

Neuronal activity in the human lateral temporal lobe

III. Activity changes during music

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Summary. During open brain surgery under local anesthesia for the treatment of medically intractable temporal lobe epilepsy we have recorded neuronal activity from the lateral temporal lobe with microelectrodes while the patients listened to short pieces of music. Three groups of music were tested: A) Simple familiar or unknown classical tunes at a simple rhythm and harmony, played on piano; B) Orchestrated folk music; C) Drumming without a tune. All types of music lead to changes of neuronal discharge rate. Musical pieces of type A produced a decrease in 48% of the recordings, an increase in about 17% and had no effect in 30%. A similar distribution of effects was found during type B-music (48%, 22%, 30%, respectively). During type C, only 26% showed a decrease and 74% an increase. When music was turned off, usually the reverse change from that caused by music was seen. In addition to changes of discharge rate, a slight entrainment of activity by single, regularly appearing notes (rhythm) was seen in some neurons. A few neurons showed a change of activity related to musical phrases (activation towards the end of a 4-bar 4/4 phrase). In contrast to the effects of verbal stimuli and overt speech, the effects of music on discharge rates did not show obvious topographical differences between superior, middle and inferior temporal gyrus. They also were bilateral with no significant right-left differences.

Key words: Neuronal activity – Temporal lobe – Music – Humans

Introduction

Lesions of either temporal lobe may seriously incapacitate musical abilities such as singing or playing

in tune, recognizing tunes or keeping the rhythm. Such disturbances are variable, however, and have been more often described after right than left temporal lobe lesions, but the localization of musical abilities is still a matter of dispute (see Clynes 1982; Critchley 1977; Kleist 1934; Luria 1966). This indicates, that it is certainly not as strictly lateralized as language and that the laterality may vary between individuals (cf. Bever and Chiarello 1974). It is also not clear which part of the temporal lobe is, in fact, indispensable for musicality. After unilateral removal of one anterior and middle temporal lobe on either side, including the temporo-basal cortex for surgical treatment of epilepsy, no serious disturbances of musical capacities have so far been reported. On the other hand, there are some observations that the right hemisphere maybe essential for singing (Gordon and Bogen 1974) and the left hemisphere for perception of rhythm (Peretz 1983; Berthold 1983). Temporal lobe seizures of the psychomotor type may be elicited in some rare cases by listening to music, particularly by pieces with a strong emotional effect (musicogenic epilepsy) (Critchley 1937; Merlis 1974; own observations). On the other hand, auditory stimuli may suppress the development of a seizure (Jung 1939, 1954).

In order to see what is going on in the temporal lobe while listening to music we played short pieces of music at the end of the microelectrode recordings from the lateral temporal cortex during epilepsy operations, and recorded the activity of single or groups of units before, during and after these pieces. The majority of units showed clear changes of mean discharge rates during music which varied to some extent with the type of music. In some units we found, in addition, a slight entrainment of single unit activity by the rhythm, or changes related to musical phrases. In contrast to the responses to language or to the patients own voice

Fig. 1. The tune “Ah, dirai-je vous, Mama” arranged by W.A. Mozart for the piano, and the first variation (KV 265). The roman numbers indicate the musical phrases, the arabic numbers the 4/4-bars (the piece is written with 2/4-bars)

(see Creutzfeldt et al. 1989a, b), the neuronal responses did not show obvious differences in the different locations of the temporal lobe, nor did they show clear lateral differences.

Methods

Of the 34 patients in which we did microelectrode recordings during various auditory, language and visual tasks, we recorded single unit activity in 15 patients while playing short pieces of tape recorded music to them. As a rule, this part of the investigation was done at the end of all testing including stimulation mapping. Patients were awake and were told that they will now hear a few short pieces of music. Before the operation they were informed about this part of the testing, but the musical pieces were not played to them before the operation. They had given their informed consent also to this short part of the investigation.

Single or multiunit activity was recorded during open temporal lobe surgery under local anesthesia for the treatment of medically intractable epilepsy as described in the preceding reports (Creutzfeldt et al. 1989a; Ojemann et al. 1988). In short, lacquer insulated tungsten microelectrodes were introduced between 1–4 mm into the cortex usually near a sulcus through a hole in a pressure foot. In some patients the activity from two electrodes were recorded simultaneously, in which cases the tips of the electrodes were 2–4 mm above each other. In some patients, two recording sites in different gyri were tested. The microelectrode activity was tape recorded at a speed of 15 inches/s, together with the audio-signal from the music and the ECoG from several epicortical electrodes, including one situated directly over the microelectrode in the pressure foot. Data analysis was done off-line and films were taken of all recordings at 2.5 cm/s or 5.0 cm/s.

