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The great tit's (*Parus major*) auditory resolution in azimuth

G.M. Klump*, W. Windt, and E. Curio

Arbeitsgruppe für Verhaltensforschung, Fakultät für Biologie, Ruhr-Universität Bochum
Postfach 102148, D-4630 Bochum 1, Federal Republic of Germany

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Summary. 1. Two male great tits (*Parus major*) were trained to distinguish between sounds from two locations in an operant two alternative, forced choice procedure with positive reinforcement.

2. The angle between the two sound sources, as experienced from the position of the experimental subject, was varied. The angle at which the birds scored 65% correct responses in 60 choices (which corresponds to $P=0.03$, two-tailed, binomial test) was defined as the minimum resolvable angle (MRA).

3. The resolution in azimuth for four natural vocalizations, the 'seeet' alarm call, the 'scolding' call, the mobbing call, and a song element, was 45°, 16°, 20°, and 18°, respectively (Fig. 2). The MRAs correlated well with the results from artificial stimuli with a comparable frequency.

4. MRAs for 300 ms sine wave stimuli were determined from 500 Hz to 8 kHz: The u-shaped function relating MRA with frequency had a minimum at 2 kHz, with a best MRA of 20°. At 500 Hz and 8 kHz the MRAs were 66.5° and 52°, respectively. MRA of a 300 ms white noise stimulus was 20.5° (Fig. 3).

5. The duration of the stimulus had no effect on the resolution in azimuth for a range of durations from 40 ms to 300 ms (Table 1). This suggests that the great tit may locate a sound source in an open loop fashion.

Introduction

In a now classical paper Marler (1955) pointed out the relationship between the structure of vocalizations and their function. He emphasized the role of the locatability of animal signals as an important characteristic which is selected in the evolutionary process. Although in some cases the detectability of a signal may play a more important role than its locatability (Klump et al. 1986; for the factors influencing detectability of signals in birds see also Dooling 1982; Wiley and Richards 1982), in other cases the locatability of easily detected signals is of crucial importance in communication.

We chose a small songbird, the great tit (*Parus major*) for our study, because much is known about its vocal behaviour (e.g. Hinde 1952; Gompertz 1961). The importance of the sound localization for the recognition of the song of territory neighbours has been demonstrated in the great tit (Järvi et al. 1977). Furthermore, the great tit's 'seeet' call was one of the examples used by Marler (1955) to discuss the functional significance of call structure. He suggested that selection should lead to differential locatability of 'seeet' and mobbing calls for the predator ('seeet' calls may also be difficult to detect for the predator, see Marler 1977; Klump et al. in press). However, the locatability of calls for other conspecifics may be important too. An easily locatable call may give the receiver additional information about the location of the predator. The study of the resolution in azimuth for acoustical signals will give us some insight in the relative differences in the locatability of these signals for the great tit.

Information about directional hearing of bird species other than the barn owl (*Tyto alba*) is relatively scarce. There is no behavioural study in which data on the directional hearing of a small songbird have been reported for a broad range of frequencies and for natural vocalizations. Our study of auditory resolution in azimuth in the great tit helps to fill this gap. Additionally, it will be

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Abbreviation: MRA minimum resolvable angle

* To whom offprint requests should be sent at the present address: Institut für Zoologie, Technische Universität München, Lichtenbergstrasse 4, D-8046 Garching, FRG

interesting to see, whether the auditory resolution in azimuth in a small songbird can be explained on the basis of the neurophysiological work with the barn owl (e.g. Takahashi et al. 1984; Sullivan and Konishi 1984), that uses pressure receivers in the range of frequencies that are localized best (Moiseff and Konishi 1981 b).

Materials and methods

Experimental subjects. Great tit nestlings were hand raised from the age of 13 days on with a diet composed of mealworms, blowfly larvae, and blowfly imagines. The diet was enriched with minerals (Ospulvit) and vitamins (Multibionta). From the age of 30 days on sunflower seeds were given which made up a major part of the diet outside experimental sessions. To control disease, oxytetracyclinhydrochloride was given with the drinking water regularly. From the age of 30 days on the birds were housed in individual cages (home-cage: 40 x 50 x 60 cm) in which they also were transported. Four great tits were selected for the experiments. Three of the four birds could be successfully trained to localize sound in a forced choice procedure described below. One of the trained birds died from diarrhoea just after finishing the shaping of the response. The experimental results are therefore reported for 2 males of the age between 4 and 9 months only.

