Music and the Auditory System

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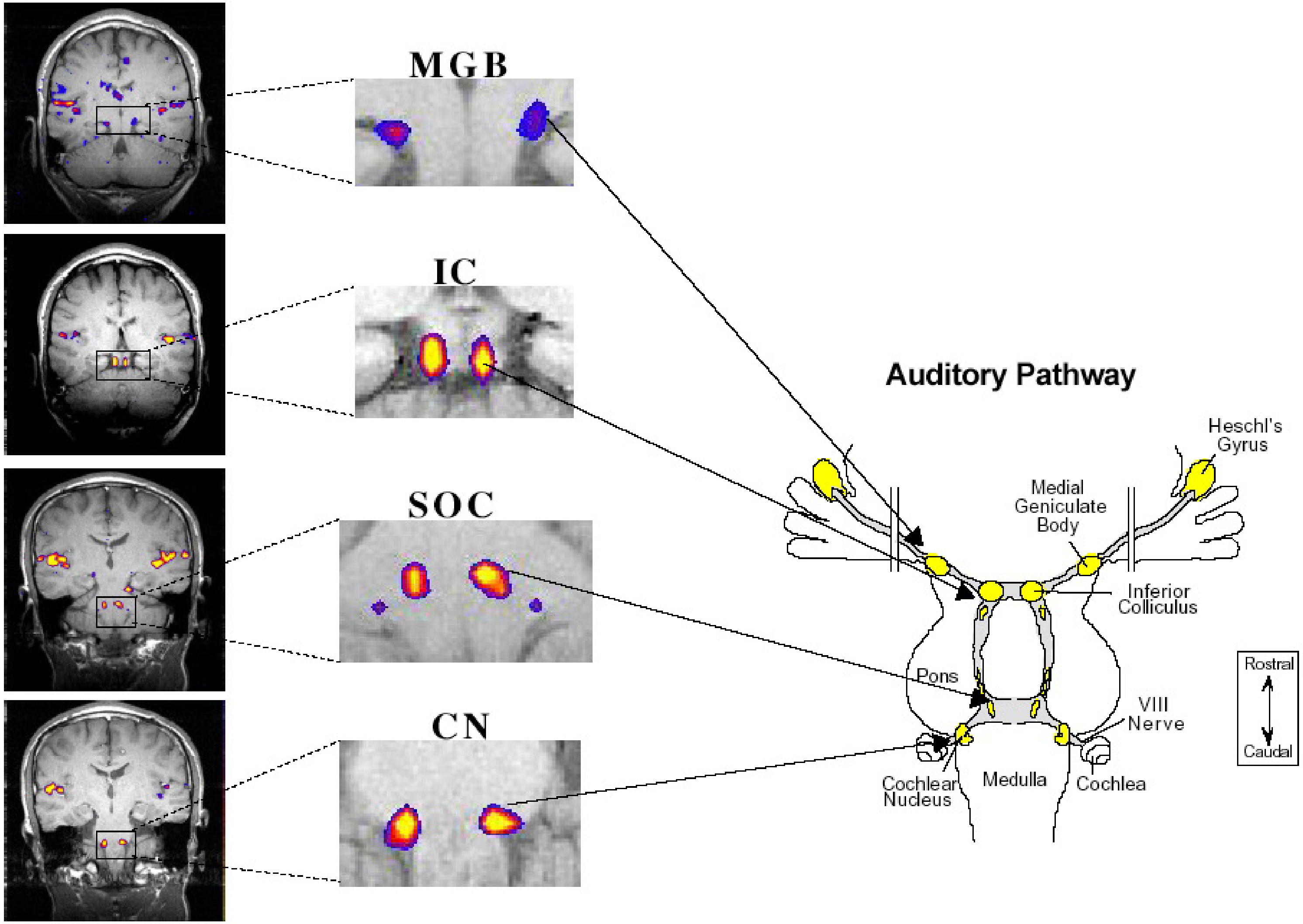
1. The neurophysiology of music perception

- 'at present, no field of the neurophysiology of music really exists' (Weinberger, 1999)
  - Most experiments carried out on anaesthetized animals.
  - Most experiments have used simple, non-musical stimuli.
- More recently:
  1. easier to produce controlled complex stimuli (e.g., by using CSound);
  2. more experiments on waking animals because this tells us much more about normal brain behaviour than experiments on anaesthetized subjects;
  3. new technologies such as MEG, MRI and PET allow brain activities in waking, behaving humans to be studied.

1. The neurophysiology of music perception

1. I was originally going to devote this fifth lecture to parallelism but after some consideration, I decided that would not be very useful.
2. So, instead, in this lecture I'm going to introduce you to some work that aims to explain music perception and cognition in terms of the neurophysiology of the auditory system.
3. Most of the material in this lecture is actually taken from Weinberger's (1999) chapter in Deutsch's (1999) *The Psychology of Music*.
4. Weinberger (1999, p. 47) claims that 'at present, no field of the neurophysiology of music really exists'.
    (a) Not ethical to do physiological experiments on humans so most experiments carried out on anaesthetized animals.
    (b) Experiments concerned with sensory physiology and have not used musical stimuli. Instead, experimenters have been aiming to understanding responses to simple sensory stimuli (i.e., usually isolated pure tones).
5. We'd like to know how musical stimuli are processed in the auditory systems of waking humans but auditory physiology provides data mainly for how non-musical stimuli are processed in the auditory systems of anaesthetized, non-human animals.
6. However, over last 20 years, some work has been done that is more obviously relevant to the physiological substrates that underlie music perception. This has come about because
    (a) it has become easier to produce controlled complex stimuli (e.g., by using CSound);
    (b) more experiments have been carried out on waking animals because this tells us much more about normal brain behaviour than experiments on anaesthetized subjects;
    (c) new technologies such as MRI (MEG), PET scans allow brain activities in waking, behaving humans to be studied remotely.