Single unit activity during music was recorded from 13 sites in the right hemisphere (8 from the middle, 4 from the superior temporal gyrus) and from 5 sites in the left, speech

dominant hemisphere (4 from the middle and 2 from the superior temporal gyrus). Recordings were all placed lateral to the somato-sensory region (see Fig. 1 of the first report). Unit discharges were counted at different trigger levels, so that from each recording two and sometimes three activity counts were available.

We had chosen musical pieces of different character, each 30–40 s long. After the tape recorder was switched on, 20–30 s passed as a control period until the music began. We thus avoided that handling and switching on the tape recorder coincided with the beginning of the music and always had a quiet period of 20–30 s before and after each piece. The music pieces were of three kinds:

A) Simple and clearly structured tunes at a quiet rhythm and played on a piano. The pieces chosen were: 1) W.A. Mozart: The childrens song “Ah, dirai-je vous, mama”, often including the beginning of the first variation (KV 265) (see Fig. 1). The tune was familiar to most patients from the childrens song “Twinkle, twinkle, little star”. 2) R. Schumann: “Nachtlied” from *Nachtstücke*, op. 23. 3) B. Galuppi: Beginning of the first movement (Andante) of *Sonata No 5 C-major*.

B) Liveley, orchestrated rhythmical music, in which a tune was clearly recognized. Here we choose well known American folk music: 1) Oh Susannah and 2) Old Folks, both arranged for orchestra by Foster, tune 1 in a rhythmical Hill-billy, and tune 2 in a soft sentimental manner.

C) Modern rock music. Here we chose, on advice of Steve Ojemann, the theme of the TV-series “Miami vice”. This is a drum piece without a tune, but with strong uniform rhythm, reinforced with synthesized sustained tones towards the end.

Results

Effects of music on discharge rate

The most prominent effects of music on single unit activities in the right and left lateral temporal lobes

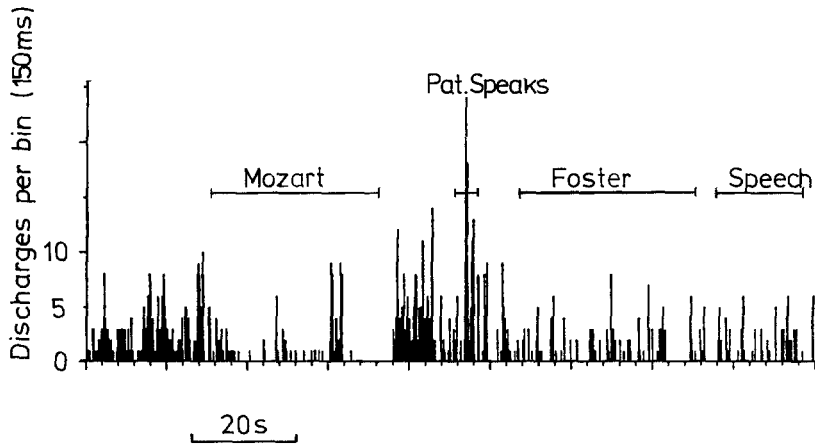


Fig. 2. Decrease of discharge rate of a group of units recorded in the right inferior temporal gyrus during music (Pat. 8529). Note, that the depression of discharge rate is stronger during the Mozart-tune than during the Foster-arrangement. The activity is slightly increased when the patient speaks, but not affected by speaking to the patient. In addition to the discharge suppression, this unit activity is also slightly entrained by the musical rhythm (cf. Fig. 5)

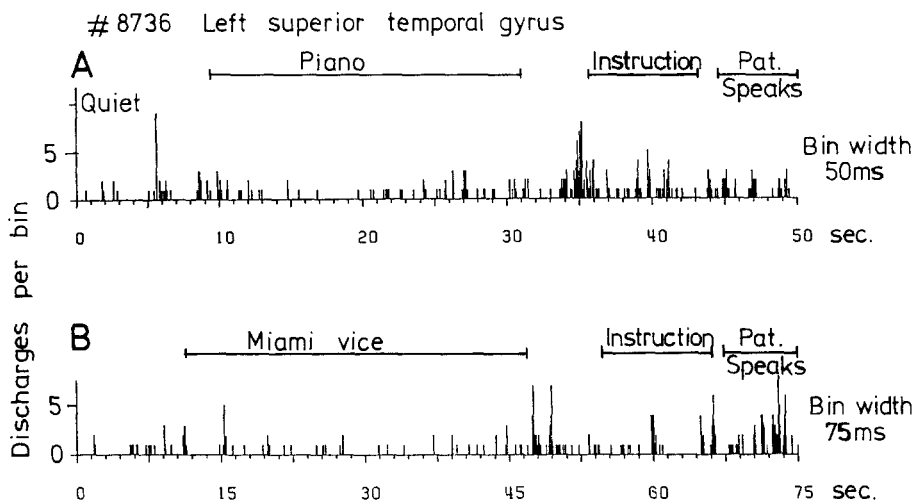


Fig. 3A, B. Decrease of discharge rate of a single unit in the left superior temporal gyrus during music (Pat. 8736). The activity is, in the average, only slightly suppressed during the piano piece (Galuppi) and the drumming (Miami Vice), but shows a strong off-discharge. This unit was activated in a specific manner when speaking to the patient and even more when he spoke himself