Apparatus. The experimental cage (see Fig. 1, shaped like a cylinder sector) was housed in a box made of 22 mm thick plywood (ca. 1 x 1 x 1.2 m) which was lined with sound absorbing wedges on the inside (Illbruck illsonic 100/70, cutoff frequency ca. 750 Hz, absorption coefficient > 0.85 for frequencies > 500 Hz). The box itself was set up in a quiet, windowless chamber with tight fitting doors insuring a disturbance-free environment during the experiments. The great tit could be observed during the experiments through a closed circuit video system. The bird could enter the experimental cage from its home cage through a tunnel. In the experimental cage were 3 perches, each 4 cm wide and attached to a microswitch (WP at the end of the tunnel; LP and RP in front of automatic feeders on the opposite side of the cage). Training and testing of the birds were performed under the control of an 8-bit microcomputer (TRS 80 Model I) which monitored the perches and controlled the feeders and the sound stimuli. Sounds were generated by a custom built interface board via an 8-bit D/A converter, a sine wave generator, or a thermal white noise generator. They were gated through an electronic switch with rise and fall times of 5 ms and switched to either of two output lines. They were amplified by a Braun A 301 stereo power amplifier and broadcast through a pair of identical midfrequency range speakers (membrane diameter 9 cm, differing by less than 4 dB in the frequency range of 200 Hz to 10 kHz, except a 200 Hz wide dip of 11 dB at 1.3 and 2.8 kHz; in control experiments these were exchanged against identical pairs of Heco HKC 38 or Isophon BPSL 65 midfrequency range speakers). The distance between the speakers could be altered so that the angle between them seen from the starting point of the bird varied between 13° and 75°. Sounds were calibrated to a level of 50 dB SPL at the position of the bird on the waiting perch (General Radio type 1933 sound level meter, exceptions from 50 dB are mentioned in the text).

Experimental procedure. The great tits were trained in a two alternative forced choice operant conditioning scheme with positive reinforcement (pieces of mealworm, a preferred food). For the shaping of the response the birds were first trained to sit on the waiting perch at the end of the tunnel (observing response) and fly to any of the two perches in front of a feeder upon sounding of a tone where they were rewarded (for more details of the initial training see Windt 1985). During the later experiments pre-tone waiting times in the observing response were randomized between 3 and 8 s, and the time to take off and reach the perches in front of the feeders was set to 2 s. No tone was given if the bird did not wait the preset time. The tone was switched off by the digital control logic with a fall time of 5 ms when the bird left the waiting perch and the microswitch opened. The side from which tones were presented was determined by a random number generator. However, to avoid the formation of a side preference no more than 3 tones were presented from each side in succession, and tones were presented from both sides in about equal number. In further training, rewards were only given if the side of the perch chosen corresponded with the direction from which the tone was given (left or right speaker). At first the great tits tended to use strategies, e.g. random choice or side constant choice, which were uncorrelated with the direction of the sound, but yielded a 50% change of getting a reward. To make these strategies unprofitable we introduced a reinforcement schedule where

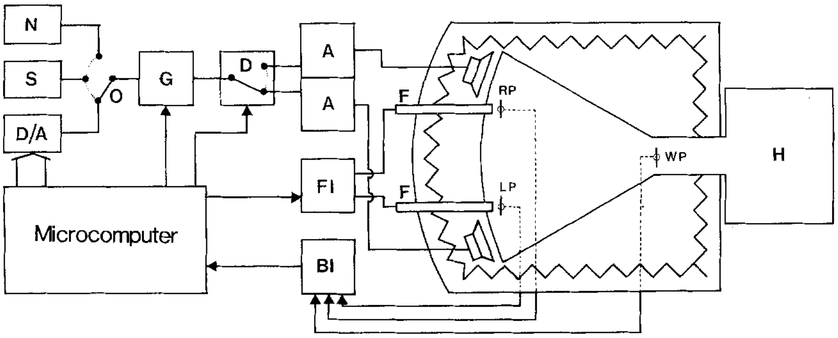

Fig. 1. Apparatus for the conditioning experiments: A Microcomputer was equipped with an interface containing a thermal white noise generator (*N*), a sine wave generator (*S*), and an 8-Bit-D/A converter, all of which could be selected by a switch (*O*). The signal was gated through a switch with rise and fall times of 5 ms (*G*), distributed to one of two channels (remotely controlled switch D) and amplified (Braun A310). The Microcomputer also monitored three perches (WP,RP,LP) through an interface (*BI*) and controlled the delivery of rewards to the bird in the test cage (interface *FI*; feeders *F*). Experimental subjects could enter the test cage from their home cage (*H*) without being handled