2. The anatomy of the auditory pathway (1)

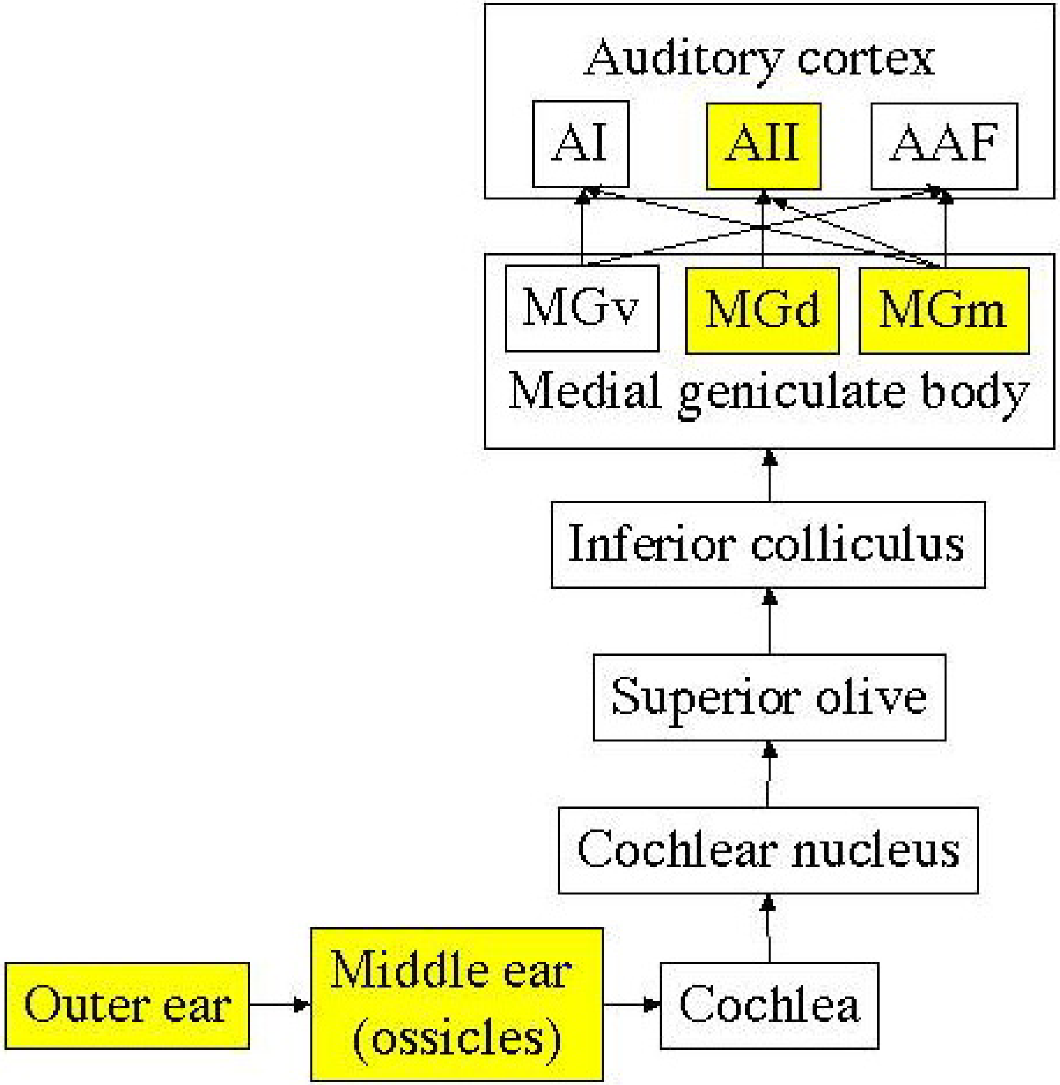


From Sigalovsky (2002).

2. The anatomy of the auditory pathway (1)

1. So I assume that we all know that when the sound enters the ear, it causes the tympanic membrane to vibrate.
2. These vibrations are then transmitted via the auditory ossicles to the cochlea which is a spiral structure containing a membrane called the basilar membrane.
3. The cochlea essentially acts as a bank of around 15000 bandpass filters, each of these filters has a nerve fibre that forms part of the auditory (VIIIth) nerve spiral ganglion.
4. As shown in the diagram on the right here, the auditory nerve fibres synapse on neurons in the cochlear nuclei in the brain stem. The nerve signal is then passed on up through the trapezoid body to the superior olivary complex. It then passes through the nuclei of the lateral lemniscus to the inferior colliculus. From the inferior colliculus it passes to the medial geniculate body which is part of the thalamus and from there it goes to the auditory cortex which forms part of an area of the temporal lobe known as Heschl's gyrus.
5. On the left hand side here you can see MRI images of the brain showing activity in these various brain structures.
6. Nerve signals are also passed *down* the auditory pathway from the cortex to the ear. This allows the basilar membrane response to certain frequency ranges to be enhanced while other frequency ranges are inhibited.
7. Much more is known about the ascending auditory pathway than the descending auditory pathway.

3. The anatomy of the auditory pathway (2)

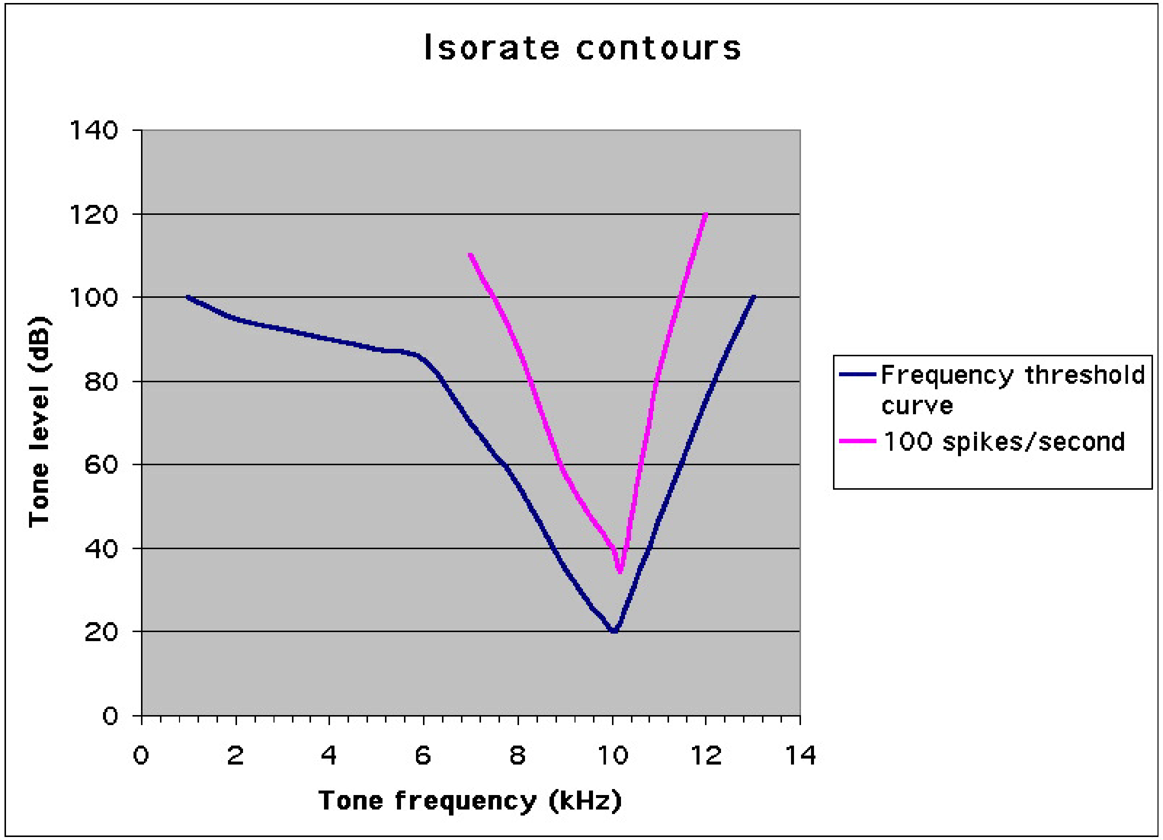


From Weinberger (1999, p. 50).