were changes of discharge rate. We have observed this in nearly 80% of our recordings and did not see, in this respect, any significant differences between the two sides. The degree of change could vary, however, and both increases and decreases could be observed. Furthermore, the different types of musical pieces from our repertoire could have different effects.

A typical example is shown in Fig. 2. In this male patient we recorded multiunit activity from the right inferior temporal gyrus. The spontaneous activity was almost completely suppressed during the Mozart tune, but less during the Foster-piece. Listening to speech did not alter the spontaneous discharge rate significantly, but when the patient spoke himself an additional activation peak could be observed (see also Fig. 9 in Creutzfeldt et al. 1989b). As will be shown later, the units recorded at this site were not simply silenced by the music but were also slightly entrained by the rhythm.

The example of Fig. 3 is from the left superior temporal gyrus. Here, the depression during the

musical pieces is only slight, but is followed by a strong off-activation after the end. During speech addressed to the patient and when he spoke himself, the unit was activated, and these activations were specifically related to phonetic speech elements as well as to word length, as documented in the preceding papers (see Fig. 6 in Creutzfeldt et al. 1989a, Fig. 5 in Creutzfeldt et al. 1989b).

The changes of activity induced by music could be quite abrupt with latencies below one sec, but could also develop gradually during the musical pieces. Moderate crescendo's and decrescendo's during a piece did not strongly affect the discharge rate, but a very strong increase of volume could additionally increase or decrease it.

Suppression of discharge rate was found most frequently and strongest during group A of our repertoire, i.e. during the simple classical piano pieces. Next came the American folk-songs (Group B), while the modern rock induced increase more often than decrease. This is shown in the summary diagram of Fig. 4. Note, that the total number of

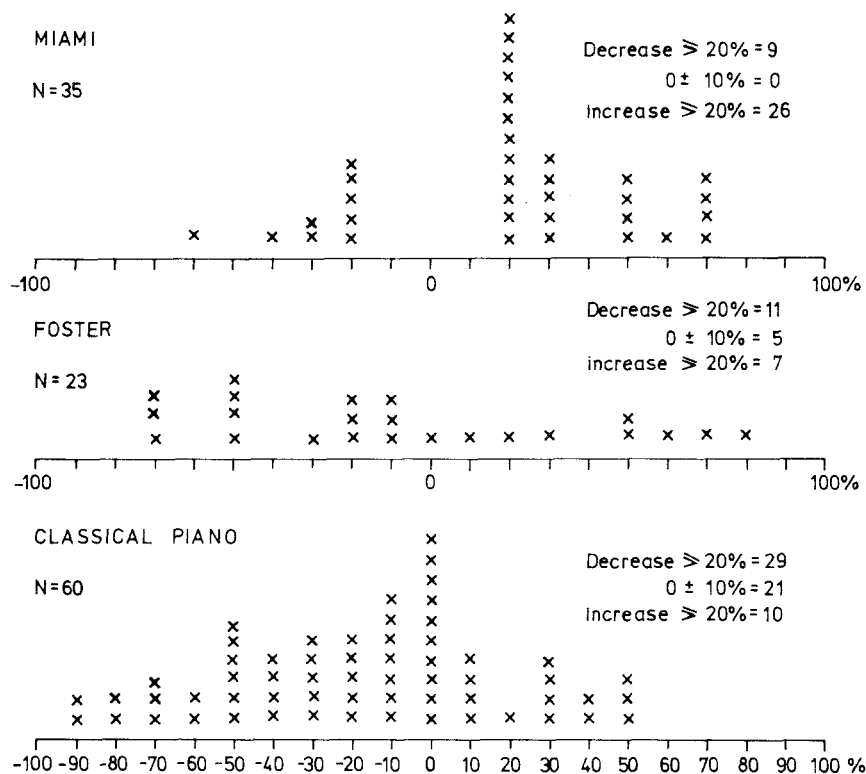


Fig. 4. Effect of the different types of music on mean discharge rates of neuronal activities in the right and left temporal lobe. Each cross represents the count from one activity. At each recording site several musical pieces were tested, some recordings were done with two microelectrodes and recordings from one electrode were split into single unit and multiple unit activity if possible. Abscissa: Decrease (–) and increase (+) of discharge rate from the last period 15 s before to the first period 15 s during music in per cent (see text). Number of recordings with increased, decreased or unaffected discharge rates are shown at the right insets

