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Anatomical bases of binaural interaction in auditory brain-stem responses from guinea pig¹

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Summary There is a non-linear interaction of binaural stimulation on auditory brain-stem potentials in both human and animals. The interaction takes the form of the binaurally evoked ABR being of smaller amplitude than the sum of the monaurally evoked ABRs. In the guinea pig this interaction occurs at the time of components P4, N4 and P5. In order to investigate the generator sites of binaural interaction in the ABR, various lesions were made in the brain-stem auditory system in 29 guinea pigs. The effects of those lesions on binaural interaction were as follows: (1) unilateral lesion of lateral lemniscus or bilateral lesions of the inferior colliculi had no significant effect on binaural interaction; (2) transection of the lateral lemnisci bilaterally was associated with a loss of the component of binaural interaction associated in time with N4; (3) a lesion just lateral to the lateral superior olivary complex resulted in an attenuation of the component of binaural interaction associated in time with P4; (4) complete section of the decussating fibers of the trapezoid body or a complete unilateral lesion of the superior olivary complex led to a loss of all components of binaural interaction.

These results suggest that binaural interaction in the guinea pig ABR requires the integrity of several distinct portions of the brain-stem auditory pathway, i.e., both lateral lemnisci are required for the interaction occurring at the time of N4; the brain-stem just lateral to the lateral superior olive participates in the interaction at the time of P4. The trapezoid body and superior olivary nucleus are required for binaural interaction at P4, N4 and P5.

Key words: Binaural interaction; Auditory evoked potentials; Brain-stem; Guinea pig

The auditory brain-stem responses (ABRs) are well known as early auditory evoked responses occurring within 10 msec after sound stimulus and consist of 7 vertex positive peaks in human (Jewett and Williston 1971; Lev and Sohmer 1972). Jewett (1970) first described binaural interaction in the ABR by showing that the ABR evoked by binaural stimuli differed from the sum of the monaurally evoked responses. Binaural interaction occurs at the time of waves V and VI of the human ABR

and of P4, N4 and P5 of cat and guinea pig ABRs (Huang and Buchwald 1978; Dobie and Berlin 1979; Hosford et al. 1979; Ainslie and Boston 1980; Dobie and Norton 1980; Huang 1980; Levine 1981; Wada and Starr 1983a, b; Wrege and Starr 1983; Caird et al. 1985; Dobie and Wilson 1985). The effects of varying interaural time and intensity differences on the amplitude of such binaural interaction have been studied in both animals and humans (Dobie and Berlin 1979; Arslan et al. 1981; Wrege and Starr 1981; Rosenhamer and Holmkvist 1983; Sontheimer et al. 1985). Moreover, lesions of the brain-stem that affect the crossing fibers of the trapezoid body (Buchwald and Huang 1975; Fullerton and Hosford 1979; Gardi and Berlin 1981) result in the loss of binaural interaction. However, the detailed neural mechanisms underlying the generation of

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binaural interaction in the ABR are still uncertain. The aim of this study is to clarify the anatomical sites in the brain-stem contributing to binaural interaction in the ABR by employing systematic lesions of the brain-stem auditory pathway and defining their effects on the various components of binaural interaction.

Methods

Twenty-nine adult guinea pigs weighing between 0.6 and 1.1 kg were used for this study: 12 of them were subjected to midline section of the trapezoid body to varying completeness and 17 guinea pigs had lesions of either the superior olive, lateral lemniscus and inferior colliculus.