3. The anatomy of the auditory pathway (2)

1. This diagram is a grossly simplified representation of the ascending auditory pathway.
2. The basilar membrane (BM) in the cochlea acts as a strip of 15000 narrow bandbass filters. Each position on the basilar membrane is therefore associated with a particular frequency, with neighbouring frequencies being represented by neighbouring points on the basilar membrane.
3. The BM therefore exhibits what is called a “tonotopic” organization and this tonotopic representation of the frequencies in the sound input is projected onto successive structures in the auditory pathway, all the way up to the auditory cortex.
4. For example, this tonotopic map is projected onto one part of the medial geniculate body known as the ventral medial geniculate nucleus (MGv).
5. The MGv then projects the tonotopic map onto a part of the auditory cortex known as the primary auditory cortex (AI).
6. In the primary auditory cortex of the cat, the tonotopic map is arranged so that the more caudal neurons (i.e., the ones closer to the tail) respond to lower frequencies and the more rostral neurons (i.e., towards the nose) respond to higher frequencies.
7. In another field of the cat’s auditory cortex, known as the anterior auditory field (AAF), the tonotopic map is reversed with the high frequency neurons towards the tail and the low frequency neurons towards the nose (rostral).
8. The frequency to which a given neuron responds can be changed with learning, however. So if a given frequency takes on special meaning for an individual, more neurons will respond to this frequency and the tonotopic map may become slightly distorted.
9. The pathway that leads from the cochlea to the primary auditory field is called the *lemniscal pathway* and it is within this lemniscal pathway that the tonotopic representation is transmitted.
10. However, there are other nuclei in the auditory cortex and the medial geniculate body of the thalamus that do not have this tonotopic organization.
11. For example, the dorsal medial geniculate nucleus which projects to the secondary auditory cortext (AII) and the magnocellular medial geniculate nucleus which projects to all fields of the auditory cortex do not have this tonotopic organization.
12. In fact, each neuron in the MGm responds to a characteristic set of frequencies which can be changed very easily by learning.
13. In this diagram, the structures marked in yellow do *not* exhibit a tonotopic representation. All the other structures do.

4. Single neurons and receptive fields



4. Single neurons and receptive fields

1. Up to now we've just been talking about anatomy—i.e., where things are and what they're called.
2. Now we start to talk about physiology which is concerned with what things do and how they do it.
3. Most physiological studies that tell us something about how various parts of the brain respond to certain stimuli have been carried out by recording the responses of single neurons or small groups of neurons using micro-electrodes.
4. This gives a detailed picture of the response properties of tiny areas of the brain (often just single neurons) and can be used to determine precisely the site within a neural structure that responds to a given stimulus.
5. What these micro-electrodes measure is the rate of discharge or firing of a neuron or small group of neurons.
6. A given neuron will not respond to all stimuli. For example, there are neurons in the auditory cortex that only respond when a stimulus sound has a frequency within a certain range.
7. The set of stimuli to which a given neuron responds is called the *receptive field* or RF of the neuron.
8. The *frequency tuning* of an auditory neuron describes the way that the neuron responds to tones with different frequencies and different intensities.
9. As I just mentioned, many auditory neurons are tuned to respond only to frequencies within some particular band. However the band of frequencies to which a given neuron responds depends on the intensity of the sound.
10. In general, the higher the intensity of the sound, the broader the range of frequencies to which a given auditory neuron will respond.
11. For example, this line on this graph here shows the sound pressure level required at each frequency to elicit a response from a particular nerve fibre in the cochlear nerve.
12. As you can see, at 100dB, a sound with a frequency anywhere between 1 and 13 kHz will elicit a response from the nerve fibre.
13. However, at 20dB, only sounds with a frequency close to 10kHz will cause the neuron to respond.
14. This curve is called the *frequency threshold curve* (FTC) and the area outlined by the FTC is called the *response area*.
15. The frequency at which the threshold is lowest is called the *characteristic frequency* (CF) of the nerve fibre. So the CF for this nerve fibre is around 10 kHz.
16. Each neuron in the cochlear nerve has its own distinct characteristic frequency. Neurons with high CFs are found near the outside of the nerve bundle and tones with lower CFs are found nearer the centre.

17. When the neuron responds, what happens is that it starts discharging or firing at a faster rate.
18. In general, the greater the intensity of the stimulus, the faster the neuron discharges.
19. The shape of this frequency threshold curve is typical of neurons in the cochlear nerve. Note that the threshold of the neuron rises quickly as the frequency rises above the CF but rises much more slowly as the frequency falls below the CF.
20. The frequency threshold curve for a given neuron is just one of a number of curves called *isorate contours*. Each isorate contour for a neuron shows all the combinations of intensity and frequency that cause the neuron to fire at a particular rate.
21. For example, this isorate contour shows for each frequency, the intensity that causes the neuron to fire at 100 spikes per second.
22. The frequency that causes the greatest response from a cell at a particular level of stimulus intensity is called the *best frequency* (BF) of the cell.
23. At the minimum point of the frequency threshold curve, the BF and CF are the same but at higher intensities, the best frequency may not be equal to the CF, as shown here.

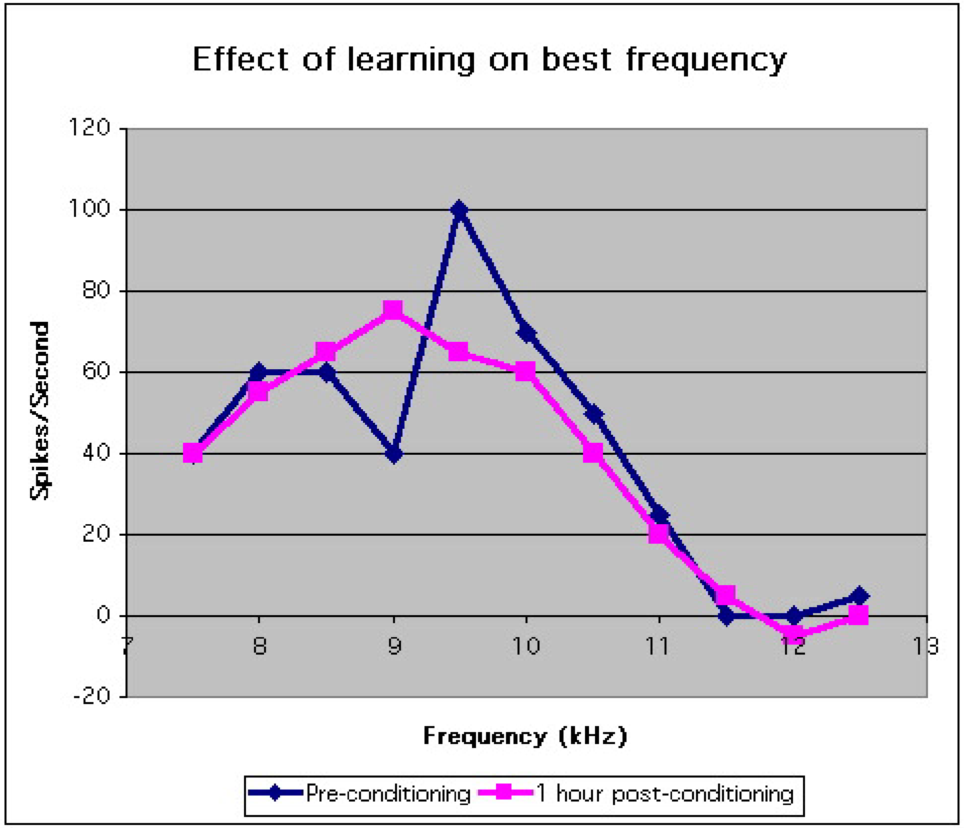
5. Other map-like representations in the auditory pathway