measurements ($N=118$) is much higher than the number of patients ($N=15$) and recording sites ($N=17$). This is not only because several classical and other pieces were played at one recording site, but also because discharge counts were done for different spike populations in multiunit recordings, and double microelectrode recordings were available in several patients. Because of the large absolute differences of discharge rates between single and multiunit activity we normalized the data for this diagram and calculated the percentage change of discharge rates between the activities during 15 s immediately preceding and during the first 15 s of the music. Percentages were always calculated relative to the higher activity which was taken as 100%. Thus, if the activity was higher during rest before the music, that was taken as 100%, but if the activity was highest during music, the latter was taken as 100%. In Fig. 4 the per cent differences discharge rates just before and during the first 15 s of music are plotted. It is obvious that the slow and simple classical piano tunes induced the strongest and most frequent suppression (in 48% of the recordings against 17% activation), and the modern rock resulted more frequently in discharge increase (74% increase against 26% decrease). The orchestrated folkmusic had a similar effect as the classical tunes, in the average (48% suppression, 22% activation).

Table 1.

N	Type of music	Relative discharge rates	
		during: before	after: during Music
59	Easy classical piano	0.6 ± 0.49 S.D.	1.65 ± 0.93 S.D.
20	Folkmusic arranged for orchestra	0.6 ± 1.7 S.D.	1.47 ± 1.68 S.D.
23	Restless drum pieces	1.69 ± 1.7 S.D.	0.59 ± 34 S.D.

Although somewhat different in the individual recordings, the change of activity from music to rest following the music were, for the whole population, mirror symmetrical to the changes from rest to music. This is shown in Table 1, where the relative discharge rates during music are compared to the resting time preceding and following the musical piece.

In all recordings in which music was tested, various speech tests preceded the music. In most cases, not the same neurons stayed throughout both tests, but the recording sites were not altered. Out of 6 recordings from the *superior temporal gyrus* the classical and/or folk music predominant-

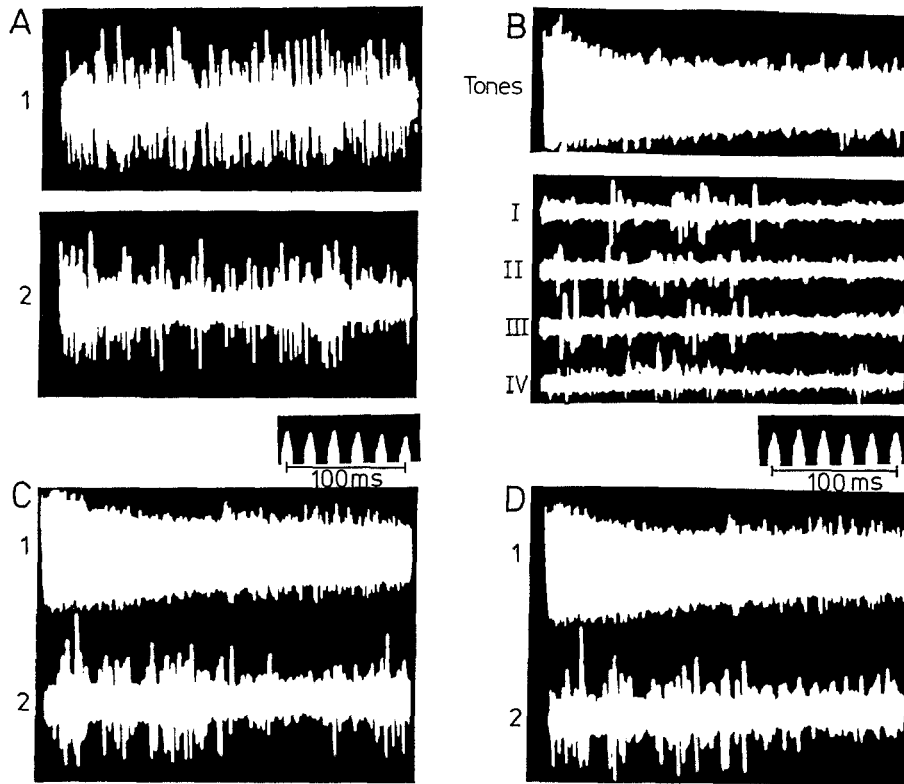


Fig. 5 A–D. Entrainment of activity by a regular rhythm (Patient 8529, right inferior temporal gyrus) (Mozart-tune). A 64 superimposed, internally triggered oscilloscope sweeps each 300 ms long. A 1 During spontaneous activity. A 2 During music. B Oscilloscope sweeps triggered by the quarter notes (see audiogram on top). I, II, III, IV: Superimposed microelectrode recordings of 15–16 notes during phrase I–IV of the tune as indicated in Fig. 1. C Sweeps triggered by quarter notes, all 62 notes superimposed. D Same as in C, but without punctuated 1/8 notes and trills in bar 4, 8, 12 and 16 of Fig. 1

