals that are frequently used by the species and are important for survival.

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References and Notes

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10. Response patterns and thresholds of single neurons studied within 2 to 4 hours after an injection of sodium pentobarbital (30 mg/kg) were similar to those 9 to 12 hours after the injection. When the animal moved too much for us to study the properties of single neurons, one-third of the initial dose was administered. There was no noticeable difference between the response pattern and threshold of neurons just before and those after such an injection. It appeared very unlikely that the anesthetic changed the mode of binaural interaction observed. It has been demonstrated that the tonotopic and amplitopic representations in the Doppler-shifted-CF processing area are not altered by the anesthetic (*6*). If sodium pentobarbital at more than 30 mg/kg was administered, there might be a noticeable effect on response properties of neurons within a few hours.
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Immunoreactive Vasopressin and Oxytocin: Concentration in Individual Human Hypothalamic Nuclei

Abstract. *Individual hypothalamic nuclei were microdissected from brain tissue of ten human subjects who had died suddenly while in apparent good health. Appreciable amounts of vasopressin and oxytocin immunoreactivity were found by specific radioimmunoassay in six hypothalamic nuclei including supraoptic and paraventricular nuclei. Vasopressin and oxytocin are presumed to be synthesized in supraoptic and paraventricular nuclei for axonal transport to the posterior pituitary for storage and release. Vasopressin and oxytocin in other hypothalamic nuclei may be a part of this system of neurosecretion or may serve some other function.*

Neurosecretion of vasopressin and oxytocin is known from studies in animals to involve biosynthesis of hormone in the hypothalamus with transport by axons to the posterior pituitary for storage and release (*1*). Both hormones have been found in supraoptic and paraventricular nuclei of the hypothalamus in numerous animal species including humans (*2*). By means of a microdissection technique and specific radioimmunoassays both hormones were found recently in the rat in six hypothalamic areas in addition to supraoptic and paraventricular nuclei (*3*). In the study reported here I determined the concentrations of immunoreactive vasopressin and oxytocin in specific anatomical areas of human hypothalamus using microdissection and radioimmunoassay.

Human brain tissue was obtained from ten subjects who died suddenly while in apparent good health. The subjects included eight males and two females (ages 17 to 58 years, mean age 37 years), and the time interval from death to removal and freezing of hypothalamic tissue was 3 to 12 hours with a mean of 9 hours. The causes of death were acute coronary occlusion (three subjects), trauma (five subjects), stabbing (one subject), and gunshot (one subject). Hypothalamic tissue was removed and frozen in Dry Ice. Alternating 300-μm and 100-μm frozen sections were cut in the frontal plane in a cryostat at − 10°C. The 100-μm sections were stained and the hypothalamic nuclei were located according to Peele (*4*). Tissue samples were removed from adjacent 300-μm frozen sections with stainless steel cannulas, 500 μm in diameter, with the aid of a stereomicroscope (*5*). This diameter is well within the diameter of the hypothalamic nuclear areas. Tissue from each mircodissected area from each human brain was homogenized in 0.4 ml of 0.1*N* HCl, and the protein content was determined by the method of Lowry *et al.* (*6*). The amount of protein per sample was between 10 and 50 μg. The remainder of each tissue sample was diluted, neutralized with buffer, and assayed for vasopressin and oxytocin (*3*). The radioimmunoassay for each hormone was sensitive to 4 pg and not interfered with by 1000 pg of the other hormone. The interassay coefficient of variation of both radioimmunoassays was less than 10 percent. All samples were assayed in at least three serial dilutions to ensure immunologic identity with pure hormone.

Similar concentrations of immunoreactive vasopressin were found in supraoptic and paraventricular nuclei, with lesser concentrations in arcuate, dorsomedial, ventromedial, and posterior hypothalamic nuclei, median eminence,

Table 1. Hormone concentration (mean picograms per microgram of protein ± standard error of the mean) in human brain (*N* = number of subjects).

Brain area	*N*	Vasopressin	Oxytocin
Nucleus supraopticus	10	440.0 ± 156	28.0 ± 4.9
Nucleus paraventricularis	10	393.0 ± 158	52.0 ± 7.9
Nucleus arcuatus	10	17.0 ± 4.7	5.2 ± 3.0
Median eminence	10	247.0 ± 60	50.0 ± 13
Nucleus dorsomedialis	4	26.0 ± 15	7.6 ± 1.4
Nucleus ventromedialis	4	19.0 ± 13	4.3 ± 1.2
Nucleus hypothalamicus posterior	4	2.2 ± 1.0	0.13 ± 0.2
Mammillary body	4	3.4 ± 0.5	2.0 ± 0.5
Pituitary stalk	2	577.0 ± 66	86.0 ± 5.2
Nucleus preopticus lateralis	4	<1	<1
Nucleus preopticus medialis	4	<1	<1
Frontal cortex	4	<1	<1
Parietal cortex	4	<1	<1
Occipital cortex	4	<1	<1
Cerebellum	4	<1	<1
Brain stem	4	<1	<1

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