the bird had to make two correct choices in succession to get a reward ('sequencing', i.e. 2 rewards with 3 correct reactions in sequence etc.). However, the first three choices of a session were invariably rewarded if they were correct. We avoided 'sequencing' in stimulus representations near or below threshold, because the birds tended to stop choosing and stayed on the waiting perch or engaged in other activities when they only rarely got a reward.

Data analysis. For each given angle the last 60 of all recorded choices of a certain stimulus by a bird were analyzed. The minimum resolvable angle (MRA) was then defined as the angle at which the choice would be significantly better than chance ($P<0.03$, two-tailed, binomial test). With 60 choices this corresponds to 65% correct responses (39 out of the 60). MRA was evaluated by linear interpolation between two angles if performance at one angle was above 65% correct and at a smaller angle for less than 65% correct. Near threshold angles tested were separated by not more than 10°. The performance for a given stimulus was usually determined by decreasing angles from session to session. (The exception was the MRA for a 500 Hz 300 ms sine wave in one bird.) Data were taken from at least two different sessions at every tested angle. Appendix A lists the performance at diffferent angles, and thresholds for a 75% correct response for comparison with other psychophysical studies which usually adopt this criterion can be calculated from these. However, the experiments reported here were aimed at detecting the 65% correct response level rather than the 75% level and often no experiments at large angles were conducted, e.g. if the experimental subject already scored 68% correct at the first tested angle.

Control experiments. First, we compared the performance at certain angles and stimulus tones with and without 'sequencing'. During the gathering of the threshold data there was no significant difference between the performance of the bird with or without 'sequencing' near the threshold (e.g. the number of errors out of 60 choices was identical in two cases and differed by two in one case). Thus 'sequencing', although necessary to maintain a response correlated with the direction of sound, did not reveal different results compared with a reinforcement schedule without 'sequencing' and vice versa. We felt it was therefore acceptable to combine results from both reinforcement schedules. Second, to test whether the birds had learned differences in the characteristics of the speakers we exchanged the pair of speakers against a new pair of speakers of a different type (Heco HKC 38, Isophon BPSL 65). We also switched the positions of the initial pair of speakers. In no case did these changes affect the performance of the birds. However, the birds reversed their choice and chose consistently the side at which the computer gave no rewards, if the speakers of an identical pair were exchanged without changing the electrical connections. Thus, they were not using clues which indicated the change of side in the stimulus, such as faint switching clicks, for their decision. All these tests show, that only the direction of the sound determined the choice.

Results

Resolution in azimuth for natural vocalizations

We studied the resolution in azimuth for four different vocalizations by means of digital replicas: the 'seeet' alarm call (described as an aerial predator call by Marler 1955), the 'scolding' call (used by the great tit when directly chased by an aerial predator, see Klump 1984), the mobbing call (see Latimer 1977), and a song element (for sonagrams see Fig. 2). The resolution in azimuth of the 'seeet' alarm call was considerably lower than that of the other three vocalizations (Minimum resolvable angle – MRA: 45°, see Fig. 2). The studied song element, the 'scolding' call, and the mobbing call were similarly well resolved with a precision of between 16° and 20° MRA. The performance of both individuals was similar: the birds differed by 5° for the song element and by 2° or less for the other three stimuli. This variation is typical of that obtained with repeated measurements of MRA for the same bird with the same stimulus (4° or less).