ly suppressed the spontaneous discharge rate in 5 recordings (3 right, 2 left), but did not have any visible effect in one recording (right hemisphere). In all these cases, speech had altered the unit activity in a specific manner as described in the preceding reports (Creutzfeldt et al. 1989a, b). Of the 16 recordings from the *middle and inferior temporal gyrus*, discharge rates were affected by music in 11 recordings. In 7 of these responsive recordings, speech had not affected the discharge rates and in 2 further cases, speech had the reverse effect as compared to music. Thus, only in three cases, the effects of music and speech were in the same direction.

Neuronal activity changes related to musical rhythm and phrases

In some unit recordings not only the discharge rates changed during presentation of music but neuronal activity could also become entrained by the rhythm of the music. Such entrainment was, however, only mild if it could be recognized at all, and was never tightly correlated to single rhythmical elements of a musical piece.

In Fig. 5 we show a recording from the right middle temporal gyrus during the Mozart tune (same recording as Fig. 2). The activity was clearly reduced during the music. This is documented in

Fig. 5A, in which 64 internally triggered oscilloscope sweeps each lasting 300 ms had been superimposed during silent rest before the music (A1) and during the music (A2). It can be seen that there were less discharges during music than preceding music (cf. Fig. 2). In fact, the discharge rate during music dropped to 25% of the premusic activity. In Fig. 5B, the sweeps were triggered by the single notes, which can be recognized in the audiogram in B 1. In B 2, 3, 4 and 5 the activity during 16 consecutive sweeps was superimposed. Each 16 tone block corresponds to a 4-bar phrase of the tune as indicated by the roman numbers (see Fig. 1). The discharge probability was elevated between 20 and 160 ms after the beginning of each tone, and no discharges appeared during the later part of the tone interval. In C, all 64 notes of the tune (four 4-bar segments) were superimposed and here again, the high discharge probability during the first 160 ms after the beginning of each tone can be recognized. During the last 150 ms of the sweeps a few discharges are seen. These disappeared when the last notes of each phrase with the trills and ritardando (see Fig. 1) were left out (D). It should be noted, that the activation did not appear after each note and that the superimposed records represent only an increased discharge probability at the times indicated. On the other hand, increased discharge probabilities were

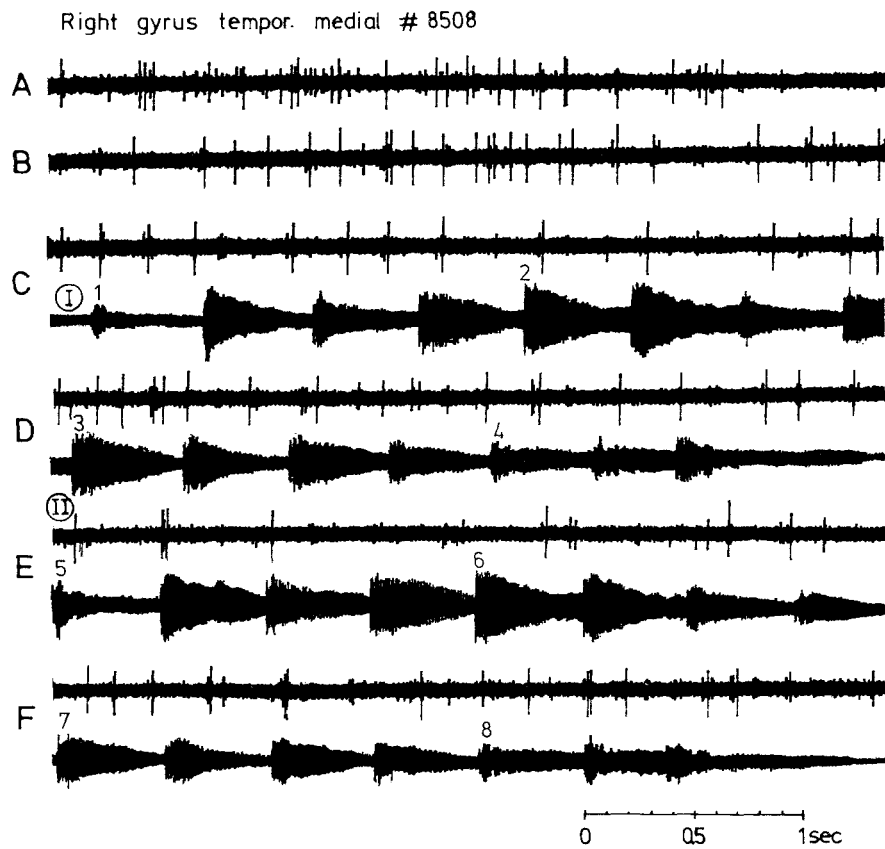


Fig. 6A–F. Unit activity recorded in the right middle temporal gyrus during rest (**A, B**) and during the first two segments of the Mozart tune (**C–F**) (Pat. 8508). Continuous recordings except for a small cut between **C, D** and **E, F**, respectively. The roman and arabic numbers refer to the phrases and bars as indicated in Fig. 1. A single unit with a large action potential and several units can be distinguished