The animals were deeply anesthetized with sodium pentobarbital (40 mg/kg intraperitoneal injection). Following a tracheotomy a small screw was fixed at a point 3 cm posterior to the bregma to serve as the 'active' electrode. The 'reference' electrode was a needle placed in the posterior neck muscles. The animals were placed in a stereotaxic frame and their head held securely by a mouth clamp and follow ear bars. In 16 guinea pigs the clivus was exposed from the neck and carefully removed with a dental drill. The brain-stem was then easily visualized and the dura was incised. In 12 animals, 1 or 2 surgical sections of the trapezoid body were made near the midline of the brain-stem with a no. 11 scalpel blade without incurring vascular damage (Wada et al. 1988). In 4 guinea pigs a unilateral lesion was made at the superior olivary complex and/or its surrounding structures by inserting an electrode into the complex from ventral approach and passing cathodal current. For the other 13 guinea pigs, a dorsal approach, consisting of removal of the occipital bone and aspiration of the cerebellum, was used for gaining access to the superior olive, lateral lemniscus, or inferior colliculus. In 3 of these animals an electrode was placed in the superior olivary complex and/or its surrounding structure and a discrete electrolytic lesion made by passing cathodal current for varying times; in 8 animals the lateral lemniscus was sectioned with a blunt spatula just caudal to the inferior colliculus. In 2 animals the

inferior colliculi were lesioned bilaterally with electrolytic currents or with aspiration.

Pulses of 100 μ sec were used to produce 'click' stimuli at a rate of 25.6/sec and were presented monaurally or binaurally through earphones coupled to hollow ear bars. Brain potentials were amplified 100,000 times with a bandpass of 100–3000 Hz (-3 dB points, 6 dB/octave). The amplified signals were led to a computer and monitored on an oscilloscope. The evoked activity was sampled at a rate of 40 kHz (25 μ sec bin width) and 150 trials were averaged. Duplicate averages were done to insure replicability of the results. The analysis epoch of 12.8 msec (512 points) consisted of a 3.0 msec prestimulus period. The digitized data were stored on disk for subsequent analysis. Binaural interaction was assessed with a computer by subtracting the ABR evoked by binaural stimuli from the sum of the ABRs evoked by monaural stimuli and measuring the residua from peak-to-trough at the time of P4 and N4 to provide a definition of wave IV and from

TABLE I

Effect of surgical section of the trapezoid body on binaural interaction (BI). Guinea pigs GPN, GB and GPL were each subjected to 2 separate cuts. TB = trapezoid body. BI = binaural interaction; 100 = BI lost. BI amplitude was measured from peak (associated in time with P4) to the following trough (associated in time with N4).

Guinea pig	Cut	% of TB cut	% decrement in amplitude as a (f) of control BI
GPF	1	100	100
GPN	2	100	100
GPM	1	93	90
GI	1	92	98
GPI	1	91	84
GB	2	90	72
GB	1	86	62
GH	1	74	67
GPK	1	60	71
GPN	1	58	40
GL	1	56	68
GPH	1	48	62
GPL	2	48	56
GPG	1	38	51
GPL	1	8	5

baseline to peak for the separate components (see Fig. 1 and Table I).

ABRs were recorded prior to and after making a lesion. The extent of binaural interaction could then be compared between the control period and after the lesion. Following the lesion, recordings were continued for 4–16 h. Rectal temperature

was monitored and maintained at 30–38°C by means of a circulating water pad.

At the end of the experiments the animals were perfused through the heart with normal saline followed by 10% buffered formalin. The entire brain was removed, the brain-stem portion blocked and stored in 10% buffered formalin for 1 week prior to processing. Serial transverse 60 μm frozen sections were made with cresyl violet and examined for evidence of lesion site or the extent of section of the fibers in the trapezoid body.