- In the lemniscal auditory pathway, the frequencies of tones are represented in tonotopic maps.
- Map-like representations also used in brain centres that deal with vision and touch.
- Knudsen (1991) showed that spatial location of a sound source is also represented by means of a map.
- Spatial location map is *computed* from physical stimulus attributes but frequency map is derived directly from physical stimulus parameters.

5. Other map-like representations in the auditory pathway

1. I mentioned earlier that within the lemniscal pathway, the frequencies of the tones that are heard are represented in a tonotopic map that is transmitted from the cochlea all the way to the auditory cortex.
2. Such map-like representations of properties of input stimuli also occur in the parts of the brain that deal with vision and touch.
3. Within the auditory system, it is not only the frequency of a sound source that is represented in this map-like manner, but also the spatial location of the sound source (Knudsen, 1991).
4. Unless a sound source is equidistant from both ears, it will arrive at different times at the ears. Also, when it arrives, because it will have travelled different distances, the intensity and phase of the sound will not be the same at both ears.
5. The first structures in the auditory pathway that receive information from both ears are the superior olivary complexes.
6. Neurons in the SOCs and higher auditory pathway components seem to be sensitive to binaural cues such as differences in intensity, time of arrival and phase between the sounds entering through the two ears.
7. Knudsen's (1991) work seems to suggest that in the inferior and superior colliculi these cues are used to compute a map-like representation of the spatial location of the sound source.
8. An important difference between the map that is used to represent spatial location and that which isused to represent frequency is that the location map has to be *computed* from two or more physical attributes of the physical stimulus whereas the frequency map is generated directly from a physical parameter of the stimulus.

6. Attention and learning in the auditory system



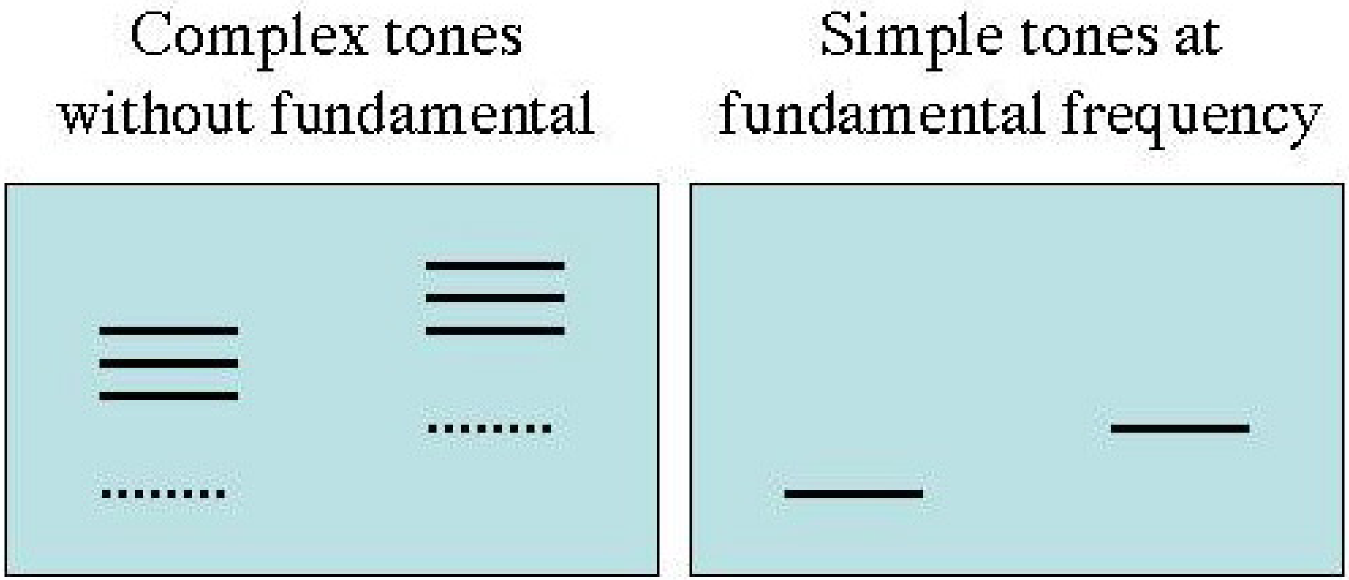
- Rate of firing of a neuron in response to an attended stimulus can be much greater than its response to the same stimulus when the subject is not paying attention.
- If the best frequency of a neuron is close to that of a conditioned stimulus, then the best frequency changes to that of the conditioned stimulus after conditioned learning.

6. Attention and learning in the auditory system

1. The rate at which an auditory neuron fires does not just depend on the frequency and intensity of the stimulus.
2. Weinberger (1999, p. 54) points out that systematic studies of monkeys have shown that the rate at which neurons fire in the auditory cortex also depends considerably on whether or not the subject is selectively attending to the stimulus, preparing to make some specific response and so on.
3. For example, the rate of firing in response to an attended stimulus can be much greater than the response to the same stimulus when the subject is not paying attention to it.
4. Recall that some of the neurons in the primary auditory cortex are tuned to specific narrow frequency bands and that each one has its own characteristic frequency and receptive field.
5. Bakin and Weinberger (1990) showed that the receptive fields or tuning curves of neurons in the primary auditory cortex can be changed by conditioned learning where an animal is trained to associate a particular stimulus, in this case a tone with a particular frequency, with a reward.
6. The tone that the animal is trained to associate with a reward is called the *conditioned stimulus* (CS).
7. Bakin and Weinberger (1990) showed that if a neuron has a best frequency near that of the conditioned stimulus, then after conditioning, the response of the neuron to the conditioned stimulus increases and the response of the neuron to other frequencies (including the former best frequency) decreases. The best frequency of the neuron therefore changes to that of the conditioned stimulus.
8. In this graph, for example, we see the receptive field of a neuron in the auditory cortex of a guinea pig changing after conditioned learning so that the best frequency is equal to that of the conditioned stimulus.
9. The result of this is that, after conditioning, more neurons in the primary auditory cortex have best frequencies that are near to or equal to the conditioned stimulus.
10. The ability of a neuron to adapt its receptive field in this way is called *receptive field plasticity.*
11. Once the best frequency and receptive field of a neuron has been changed by conditioning, the effect can last for weeks.
12. Weinberger *et al.* (1990) showed that the fact that the receptive fields of primary auditory cortex neurons can be changed by conditioning means that the actual tonotopic frequency map of the primary auditory cortex can be changed, with frequencies that have important associations being more highly represented than less important frequencies.
13. However, this increase in response to particular frequencies only occurs if the animal learns to associate a reward or some other important meaning to the frequency. It cannot be induced simply by presenting the animal repeatedly with the same frequency.