not related to notes of certain pitch. Thus, our results do not give an indication for pitch dependent activations in the lateral temporal lobe. This is consistent with the analysis of speech responses, where we also did not find activations specifically related to certain vowel formants (Creutzfeldt et al. 1989a).

Another example is shown in Figs. 6 and 7 from a recording in the right middle temporal gyrus of another patient during the Mozart tune. In the original recording (Fig. 6), one large single and some small units could be distinguished. The resting discharge rate of the units (Fig. 6A, B) dropped during the first bars of the music (C, D). Only the first two parts of the tune are shown (compare roman numerals with those in Fig. 1). When counting the discharge rates of the large and the small action potentials over the whole resting and the music period, one sees that both were suppressed by about 50% during the music (Fig. 7A). When counting the discharges at different 100 ms-intervals during each tone interval (450–500 ms, quarter notes), the averaged discharge probability of the large unit was 0.78 per note during the first 200 ms following each interval, in contrast to only 0.42 during the last 300 ms (Fig. 7B, upper, continuous curve). The separate plots for the successive 4-bar

segments of the tune at the lower part of Fig. 7B show entrainment of variable strength only during phrases I–IV (the original tune), but not during V and VI, the first variation with 1/16-notes (see Fig. 1). Also in this unit, the variation of discharge entrainment during tone intervals was not related to pitch. The small unit was not significantly affected by single tones (broken line in Fig. 7B).

As seen in Fig. 1, the Mozart tune consists of 4 phrases or segments, each of them four bars 4/4 long (or, in this notation 8 bars with 2/4 notes). The last note in the last bar of each phrase is a half note and is preceded by a prolonged 1/8 with a trill followed by a 1/16 which has the effect of a ritardando and thus accentuates the end of the phrase. Some units were specifically activated during this terminating figure of each phrase. Such an effect is suggested already by the recording of Fig. 5C, but this activation could also be interpreted as a tone related activation during the trill. A more clearly end-of-phrase related activation is shown in Fig. 8. This is from a unit recorded in the right middle temporal gyrus. The discharge rate of this unit was low during the first 3 s, but increased during the last 3 s of each phrase. In Fig. 8B the mean discharge rates during one second-intervals are summed up for all 4 phrases (continu-