Results

(1) Normal ABR and the binaural interaction in guinea pig

Auditory brain-stem responses in guinea pig consist of up to 5 positive and 4 negative peaks in the first 10 msec after stimulus onset (Wada and Starr 1983a). Each component is designated by their polarity at the vertex (P for positivity and N for negativity) and their approximate latency in msec. In a previous paper (Wada and Starr 1983c), we suggested the following approximate locations of the generator sites: components P1 and N1 from the ipsilateral VIIIth nerve, P2 and N2 from the ipsilateral cochlear nucleus, P3 from the superior olive contralateral to stimulated ear, N3 from the lateral lemniscus contralateral to stimulated ear, P4 from both sides of the brain-stem just lateral to the superior olivary complex and N4 from both lateral lemnisci. Fig. 1 shows ABRs evoked by stimulation of the right ear, the left ear and both ears (solid line in the third tracing). The algebraic sum of the ABRs evoked by the 2 monaural stimuli is included in the third trace as a dotted line. The bottom trace reflects binaural interaction as the sum of ABRs evoked by monaural stimuli minus the ABR evoked by binaural stimulation ($R + L - \text{binaural}$). Binaural interaction represents a non-linear processing of binaurally evoked ABRs when compared to the sum of the ABRs evoked by separate monaural stimulation. In the guinea pigs binaural interaction takes the form of a lowered amplitude of the binaurally evoked ABR compared to the sum of the separately evoked monaural ABRs. The amplitude

Fig. 1. ABRs in the normal guinea pig to right ear (R), left ear (L), and to binaural stimulation (solid line, third trace). The algebraic sum of the ABRs to monaural stimulation ($R + L$) is the dotted line in the third trace. The bottom trace is binaural interaction representing the sum of the ABRs to monaural stimulation minus the ABR to binaural stimulation (binaural interaction). A cross-section of the brain-stem is above. LSO, lateral superior olive; MSO, medial superior olive; DCN, dorsal cochlear nucleus; VCN, ventral cochlear nucleus.

Fig. 2. The effects of complete transection of the trapezoid body on the ABR. In this and all subsequent figures, the ABR recorded after the lesion is plotted with the dark lines that also are occasionally dotted. To monaural stimulation components P3 and N3 are lost, P4 is preserved but shortened in latency. Binaural interaction is lost following the section. The darkened area represents the site of the lesion.

disparity occurs in the time domain of components P4, N4 and P5 and amounts to up to a 60% reduction in the amplitude of these components (Fig. 1).

(2) Brain-stem lesions and binaural interaction

(A) *Surgical section of the trapezoid body.* Following the complete section of the trapezoid body (Fig. 2, in this and all subsequent figures the ABRs recorded after the lesions are indicated by thick darker tracings that also appear as a dotted line in some portions of the tracing), components P3 and N3 to monaural stimulations were lost, N4 was reduced in amplitude, and P4 was of the same

amplitude but of shorter latency. To binaural stimulation component P4 increased in amplitude by 50–60%. In this example, with complete section of the trapezoid body, binaural interaction is lost at the time of P4 and N4. Table I compares the percentage of decussating fibers sectioned in the trapezoid body and the percentage decrement of binaural interaction in 12 guinea pigs (15 cuts). The relationship is linear with the reduction of binaural interaction being almost proportional to the volume of the decussating fibers sectioned in the trapezoid body ($r = 0.87$, $r^2 = 0.76$, $P < 0.001$).

(B) *Lesions of the superior olivary complex.* In 2 guinea pigs, an extensive lesion was made in the superior olivary complex with an effect on binau-

Fig. 3. The effects of a lesion of the superior olivary complex on ABRs. Binaural interaction is lost following the lesion. Components P3, N3 and N4 are attenuated to contralateral monaural stimulation (L) and only N4 is attenuated to ipsilateral stimulation (R).

Fig. 4. The effects of a unilateral transection of the left lateral lemniscus just caudal to the inferior colliculus. Binaural interaction was not affected by the lesion whereas N3 was attenuated to contralateral monaural input (R).

ral interaction similar to that seen with complete trapezoid body section through with differing effects on monaural stimulation. The example shown in Fig. 3 shows that the lesion destroyed the entire medial superior olivary nucleus and the medial part of the lateral superior olivary nucleus without damaging other auditory structures such as the trapezoid body or the dorsal and intermediate acoustic striae. To monaural stimulation there was an attenuation of components P3 and N3 to stimulation of the ear contralateral to the lesion (L) and a moderate attenuation of N4 to both right and left stimulation. To binaural stimulation there was a decrease of component P3 by 39%, N3 by 38%, and N4 by 40%, while component P4 increased in amplitude by 70%. Binaural interaction was absent after the lesion.