14. In fact, Condon and Weinberger (1991) showed that when an animal is repeatedly presented with a tone of a particular frequency, the neurons in its auditory cortex quickly become *habituated* to the frequency and their response to the stimulus frequency *decreases*, while their response to frequencies near the stimulus *increases*.

7. Do animals perceive pitch?



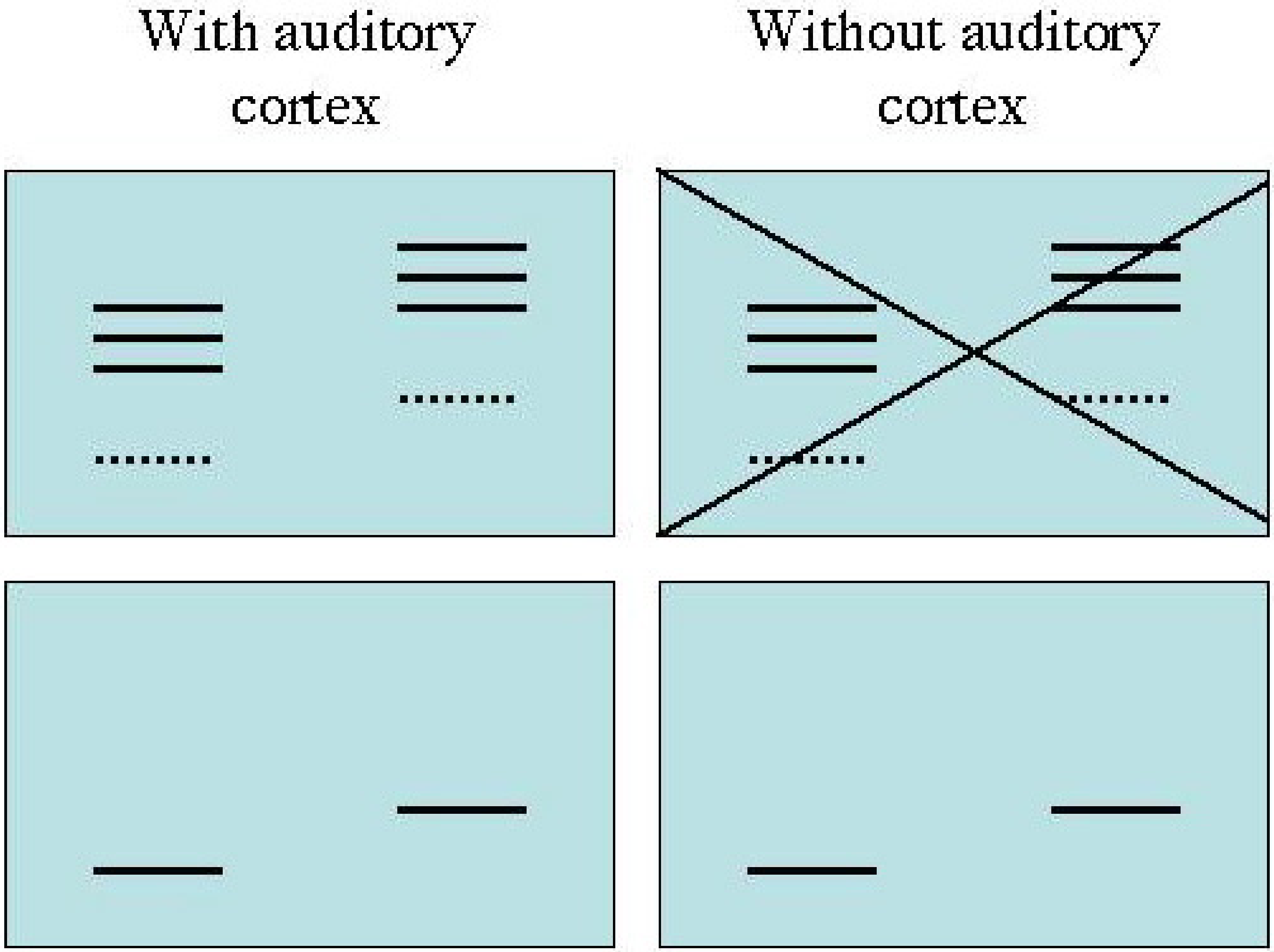
Complex tones without fundamental

Simple tones at fundamental frequency

7. Do animals perceive pitch?

1. Weinberger (1999, pp. 61–67) then goes on to and answer a number of questions concerning the auditory system and pitch perception.
2. The first of these is, “do animals perceive pitch?”.
3. Weinberger (1999, p. 62) describes experiments carried out by Chung and Colavita (1976) and Heffner and Whitfield (1976) that seems to suggest that they do.
4. In this experiment, cats are first trained to distinguish between two complex tones, each containing harmonics of some missing fundamental.
5. Although the fundamental is not present, the pitch of the complex tone is perceived by humans to be equal to that of a simple tone with a frequency equal to the fundamental. This is only possible if the fundamental frequency is less than about 2000 Hz.
6. Having been trained to distinguish between complex tones with missing fundamentals, the cats were then presented with tones consisting just of the fundamentals that had been missing in the earlier stimuli.
7. The cats discriminated between the fundamentals in the same way they had learnt to discriminate between the complex tones without the fundamentals.
8. This experiment suggests that cats perceive periodicity pitch. Other experiments have been performed that suggest that birds and monkeys also perceive periodicity pitch.