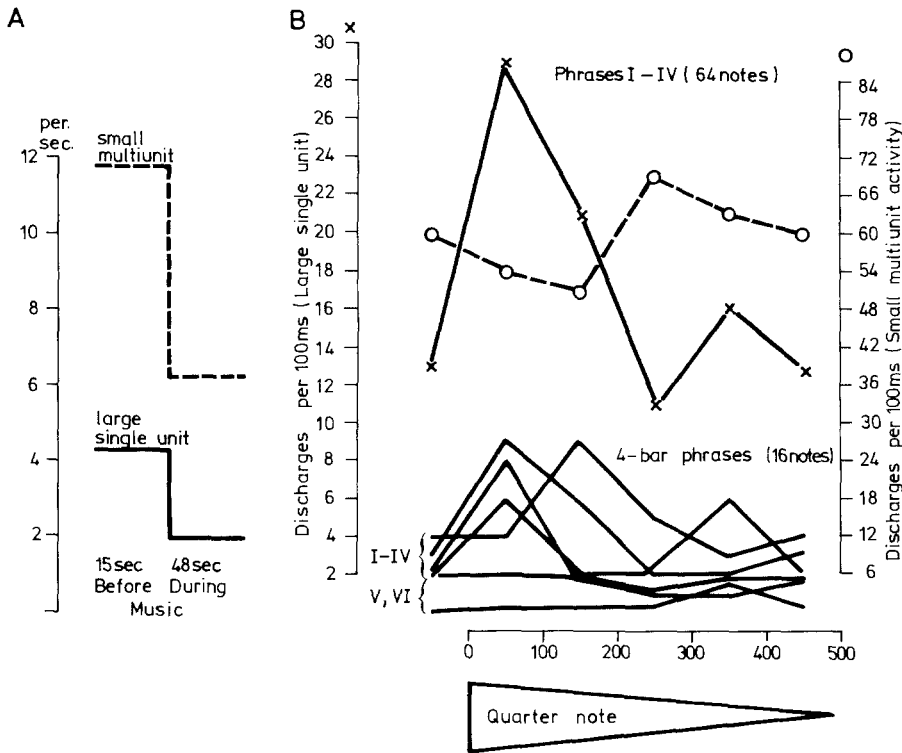


Fig. 7 A, B. Mean discharge rates **A** and entrainment of activity by single tones **B**. From same record as Fig. 6, but counted over the whole Mozart tune. **A** Discharge rates of the large single unit (continuous line) and the small multiunit activity (broken line). **B** Lower curves: I-IV: Counts of discharges during 100 ms intervals between the sixteen notes of the respective 4-bar phrases (15-16 notes each). V-VI: Counts during the first 2 phrases of the first variation (see Fig. 1). Continuous curve on top: Sum of discharges during 100 ms intervals between all 62 1/4-notes of the tune. Broken line: Same count for the small multiunit activity. Note different ordinate scale for large single (left) and small multiunit activity (right)

ous line). The counts of spontaneous activity preceding music for successive periods of phrase length (broken lines) show that there was no significant spontaneous periodicity of discharge rate.

We have also seen such rhythm and phrase related activations in other units and during other pieces. Thus, for example the rhythmical beats towards the end of the drum solo of the rock music or the rhythmical banjo beats at the beginning of the Foster piece "Oh Susannah" tended to entrain the activity of some units. However, the activations were always rather loosely coupled to the respective beat notes, so that the latencies and discharge probabilities could vary considerably.

In spite of these impressive examples, it must be emphasized that distinctively single note, rhythm or musical phrase related activations were weak and could be recognized only in a minority of recordings, so that with the described variabilities in discharge probabilities and latencies the whole population of units from which we recorded was far from synchronized with the beat and rhythm of the musical pieces, at least for the short recording times of each piece (20-30 s).

The examples we have shown for note and phrase related activations were from the right middle temporal gyrus, i.e. from the non-speech dominant hemisphere. However, we have seen the same phenomena also in the middle and superior temporal gyrus of the speech dominant left side, and

our material is not sufficient to make any firm statement on the laterality of these phenomena.

Discussion

The neuronal activity changes observed in the lateral temporal lobe on which we reported do not appear to represent essential aspects of music and therefore probably do not play a decisive role for music representation in the brain. On the other hand, our findings indicate that music appears to affect neuronal activities in this region of the brain in a characteristic manner. The most prominent effect was a change in spontaneous discharge rate. When playing simple tunes in pleasant harmony such as the piano pieces of Mozart, Schumann and Galuppi, discharge rates dropped in nearly half of the neuron recordings or increased only slightly in a minority. Also the more lively orchestrated folk tunes caused a decrease of discharge rates more often than an increase. In fact, the neuronal activity in the lateral temporal lobe was reduced to 60% of the resting level in the average during these types of music. During the unmelodic and only slightly structured drum beat of the rock music, on the other hand, increase of discharge rate was seen more often than decrease. These changes of discharge rates were recorded in the superior temporal gyrus of both sides, where speech usually evoked neuronal activations, often quite specifi-