In 2 other animals an electrolytic lesion of the superior olivary complex also involved a small part of the decussating fibers in the trapezoid body, and in these animals binaural interaction was also completely abolished.

(C) *Unilateral lesion of the lateral lemniscus.* A unilateral lesion of the lateral lemniscus was made in 8 guinea pigs; 2 by electrolysis and 6 by surgical section. All instances with unilateral lateral lemniscus lesion showed similar results and an example is given in Fig. 4. There was a significant reduction of N3 only to stimulation of the ear contralateral to the lesion and an attenuation of N3 of the same magnitude to binaural stimulation. Binaural interaction was not significantly affected following the lesion.

(D) *Bilateral lesions of the lateral lemniscus.* Two animals with unilateral lateral lemniscus sec-

Fig. 5. The effects of bilateral transection of the lateral lemnisci on binaural interaction. N3 was lost to monaural inputs. Binaural interaction at the time of component P4 remained while interaction at the time of N4 was lost.

tion were subjected to sectioning of the other lateral lemniscus within 1 h following the first section. The histological examination indicated that both lateral lemnisci were completely transected just caudal to the inferior colliculi. Following the lesions, the ABR showed an attenuation of component N3 to both ipsi- and contralateral monaural stimulation as well as to binaural stimulation. Component P4 showed no significant change to both monaural and binaural stimulation. Component N4 decreased in amplitude by 50% to contralateral (left-sided) stimulation and was not changed to both ipsilateral monaural right and to binaural stimulation. Binaural interaction

Fig. 6. The effects of a unilateral lesion of the lateral portion of the pons adjacent to the superior olive on binaural interaction. P4 was delayed to ipsilateral input (R). Binaural interaction at the time of component P4 was attenuated with only a small reduction of interaction associated in time with N4.

Binaural Interaction

Fig. 7. A summary of the effects of various lesions of the brain-stem on binaural interaction.

was unchanged at the time of P4 but was lost at the time of N4 (Fig. 5).

(E) *Lesions adjacent to the lateral aspect of the superior olivary nucleus.* In 3 guinea pigs the lesion was dorsolateral to the superior olivary nucleus impinging on the lateral aspect of the lateral superior olivary nucleus, the dorsal and intermediate acoustic striae, as well as those fibers of the ventral acoustic striae entering the ipsilateral superior olivary complex. The ABR to monaural stimulation of the ear ipsilateral to the lesion (R) showed a decrease in the amplitude and a delay in latency of components P4 and N4. Component N3 increased in amplitude without a latency shift. Component P4 to binaural stimulation increased in amplitude and was slightly delayed in latency along with N4. The component of binaural interaction associated in time with P4 was reduced by 60% with a smaller reduction of

the component of the binaural interaction associated in time with N4 (18%) (Fig. 6).

(F) *Lesions of the inferior colliculus.* In 2 guinea pigs, the inferior colliculus was completely destroyed either by aspiration or by electrolysis. There were no changes in the ABR to monaural or binaural stimulation and no effect on binaural interaction.

Fig. 7 summarizes the effects that these various lesions of the brain-stem auditory pathway had on binaural interaction components of the ABR: (1) Inferior collicular lesions or unilateral lesions of the lateral lemniscus were without effect. (2) Bilateral lateral lemniscal lesions were associated with the loss of only the component of binaural interaction associated in time with N4. (3) Section of all of the decussating fibers in the trapezoid body was accompanied by a loss of all binaural interaction. (4) A unilateral complete lesion of the superior olivary complex was associated with a similar complete loss of the binaural interaction. (5) A lesion just lateral to the superior olivary complex was associated with an attenuation of the component of binaural interaction associated in time with P4 and a smaller attenuation of N4.