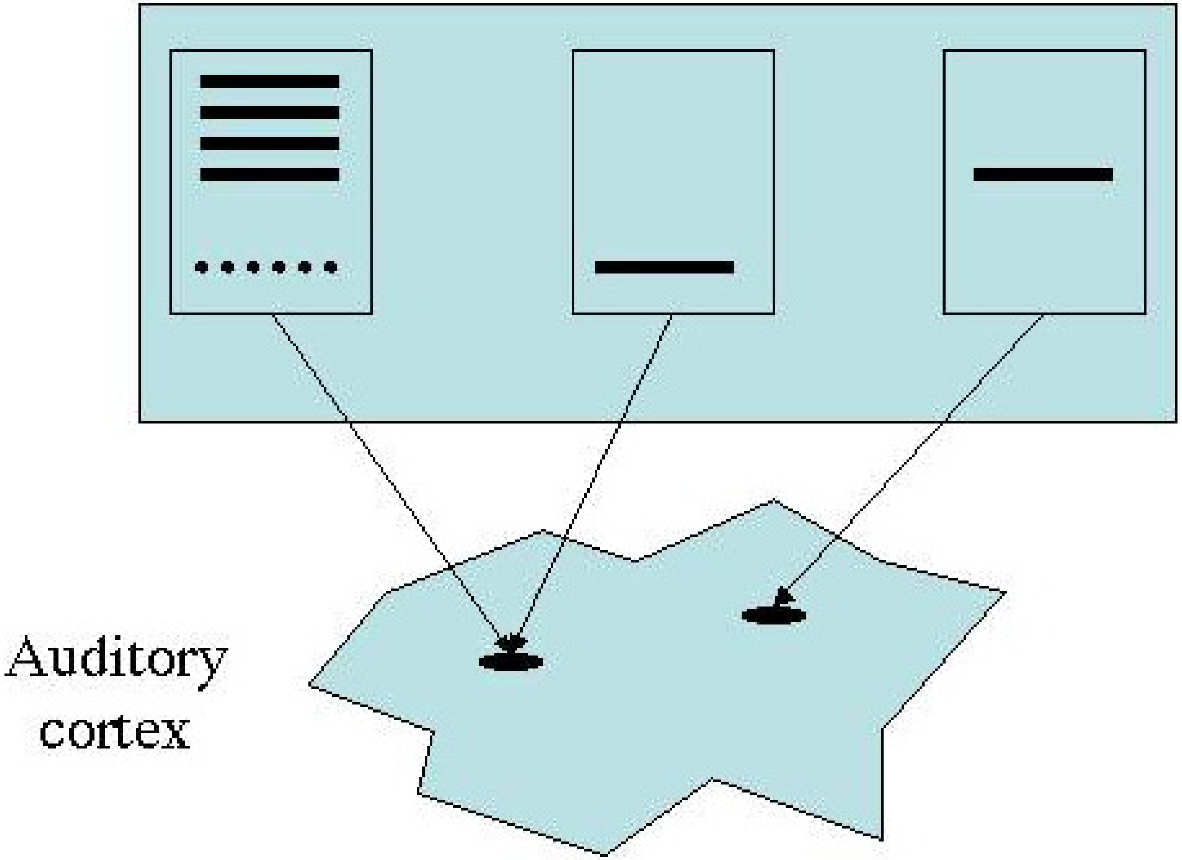
8. Is the auditory cortex necessary for the perception of pitch?



8. Is the auditory cortex necessary for the perception of pitch?

1. Weinberger (1999, p. 63) then asks whether the auditory cortex is necessary for the perception of pitch.
2. Whitfield (1980) carried out an experiment that seems to show that this is indeed the case.
3. In this experiment, Whitfield first trained cats to discriminate between harmonic complex tones without the fundamental frequencies and also to discriminate betwen various pure simple tones.
4. As I mentioned on the previous slide, Heffner and Whitfield (1976) showed that cats identified a complex tone without its fundamental with a simple tone at the same frequency as this missing fundamental, suggesting that they can hear periodicity pitch.
5. Whitfield (1980) showed, however, that when the auditory cortexes of the cats were removed, they were no longer able to hear the missing fundamental, even though they still responded to the simple tone stimuli.
6. This seems to suggest that the frequencies making up a complex tone are unified into a unitary pitch percept in the auditory cortex.

9. Is tonotopic organization based on frequency or on pitch?



9. Is tonotopic organization based on frequency or on pitch?

1. Weinberger (1999, p. 63) then asks whether tonotopic organization is based on frequency or on pitch.
2. Pantev *et al.* (1989, 1991) investigated this question by presenting human subjects with three different types of tone:
   (a) a complex tone consisting of the fourth to seventh harmonics of a fundamental at 250Hz without the fundamental itself;
   (b) a pure tone at 250Hz; and
   (c) a pure tone at 1000Hz.
3. Pantev et al showed that the position of response in the auditory cortex for the 250Hz pure tone was the same as that of the complex tone without its fundamental and different from the position of response for the 1000Hz tone.
4. The positions of the responses were confirmed using MRI to be in the primary auditory cortex.
5. The authors therefore concluded that the tonotopic organization in the auditory cortex is actually based on pitch rather than frequency.

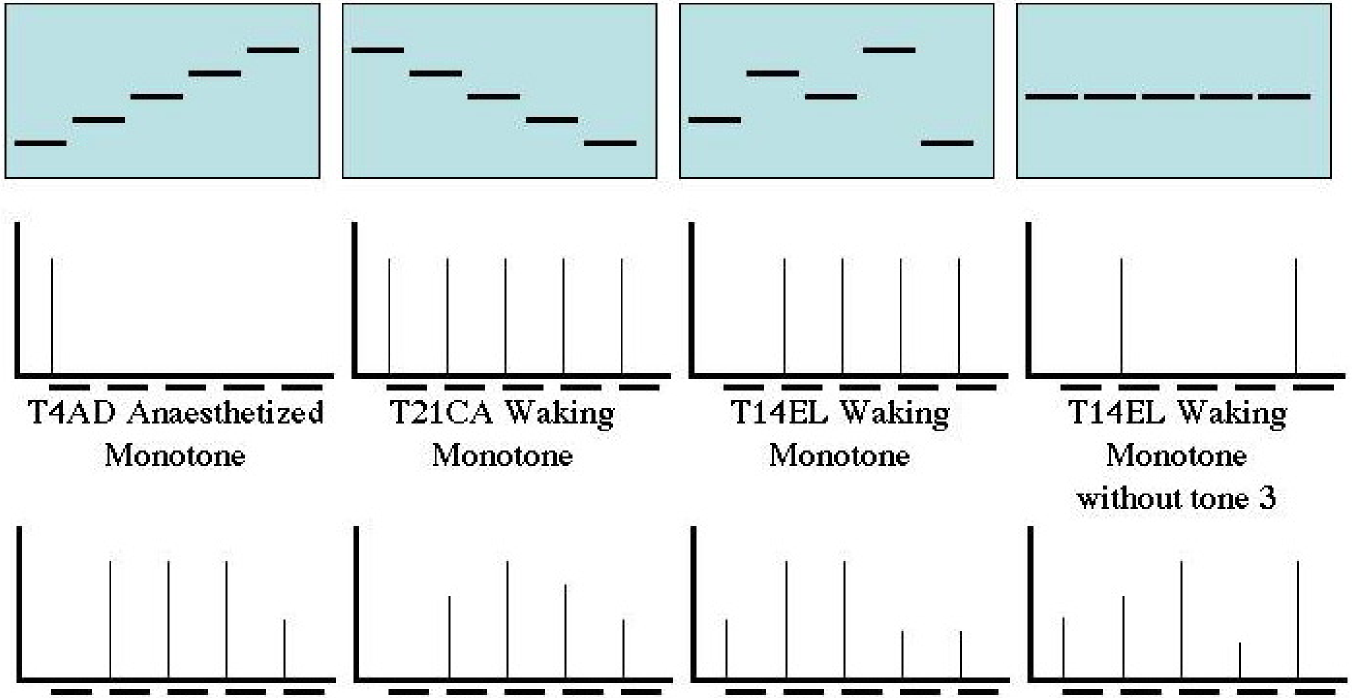
10. Do single neurons encode pitch?