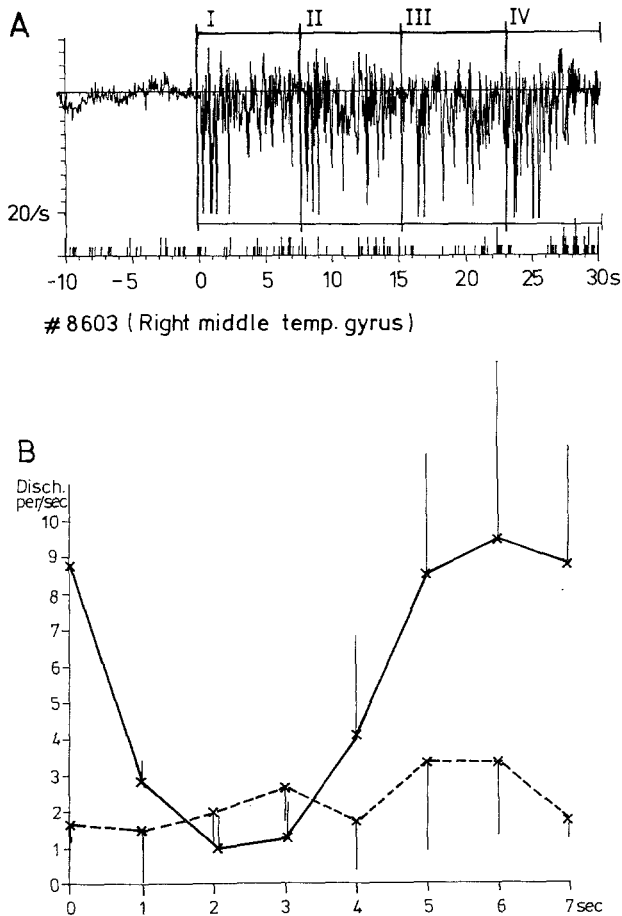


Fig. 8A, B. Activation of a neuron in the right middle temporal gyrus at the end of a musical phrase (Patient 8603). **A** Digitized audiorecord (top) and discharge counts of the neuronal activity (bottom). The vertical lines mark the phrases I–IV as indicated in Fig. 1. Binwidth 50 ms. **B** Continuous line: mean discharge rates with standard deviations at 1 s-intervals during the 4 musical phrases (the phrases begin at 0 s). Broken line mean discharge rates during rest preceding music over 4 successive 7 s-long periods (corresponding to the length of the musical phrases)

cally related to phonemic and temporal aspects of spoken language and the patients own voice, as well as in the middle and inferior temporal gyrus, in which neurons were either unresponsive to speech or only unspecifically activated (cf. Creutzfeldt et al. 1989a, b). Only in three recordings the changes of discharge rate during speech and music were in the same direction.

We conclude from these observations and with all caution, which is necessary in the light of the large variability, that music has a specific effect on neuronal activity in the lateral temporal lobe and that this effect is predominantly in the direction of silencing down the spontaneous discharge rate. It is tempting to relate this observation to the quieting effect of this type of music.

We have observed a similar effect on spontaneous discharge rate in the same neuronal population also during a complex memorizing task as will be described in a subsequent report (Creutzfeldt, Ojemann, Lettich, in preparation; see also Ojemann et al. 1988). Is the common denominator in both situations the reduction of “noise in the system”? We shall discuss this with respect to the mental tasks in some more detail in the next paper. Interestingly, the EEG also shows a decrease in power over both temporal lobes during listening to music as well as during various mental tasks (Petsche et al., in press). This decrease of power is mainly restricted to the α - and θ -range, but spontaneous unit discharges may also be closely related to the α - and θ -waves at the recording site as we will describe in a forthcoming paper (Creutzfeldt, Gädicke, Ojemann, in preparation). Local cerebral metabolism was reported to increase over both temporal lobes during music stimulation (Mazziotta et al. 1982). This is unexpected in view of the generally suppressed neuronal activity in this region, but if this turns out to be a consistent finding, the metabolic activation might reflect activation of neurons in the primary auditory cortex or increased activation of inhibitory neuronal mechanisms.

The other effects of the music we presented were somewhat more specific in that we could demonstrate some entrainment of neuronal activities by single tones and changes of activity related to the completion of musical phrases. The effects were slight and we only recognized them in a minority of recordings. Yet, they indicate that rhythm and segmentation of music into phrases may entrain neuronal activities that are apparently not strictly involved in the representation of melody. Such a synchronizing effect of music on a larger population of neurons, even if it is only slight and obvious in a minority of neurons, must have an effect on the general state of mind, attention, emotion etc. This even more so if one can assume that these general effects of music on neuronal activities may not be restricted to the lateral temporal lobe but may also affect other regions of the brain including the motor system as the EEG-data and behavioral observations (“beating the rhythm”) suggest. The situation and position during which the patients listened to the music was clearly abnormal and did not allow for any overt emotional or motor response. Yet, the changes of neuronal discharge rates induced by music and the entrainment of neuronal activity by tones and musical phrases may be related to one of various known effects of music on vegetative phenomena such as heart rate, mus-

cle tone, the state of mind, on mood, attention and motor activity known from soothing, march and dance music.

In all this one should not forget, however, that music is not a natural signal. It is a creation by human beings and therefore the form and constraints of musical composition are those dictated by the conditions of auditory perception which are the conditions for the appreciation of music. On the other hand, none of our observations can be related in any way to the richness of experience and analytical perception of music, a capacity specific to humans.

This implies that we have not tapped with our microelectrodes a region in which specific aspects of music are neuronally represented. Even the distinction between harmonic and disharmonic sounds which, if presented alone, appears to be related to specific activity changes in the EEG in the hippocampal region and, to some extent also in the auditory cortex of both sides (Wieser and Mazzola 1986; Mazzola et al. 1988) is not reflected in our recordings. On the other hand, our findings may give a clue to the phenomenon that temporal lobe seizures maybe in some rare cases triggered while listening to music, especially to emotionally involving music. A general reduction of spontaneous discharge rate and a slight but probably inter-individually variable degree of synchronization induced by the beat of music could indeed facilitate (or disinhibit) epileptogenic activity. The type of activity changes observed in our study during music could also interfere with the understanding and production of language while listening to music, considering the involvement of the same population of neurons in listening to speech and speaking.

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