Discussion

The results of this paper demonstrate that lesions of the brain-stem portions of the auditory pathway alter binaural interaction components of the ABR in selective ways. Complete destruction of the trapezoid body or the medial superior olivary complex abolishes binaural interaction. This finding is in agreement with many previous studies demonstrating the necessity of the crossing fibers of the trapezoid body and the superior olivary complex for binaural interaction in the ABR (Buchwald and Huang 1975; Fullerton and Hosford 1979; Gardi and Berlin 1981). Our results further establish the role of particular auditory brain-stem structures of the various components comprising binaural interaction. Bilateral lesions of the lateral lemniscus abolished that portion of binaural interaction coincident in time with the N4 component, while unilateral lemniscal lesions were without effect. Lesions just adjacent to the

lateral portions of the lateral superior olivary nucleus and the middle acoustic striae principally diminished binaural interaction occurring at the time of component P4. Thus, distinct portions of the brain-stem auditory pathway are essential for the occurrence of particular portions of binaural interaction in the ABR.

Binaural interaction of the ABR has been defined as those potentials remaining after summing the ABRs evoked by monaural stimulation and subtracting from this sum the ABR evoked by binaural stimulation (Dobie and Berlin 1979). This method is based on one used by Rosenzweig and Amon (1955) more than 30 years earlier for analyzing binaural processing by the brain. Wernick and Starr (1968) used this method with direct brain-stem recordings from cats to parcel out the binaural interaction component accompanying stimuli that evoked the percept of 'binaural beats.' The criticism that the residua from this simple algebraic procedure do not reflect binaural processes but are due to acoustic crossover (Ainslie and Boston 1980) has not been substantiated (Levine 1981; Dobie and Wilson 1985; Özdamar et al. 1986). Binaural interaction of the ABR as defined by this algebraic method is an acceptable method for quantifying the extent to which binaural processes are reflected in evoked potentials.

The potentials remaining after these algebraic procedures must reflect inhibitory and excitatory events specific to binaural stimulation. At the time of P4 and N4 binaural interaction in the ABR represents a diminution of activity to binaural versus the sum of monaural stimulation. There is no evidence in the binaurally evoked ABR of an enhancement of activity above that to be expected by summing the potentials evoked from monaural stimulation.

Binaural neural processes involved in integrating the inputs from two ears have been well studied. The accessory or medial nucleus of the superior olivary complex is the first nucleus in the classical ascending auditory pathway that received bilateral auditory input. There are at least 2 kinds of binaural neurons in the superior olivary nucleus, i.e., one group excited by inputs from both ears (excitatory-excitatory = EE) and another group excited by input from one ear and inhibited by

input from the other ear (excitatory-inhibitory = EI). Both types of units are present in the superior olivary complex (Galambos et al. 1959; Caird and Klinke 1983; Moushegian et al. 1985). Furthermore, Irving and Harrison (1967) reported that the EI cells are chiefly in the lateral superior olivary nucleus and that EE cells are chiefly in the medial superior olivary nucleus. The medial superior olive cells are sensitive to interaural time while the lateral superior olive cells are sensitive to both interaural time differences and interaural intensity differences (Caird and Klinke 1983). Thus, there are cells in the superior olivary complex that are differentially sensitive to binaural inputs leading to either enhanced (EE cells) or diminished (EI) outputs relative to monaural stimulation. Binaural interaction in the ABR at the time of both P4 and N4 represents a diminution of activity to binaural stimulation relative to the sum of monaural stimulation, a function best described by activity of binaural units of the EI type. Since there is no amplitude increment of the ABR to binaural stimulation relative to the sum of the monaural inputs, the participation of EE cells activity in accounting for binaural interaction of the ABR is not in evidence.