Resolution in azimuth for pure tones and white noise

We studied the performance of the two birds with pure tones of 500, 750 Hz, 1, 2, 4, 6, 8 kHz, and with white noise. All these stimuli had a duration of 300 ms. As found in the study of natural vocalizations the performance of the two birds was rather similar (see Fig. 3). MRA differed by 15° only for the 500 Hz tone, and by 4° and less for all other 300 ms stimuli. The resolution in azimuth for pure tones was clearly frequency dependent. MRA was best at 2 kHz, which is also the best frequency in the audibility threshold curve for unmasked pure tones of 300 ms (see Klump et al. in press). The resolution in azimuth for pure tones was also very good at 1 kHz and 4 kHz and decreased considerably below 1 kHz and above 4 kHz. At 8 kHz, the dominant frequency of the 'seeet' alarm call, the great tits' MRA was about 2.5 times larger than their best MRA. The two birds' resolution in azimuth for broadband noise (thermal white noise) was as precise as for the optimum resolvable pure tone (MRAs being 21° and 20°, respectively).

The resolution in azimuth was not influenced by the duration of the stimulus (Table 1). We measured the MRA of one of the birds for a range

Table 1. MRA (deg) of the great tit in relation to tone duration

Duration (ms)	Frequency (Hz)			
	1,000	2,000	4,000	8,000
40	–	21	24	–
100	20	18	27	52
150	–	21	23	–
300	25	18	26	51

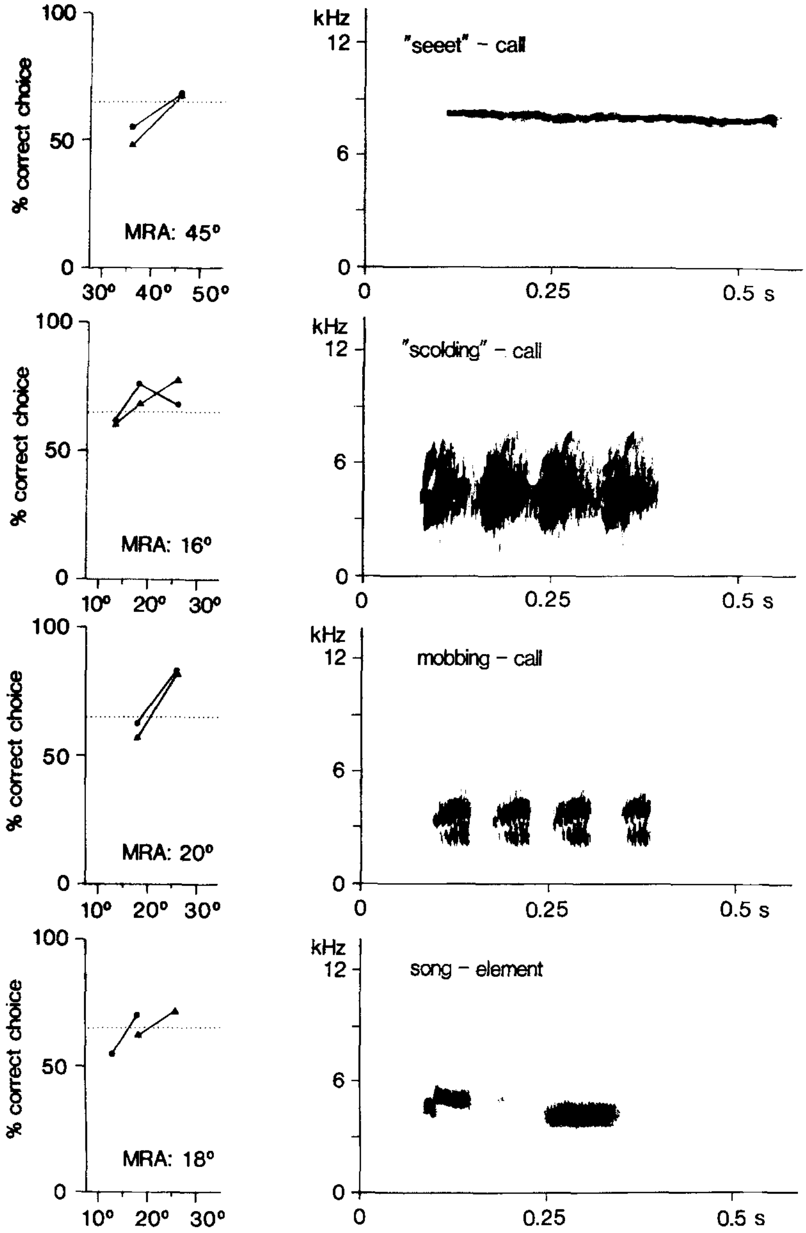

Fig. 2. Minimum resolvable angle of the great tit for four vocalizations (two subjects). Threshold criterion is a 65% correct choice by the experimental subject which corresponds to a significantly nonrandom choice ($P = 0.03$, two tailed, binomial test, all $n = 60$ choices per data point). Thresholds were estimated through linear interpolation between the performance just below and just above threshold. The sonagrams show the digitized stimuli used in the experiments