- Pitch of complex tones encoded in cochlear nerve by distribution of spike intervals across nerve fibres (Cariani and Delgutte, 1996a,b; Cariani *et al.*, 1992).
- Cells in dorsal part of AI each respond to two frequencies, usually about a perfect fifth apart (frequency ratio= 3/2) (Schreiner and Sutter, 1992; Sutter and Schreiner, 1991).
- Single neurons do not respond in the same way to a complex tone as they do to a simple tone with the same frequency as the fundemantal of the complex tone (Schwartz and Tomlinson, 1990).
- Pitch may be encoded by *groups* of neurons even if single neurons only encode frequency (Weinberger, 1999, p. 66).

10. Do single neurons encode pitch?

1. It is now reasonably well accepted that the pitch of complex tones is encoded in the pattern of distribution of spike intervals across the nerve fibres in the auditory nerve (Cariani and Delgutte, 1996a,b; Cariani *et al.*, 1992).
2. Cariani et al. showed that different stimuli that are all perceived to have the same pitch generate the same pattern of distribution of spike intervals across the auditory nerve.
3. It is therefore pretty clear that each cochlear nerve fibre does not single-handedly encode pitch.
4. Schreiner and Sutter (1992) and Sutter and Schreiner (1991) showed that neurons in the dorsal part of the primary auditory cortex have not one but *two* characteristic frequencies—that is, for these cells there is more than one frequency with the lowest threshold.
5. Moreover, they found that the median ratio of the characteristic frequencies for such two-peaked neurons is 1.56, which is very close to 1.5 which is the frequency interval of a perfect fifth.
6. Schwartz and Tomlinson (1990) made a direct study to investigate whether or not single neurons respond to pitch or frequency. If the neurons responded to pitch, then they should respond equally to both a simple tone and a complex tone with the same pitch. However, if they respond only to frequency, then the neurons would respond differently to complex and simple tones even if they are perceived to have the same pitch.
7. Schwartz and Tomlinson (1990) failed to find a single neuron that responded in the same way to a complex tone as it did to a simple tone with the same frequency as the fundemantal of the complex tone.
8. However, as Weinberger (1999, p. 66) points out, even if single neurons in the primary auditory cortex do not encode pitch, this does not exclude the possibility that the primary auditory cortex is organized by pitch rather than frequency.
9. Weinberger (1999, p. 66) suggests that pitch may be coded by groups of neurons within the auditory cortex even if single neurons only encode frequency.

11. Studies relating to the perception of contour and melody



T4AD Anaesthetized Monotone

T21CA Waking Monotone

T14EL Waking Monotone

T14EL Waking Monotone without tone 3

T14ELWaking Ascending

T14EL Waking Ascending (+45 mins)

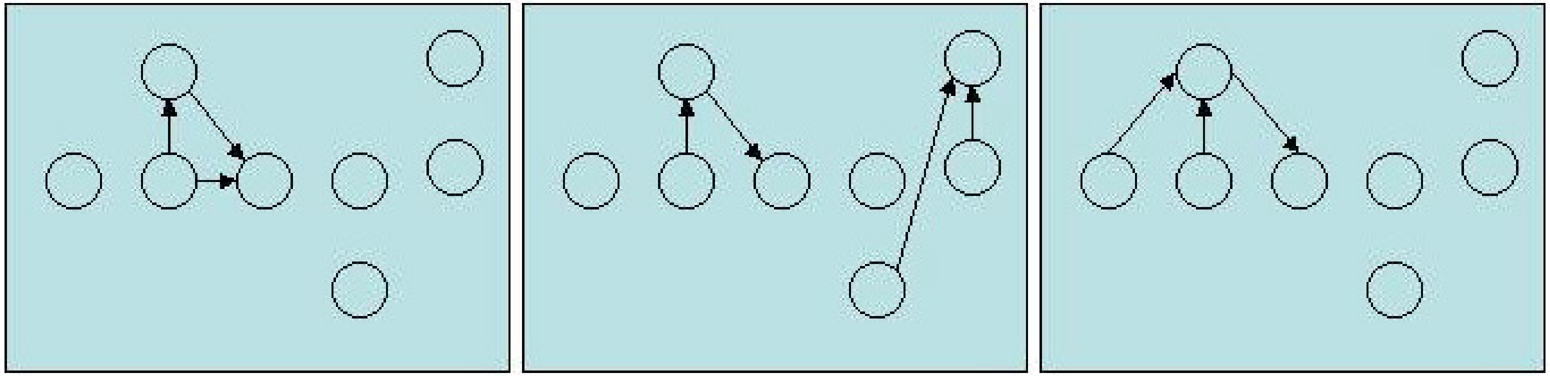
T14EL Waking Descending

T14EL Waking Mixed

11. Studies relating to the perception of contour and melody

1. Weinberger and McKenna (1988) and McKenna *et al.* (1989) investigated the responses of single neurons in the primary and secondary auditory cortex in waking and anaesthetized cats, when presented with sequences consisting of five pure-tones.
2. Each five-tone sequence either had an ascending contour, a descending contour, a mixed contour or a monotone (i.e., all five tones the same), as shown here.
3. In some of the five-tone sequences, the third tone was omitted. In all the others, the third tone was the same.
4. The response of each cell to each frequency in the five-tone sequence was determined for all contours and each five-tone sequence was presented 25 times.
5. In the first part of the experiment they presented just the monotone pattern to anaesthetized cats and found that the neurons only responded to the first tone in each five-tone sequence (see diagram). However, in waking cats, the neurons responded to all five tones in each sequence.
6. In the second part of the experiment they therefore examined the neuronal responses to the tone sequences in waking cats.
7. They also found neurons such as T14EL that only responded to the second tone in every pair of tones. This was demonstrated by the response of these neurons when the middle tone of the five was omitted (see diagram). This result seems to be suggestive of Povel and Essens's (1985) rule that the second tone in a pair of tones is heard to be stressed.
8. In the ascending, descending and mixed stimuli, they found that the response of a T14EL neuron to a given frequency depended on the position of the tone with that frequency in the stimulus.
9. They found that the best frequency of the neuron for the descending and mixed sequences was 13kHz and 12kHz for the ascending sequence.
10. They hypothesized that this effect was caused by complex patterns of excitation and inhibition of neurons by the responses of neighbouring neurons.