The relationship between the location of the generator sites for the components of the monaurally evoked ABR components and the location of the generators for binaural interaction is complex. In the guinea pig components P3 and N3 are lost following a midline lesion of the trapezoid body or the medial superior olive contralateral to the stimulated ear, whereas only N3 is lost following a unilateral lesion of the lateral lemniscus also contralateral to the stimulated ear. Both of these findings suggest that the P3-N3 components, or wave III, are generated in the brain-stem contralateral to the ear being stimulated with the trapezoid fibers providing the inputs to the region of the medial superior olive, where P3 is generated, and to the region of the lateral lemniscus, where N3 is generated. Lesions of the trapezoid body and superior olivary complex do not affect the amplitude of P4 to monaural stimulation though its latency is shortened whereas N4 is only slightly attenuated. These data suggest that both P4 and N4 are generated at site(s) distinct from

both the superior olivary complex and trapezoid body. Other experiments indicate that for P4 the generator sites are bilateral, involving lateral structures in the brain-stem adjacent to the lateral superior olive for P4 and slightly more rostral, in the region of the lateral lemnisci, for N4 (Wada and Starr 1983c).

Binaural interaction at the time of component P4 and N4 is abolished by a complete lesion of one of the superior olivary complexes indicating the essential role of these structures for binaural processes but not their identification as the generator sites for binaural interaction components. We suggest that the binaural processes, reflected in the ABR, require the crossing fiber input of the trapezoid body to the superior olivary complex but that the sites of generation of binaural interaction components at the time of P4 and N4 are rostral to the superior olivary complex. The location of the generator portions along the superior olivary complex output pathways must be in at least 2 distinct areas: a unilateral lesion just adjacent to the lateral superior olive affects principally the P4 component of binaural interaction whereas lesions of the lateral lemnisci affect principally the N4 component of binaural interaction. Thus, the components P4 and N4 to binaural stimulation must include the output activities of binaural cells of the superior olivary complex as well as cells that are also only monaurally driven.

In the guinea pig the contribution of binaurally sensitive cells to the ABR is considerable since binaural interaction accounts for approximately a 50% difference in the amplitudes of P4 and N4 expected from the sum of monaural stimulation. The site of binaural processes in the auditory pathway is in the superior olivary complex, with its output fibers traversing dorsal and lateral in the brain-stem. Thus, a unilateral lesion just adjacent to the lateral superior olive impinges on this output pathway and affects both the ipsilateral monaural and binaural ABRs at the time of P4 and N4. The output systems of the superior olivary complex must then diverge with the portion of the pathway related to component N4 traveling bilaterally in the lateral lemniscus where bilateral lesions affect binaural interaction of this component (N4) but not of P4. The location of the

portion of the pathways, accounting for binaural interaction of P4, is not known since we did not observe a complete loss of binaural interaction at the time of P4 with any of the lesions of this study. However, we would expect that bilateral lesions of the brain-stem just lateral to the superior olivary complex would result in the complete loss of binaural interaction at the time of P4.

These experiments suggest the importance of fiber pathways for the generation of components of both the monaural and binaural portions of the ABR. The results cannot distinguish whether the fiber pathways are the actual generators for these components or whether they merely provide input to other structures that are responsible for the appearance of these components in the far-field.

In humans, binaural interaction in the ABR consists of an initial component associated with the IV-V complex and a second component associated with the wave VI (Dobie and Norton 1980; Levine 1981; Wrege and Starr 1981). The relative proportion of binaural interaction found in the ABR in humans is approximately one-half of that defined for cat and guinea pig. We are not aware of studies examining binaural interaction in the ABR and the site of brain-stem lesions in humans. This is most likely due to difficulties in detecting binaural interaction components in humans due both to their relatively small contribution to the ABR (25%) and to the 10-fold reduction in amplitude of the ABR in humans relative to animals, such as the cat 0.5 μ V in humans, 5 μ V in cats. If the technical problems compromising the detection of binaural interaction of the ABR in human could be overcome, this method might lead to precise definition of focal brain-stem lesions to complement current imaging abilities.

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