of tone durations from 40 ms to 300 ms. At no angle was there a significant difference in performance with different tone durations (χ^2-test, $n = 120$ choices, all $P > 0.38$, two-tailed). The variation of MRA shown in Table 1 is within the range of variability of repeated measurement of the MRA of the same bird and same stimulus (see above). We also videotaped the behaviour of the birds in some sessions and used single 40 ms frames to analyse 387 choices with a stimulus duration of 300 ms. In 72% of the observed choices the bird did not turn its head during the presentation of the tone at all. Head turning started after the onset of the stimulus within the first 40 ms in only 4.4% of all cases. If the head was turned, this was done on average 180 ms (±124 ms SD) after the onset of the stimulus. Hence, we conclude that the bird was mostly using an open loop system for sound localization (see Knudsen and Konishi 1979 for definition), at least for the tone duration of 100 ms and below. However, even with the 300 ms stimulus the birds rarely took the opportunity to turn their heads, indicating a similar strategy of localizing sound.

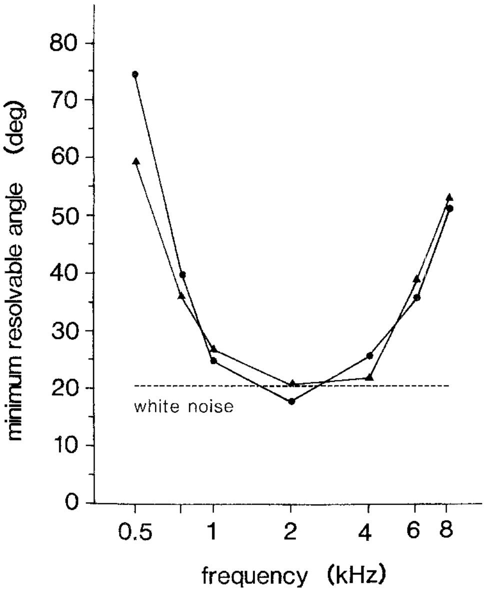

Fig. 3. The great tit's minimum resolvable angle for pure tones of 300 ms duration (solid lines, performance of the two experimental subjects) and a 300 ms white noise stimulus (dashed line, average of the two individuals which had an accuracy of 20 and 21 deg, respectively)

Discussion

Correlation of resolution in azimuth for natural vocalizations and simple artificial stimuli

The results from the study of natural calls correlate very well with the results of the study of sine waves and white noise. The 'seeet' call, which is essentially a tone of about 8 kHz (with some fluctuations in the envelope), is resolved about as precisely as a sine wave stimulus of 8 kHz. The 'scolding' and mobbing calls are resolved about as well as the artificial broad band signal, white noise (cf. Figs. 2, 3). The song element is resolved somewhat better than would be expected from results for pure tones of 4 to 6 kHz. However, the song element had a greater bandwidth than a pure tone, which may explain the better performance of the birds.

The results of this study confirm the predictions of a classical paper by Marler (1955) that 'seeet' alarm calls are less easily locatable than broadband mobbing calls (in some avian predators similar evidence has been found (Brown 1982; Kretzschmar 1982), in others no difference was detected (Shalter 1978)). The differences in the resolution in azimuth for the calls seem not to result from differences in bandwidth of the signal alone, but is also very likely influenced by differences in the dominant frequency in the signal's spectrum. The small difference between the resolution of a sine wave of 2 kHz and white noise (Fig. 3) serves to emphasize this point. The less precise resolution of the 'seeet' call cannot be attributed to ambiguities resulting from interaural phase differences of more than $\lambda/2$, because these would occur only for frequencies of above 9.3 kHz (calculated after Kuhn 1977, see below). It is also unlikely that the frequency dependence on MRA is explained by differences in suprathreshold stimulation. We repeated sessions at 500 Hz and 8 kHz with a SPL of 55 dB and 63 dB (50 dB SPL in all standard sessions) and found no difference in the performance of the birds (χ^2-test). These results parallel findings of Konishi (1973) in a behavioural study of sound localization in the barn owl. Our results on resolution in azimuth lead us to conclude that most auditory signals in the great tit are about equally well localized by conspecifics if their sound energy is concentrated in the range of 1 to 5 kHz. Sounds with a higher pitch than 5 kHz seem to be less well localized, especially if they are pure tones, and the great tits seem to trade off between ease of localization and ease of detection by conspecifics in a noisy environment (see Klump and Curio 1983) or crypsis with regard to detection by predators (Klump and Shalter 1984; Klump et al. 1986).