12. Responses of groups of auditory neurons to 3-tone sequences



CBA

BCA

ACB

12. Responses of groups of auditory neurons to 3-tone sequences

1. Espinosa and Gerstein (1988) presented lightly anaesthetized cats with all possible permutations of a three-tone sequence and measured the responses of 8–24 neurons local networks.
2. They were able to work out the connectivity pattern of the neurons for each of the stimulus sequences and they showed that the connectivity pattern of the neurons was different for each sequence, as though the pattern of connectivity in some way represented the complete sequence.
3. In other words, they provided the first direct evidence for what is called a distributed representation of melodies in the auditory cortex.
4. Their results also show that the functional connections between neurons are not fixed.

13. Rhythm perception and auditory neurophysiology: Amplitude modulation and metre perception

- Langner (1992) emphasizes importance of AM in animal, human and natural sounds.
- AM may be a cue for metre perception.
- Some computational theories of metre perception try to find oscillations that best match the music at frequencies corresponding to beats (tactus) and bars.
- Modulation transfer function measures how well a neuron responds to a particular AM rate.
- Best modulation frequency (BMF) is the AM rate to which a neuron responds best.
- BMFs of neurons decreases as ascend auditory pathway.
- MGm responds throughout duration of tone whereas higher, auditory cortex only responds at beginning of tone.
- Topographic map of BMF found in inferior colliculus of cat and field L of myna bird: are these fields therefore very important for rhythm perception?

1. Langner (1992) has emphasized the importance of periodic fluctations in amplitude in animal communication sounds, human speech, many important natural sounds (e.g., wind, water) and music.
2. Such periodic fluctuations in amplitude (or loudness) are known as amplitude modulation.
3. In music, amplitude modulation often corresponds to the patterns of stress in metrical structure and is thus an important cue for rhythm perception.
4. This seems to relate to the work of Todd (1994), Large and Kolen (1994), Parncutt (1994) and Scheirer (2000) who have proposed theories of metre and tempo perception that essentially involve finding those oscillations that best match the music at frequencies corresponding roughly to perceived beat rates and bar rates.
5. Just as different neurons respond differently to tones with different frequencies, so they also respond differently to sounds with different amplitude modulation rates.
6. One way of measuring how well a neuron responds to a particular amplitude modulation rate is called the "modulation transfer function" (Weinberger, 1999, p. 77).
7. The rate of AM to which a neuron responds best is called the "best modulation frequency" or BMF.
8. Langner showed that the BMFs of neurons in the auditory pathway generally decrease as you ascend. For example, BMF of neurons in the auditory nerve might be 370 Hz while the inferior colliculus cells generally have BMFs in the range 20–120 Hz and the auditory cortex cells have BMFs of around 4–28Hz.
9. This may correspond to successively more "summarised" representations of the input stimulus as you rise up the auditory pathway.
10. This idea is supported by the results of Creutzfeld *et al.* (1980) who showed that while the cells in the magnocellular medial geniculate body of the guinea pig respond continuously to tones throughout their duration, cells in the auditory cortex only respond to the onsets of the tones.
11. Again, this seems to correspond nicely to the well established fact that human listeners are far more sensitive to tone onsets than tone offsets.
12. Creutzfeld *et al.* (1980) also found that while MGm cells could follow AM rates of around 100Hz, the BMFs of cortical cells were 20Hz or lower.
13. Interestingly, these BMF rates correspond to the AM rates found in species-specific vocalizations.

14. The idea that AM characteristics of sound are perceptually important is supported by the findings of Langner and Schreiner (1988) and Schreiner and Langner (1988) who found that the there is a systematic topographic distribution of BMFs in the inferior colliculus of the cat.
15. Hose *et al.* (1987) similarly found that in the field known as L in the myna bird (which roughly corresponds to the auditory cortex in mammals), there is also a systematic arrangement of the cells according to their BMFs, prompting the authors to conclude that the field L is the dominant site for rhythm analysis.

14. Rhythm perception and auditory neurophysiology: a neurophysiological correlate of grouping stress

- An event that begins a long run of similar events is more likely to be heard as beginning a perceptual group (Garner, 1974; Lerdahl and Jackendoff, 1983; Povel and Essens, 1985).
- Robin *et al.* (1990) presented cat subjects with two different sequences:
  1. UNAMBIGUOUS: `XXXOOXOOO`;
  2. AMBIGUOUS: `XXOXOXXOO`.
- Measured rates of discharge for neurons at various points in the auditory pathway.
- All neurons responded strongly to first event in UNAMBIGUOUS sequence but no regularity observed in response to AMBIGUOUS sequence.

14. Rhythm perception and auditory neurophysiology: a neurophysiological correlate of grouping stress

1. You may recall from the first lecture that one of the rules that Povel and Essens (1985) used to predict the perceived metre was based on the idea that an event is more likely to be heard as stressed if it begins a run of similar events. This idea seems to have been originally due to Garner (1974). It also corresponds to the 'Strong Beat Early' rule of Lerdahl and Jackendoff (1983, p. 76).
2. Robin *et al.* (1990) have carried out some experiments that seem to suggest a neurophysiological basis for this behavioral rule.
3. They obtained recordings of the discharge rates of neurons at various points in the auditory pathway when the subjects were presented with two different event sequences.
4. The first event sequence contained noise bursts and silences of equal length, arranged into the order xxxooxooo where x represents a noise burst and o represents a silence.
5. This event sequence was considered to be 'unambiguous' because the rule that events beginning longer sequences of similar events tend to be heard as stressed unambiguously predicts that the first event in this sequence will be heard as stressed.
6. In the second event sequence, the noise bursts and silences were arranged in the order xxoxoxxoo. In this sequence, the two longer sequences are not as isolated by silence as the longer sequence in the unambiguous pattern is. Also they are shorter. This pattern was therefore labelled as being 'unambiguous'.
7. Also, another rule used by Povel and Essens (1985) predicts that the second event in any isolated pair of events will be heard as stressed. This rule would predict stresses on the second and seventh events in the unambiguous sequence.
8. Robin *et al.* (1990) found that when the unambiguous pattern was presented, all the neurons they tested at various points in the auditory pathway responded more strongly to the first event in the sequence than to any of the others.
9. However, when the ambiguous sequence was presented, no such clear outcome was observed. It would be worth looking more closely at their results to see if the responses of the neurons to the ambiguous sequence can be explained using the rule that predicts a stress on the second event in any isolated pair.
10. Nonetheless, the results seem to provide a neurophysiological basis for the observation that grouping (and metrical structure) are strongly influenced by the first events in runs of similar events.

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