Comparison with other bird species

The study of acoustical resolution in azimuth in the great tit is the first comprehensive study of locatability of sounds in a small songbird. However, results limited to only a few frequencies are available from earlier studies. The resolution of sounds in azimuth in the great tit is comparable to the precision of resolution found in studies of other small songbirds. In the bullfinch (*Pyrrhula pyrrhula minor*) Schwartzkopff (1950) found a MRA of 24° at 1,500 Hz. He also found that the precision of sound localization was lower at 850 Hz which parallels the findings in the great tit. Granit (1941) found MRAs of 20° to 23° for pure tones (unfortunately there is no information on the frequency of the Edelmann-whistles) in pine grosbeaks (*Pinicola enucleator*). Bobwhites (*Colinus virginianus*, see Gatehouse and Shelton 1978) localize pure tones of 1 kHz less well than pure tones of 2 kHz, which again parallels the results in the great tit that the locatability of pure tones decreases with decreasing frequency below 2 kHz. Both, the barn owl (see Knudsen and Konishi 1979) and the European sparrowhawk (*Accipiter nisus*, Kretschmar 1982) localize pure tones in azimuth more precisely than great tits (10° and 15°, respectively). However, in the study of the sparrowhawk up to 30 stimuli were presented before the bird indicated its choice. In both these species, as in the tit, the precision of localization was lower at 8 kHz than in the midfrequency range of 2 to 4 kHz. In sparrowhawk and barn owl no decrease of azimuth-locatability of pure tones was found for frequencies below 2 kHz. The results of the study of the great tit differ considerably from a study of azimuth sound localization in the pigeon (*Columba livia,* Jenkins and Masterton 1979). Contrary to the results from the great tit the precision of localization in the pigeon is poorer in the midfrequency range than at lower or higher frequencies. However, in the study of the pigeon only an angle of 120° between the sound sources was used and no attempt was made to determine resolution in azimuth by varying the angle between the sound sources. The percentage of correct choices at one angle was used to estimate the precision of localization.

The mechanisms of sound localization

Different mechanisms have been described which give rise to the directional sensitivity of the avian ear (see reviews by Knudsen 1980; Lewis 1983). Some studies indicate that some bird species may use a pressure gradient system (Coles et al. 1980; Rosowski and Saunders 1980). Other studies show that the barn owl does not use a pressure gradient system over the whole range of its hearing, but that the ears function as two separate pressure receivers in the frequency range in which localization is most accurate (Moiseff and Konishi 1981b). Neurophysiological studies of the barn owl (Takahashi et al. 1984; Sullivan and Konishi 1984) indicate that time and intensity differences between the two ears are processed in two separate neural pathways. In the barn owl, interaural time differences code the azimuth of the sound source whereas interaural intensity differences code the elevation of the sound source (Knudsen and Konishi 1979; Moiseff and Konishi 1981a). Onset time differences play no role in azimuth localization, and azimuth is perceived on the basis of phase differences or, more general, ongoing time differences (Moiseff and Konishi 1981a).

The shape of the function relating the resolution in azimuth to frequency in the great tit could be explained by the ability of birds to code phase differences or ongoing time differences (see Knudsen 1980). In both the redwinged blackbird (*Agelaius phoeniceus*) and the barn owl the amount of phase locking in the nervous system decreases with increasing frequency. In the barn owl, phase locking in nucleus magnocellularis breaks down at 8 to 9 kHz (Sullivan and Konishi 1984), whereas the auditory nerve of the redwinged blackbird shows phase locking with sine waves up to 4 kHz (Sachs et al. 1980). The decrease in resolution in azimuth above 4 kHz could be explained by the decreasing ability of auditory neurons to fire in a fashion correlated with the phase of the signal. With decreasing frequency below 1 kHz phase locking of auditory fibers decreases only slightly in the redwinged blackbird (Sachs et al. 1980). However, with a constant interaural time difference, the difference in the phase angle will decrease with decreasing frequency. If the resolution of phase angle is relatively constant, this means that precision of localization should go down with decreasing frequency. Thus the limits to the coding of phase or ongoing time differences alone could explain the form of the frequency-dependency of MRA. Using the model of Kuhn (1977), which is more appropriate for the great tit with its small interaural distance than the model of Woodworth (1962), which was used for similar calculations for barn owls, (see Knudsen 1980) we calculated the minimum resolvable phase angles from MRAs assuming that the birds would point at one of the speakers when making the decision (Table 2). The results of this calculation nicely parallel findings of the degree of phase locking in the redwinged blackbird (Sachs et al. 1980) which similarly show the best phase locking at 1 kHz with a steep decrease above 1 kHz and a small decrease with frequency below 1 kHz.

Table 2. Minimum resolvable time (MRT) and phase (MRP) differences calculated from the average minimum resolvable angle (MRA) for sine wave stimuli of 300 ms duration (estimated by using the formula given in Kuhn 1977 for $k \cdot a < 1$)

Frequency (Hz)	MRA (deg)	MRP (deg)	MRT (μs)
500	66.5	8.9	49.4
750	38	9.0	33.2
1,000	26	8.5	23.6
2,000	19.5	13.0	18.0
4,000	24	31.6	21.9
6,000	37.5	70.9	32.8
8,000	52	122.3	42.5

Intensity differences between the external ears created by the sound shadow of the head are rather insignificant. Measurements of the sound attenuation by the head of the great tit (made in a free field in an anechoic room using a B&K Type 4170 probe microphone with the opening located at the outside of the birds tympanic membrane) showed a maximum difference between the ipsi- and contralateral ears of less than 4.5 dB at 4 kHz and below. At 8 kHz the maximum difference between the two ears was 7.5 dB. Thus small intensity differences are available for the birds in the high frequency range of their hearing. It cannot be ruled out that the great tit uses these intensity differences, e.g. at 8 kHz. However, as the results show, they do not lead to an accurate localization of tones at high frequencies. It is also unlikely that the frequency dependence of the MRA is explained by differences in suprathreshold stimulation (see above). This result is paralleled by neurophysiological evidence showing that the degree of phase locking in auditory nerve fibers of the redwinged blackbird is independent of SPL once a certain level has been reached (Sachs et al. 1980).

Using the information about the best MRA (20°, average of the two birds at 2 kHz) we can calculate the minimum time difference that the birds must be able to resolve (for the method of calculation in the great tit see low frequency model in Kuhn 1977; for the barn owl see Woodworth 1962; Knudsen 1980). We measured an interaural distance of 12 mm in the great tit which leads to a minimum detectable interaural time difference of 18.0 μs (see also Table 2). The maximum interaural time difference that is available in the great tit is about 54 μs. The great tit's minimum resolvable interaural time difference is larger than that found by Knudsen (1980) in the barn owl (8 μs), but in approximately of the same order to magnitude.

Our results do not allow to conclude whether the great tit is using a sound pressure gradient system or whether the two ears are not acoustically coupled. However, the results of this study would not require other neural mechanisms than those described in the barn owl for the detection of time differences in acoustically uncoupled ears (see Takahashi et al. 1984). To solve the question of the mechanism of the directional sensitivity of the great tit's ear more behavioural experiments are needed in which the intensity differences and the ongoing time differences between the two ears can be varied independently.

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Appendix A:

The percentage of correct choices in relation to frequency and angle between speakers. The tables show averages of at least two sessions

Bird 'Red':

Frequency (Hz)	Angle (deg)									
	13	18	23	26	31	36	46	56	66	75
500								50	55	67
750						57	80		75	
1,000		60		67	78			70		
2,000	50	67	88			73				
4,000				63	78		71	65	85	
6,000					57	65	82	70		
8,000						52	62	68		

Bird 'White':

Frequency (Hz)	Angle (deg)									
	13	18	23	26	31	36	46	56	66	75
500								62	75	
750				57		65	86			
1,000				62	73					
2,000		57	67	72		75		94		
4,000		52		77		69				
6,000						60	75			
8,000							55	70		

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