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Full title: Dynamic adaptations in the echolocation behavior of bats in response to acoustic interference

Short title: Dynamic adaptations to avoid acoustic interference

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Abstract

Animals must extract relevant sensory information out of a multitude of non-informative and sometimes interfering stimuli. For orientation, bats rely on broadcasted calls and they must assign each echo to the corresponding call. When bats orient in acoustically enriched environments, call-echo assignment becomes challenging due to signal interference. Bats often adapt echolocation parameters which potentially improves signal extraction. However, they also adjust echolocation parameters with respect to target distance. To characterize adaptations that are exclusively elicited to minimize signal interference, we tested the effect of acoustic playback on the echolocation behavior of the fruit-eating bat, *Carollia perspicillata*. Hereby, distance-dependent changes were considered by swinging bats in a pendulum and directly measuring the object distance. Acoustic playback evoked different call adjustments in parameters such as bandwidth, peak-frequency, duration and call level. These adaptations were highly dynamic and could vary across individuals, days, trials, and even within trials. Our results demonstrate that bats do not only change one echolocation parameter when orienting in acoustically enriched environments. They rather have a tool-kit of different behavioral adaptations to cope with interfering acoustic stimuli. By dynamically switching between different adaptations, bats can maximize the extraction of their biosonar signals from the background.

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Introduction

Animals extract behaviorally relevant information (signal) out of the mass of stimuli that they are daily confronted with. Echolocation represents a popular example where the broadcaster needs to discriminate its biosonar signals from the signals of adjacent conspecifics (background) (1, 2). For orientation, bats emit biosonar calls and listen to echoes arising from call reflections off surrounding objects (3-5). Spectro-temporal parameters of the echoes inform the animals about position and identity of close-by obstacles (6). To gain spatial information, bats need to assign the echoes to the corresponding calls (2, 7, 8). Call-echo assignment becomes challenging when biosonar signals broadcasted by multiple bats overlap with each other (9, 10). Under these circumstances, bats demonstrate different behavioral adaptations that have been discussed to improve call-echo assignment (7, 11-30). These adaptations range from spectro-temporal changes of the call design, to changes in the call emission pattern. This large variety of adaptations is contrasted by the adaptation that electrolocating fish demonstrate (31, 32). Here, the fishes shift their signal frequency away from each other so that each individual fish occupies a specific frequency. It remains controversial, why bats employ such a large variety of different adaptations when biosonar signals from multiple bats overlap with each other.

The present study answers three different questions that may explain the large variability of adaptations seen in bats: i) is there an individual-specificity in which each individual-bat shows ("prefers") a particular adaptation? ii) is there context dependency? If there is context dependency, then individual bats should show the same adaptations under a constant behavioral context. iii) do bats follow multiple adaptation-strategies in parallel and can they dynamically switch between different adaptations? If this is the case, then bats may be able to switch their adaptations strategies while echolocating.

To answer these questions, individual bats of the species *Carollia perspicillata* were attached on a platform in the mass of a swinging pendulum (Figure 1A). During the forward swing – which mimicked an approach flight – the animals were acoustically stimulated with patterned echolocation calls broadcasted from a speaker that travelled with and was pointing towards the animal (test trial). Call design and emission pattern of test trials were compared with the ones recorded during control

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trials where bats were swung in the absence of playback stimuli. We observed that during test trials, bats changed different echolocation parameters including call level and call frequency composition. These parameters were changed independently from each other indicating that bats could dynamically adjust their biosonar emissions to improve signal discriminability from the playback stimuli. To our surprise, bats dynamically varied the adapted echolocation parameters across days, trials and even within trials. The large variability of adaptations can neither be explained by individual-specificity nor by context dependency because individual bats dynamically switched between adaptation strategies when they were repetitively confronted with the same behavioral context. We argue that each individual bat may profit from a tool-kit of different behavioral adaptations. By dynamically combining different adaptations, bats can create unique and distinguishable echolocation streams which may support correct call-echo assignment in natural scenarios where many bats echolocate in proximity to each other.

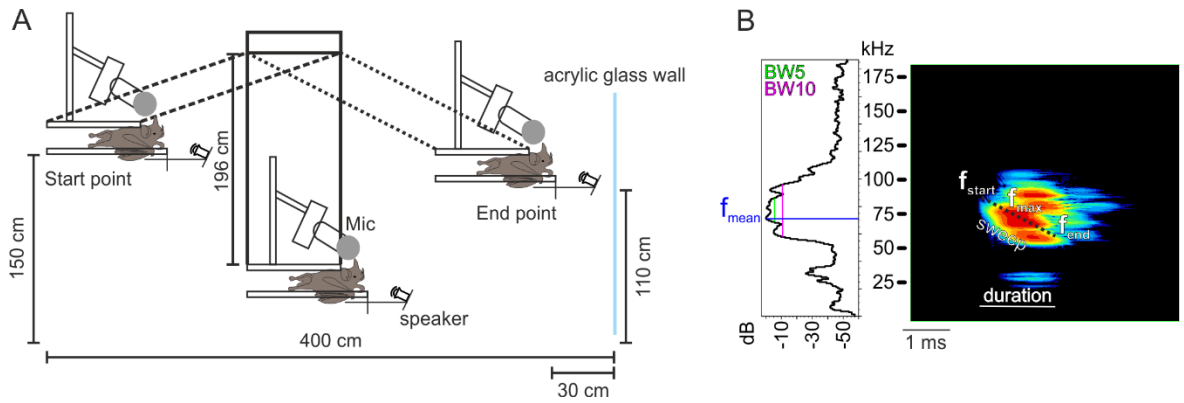

Fig. 1 Behavioral paradigm and representative echolocation call

(A) Schematic side view of the pendulum paradigm. The bat was positioned in the mass of a pendulum and it was swung towards an acrylic glass wall. During the swing the bat emitted echolocation calls which were recorded together with the echoes by an ultrasound microphone (Mic). For test trials, the bat was stimulated with playback echolocation sequences that were composed of a previously recorded echolocation call of the tested bat. The playback stimuli were emitted with a speaker that was pointing towards the bat's head. Microphone and speaker were travelling with the bat and had a constant distance to the bat's head throughout the experiments. (B) Power spectrum (left) and spectrogram (right) of a representative echolocation call recorded with the pendulum paradigm.

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Different call parameters were measured to characterize spectro-temporal call properties. Spectral parameters that were measured included initial (f_{start}), centre (f_{centre}), terminal (f_{end}), mean (f_{mean}), maximum amplitude (f_{max}) peak frequency, and bandwidths at five (BW5) and ten dB (BW10) below the f_{mean}. Call duration represents one of the temporal echolocation parameters that were considered in the analysis. The sweep rate represents the difference of f_{end} and f_{start} ($f_{end} - f_{start}$) divided by the call duration.

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Results

Playback stimuli evoke individual specific changes of the echolocation behavior

To exclude changes in the echolocation behavior associated with the behavioral context – like the animal's flight path –, we repetitively presented the bat with an invariant context. This was achieved by positioning a bat in the mass of a pendulum and swinging the animal towards an acrylic glass wall (Figure 1A). The forward swing mimics an approach flight and the bat broadcasted echolocation calls (Figure 2) during the swing. Echolocation calls and echoes were recorded by an ultrasound sensitive microphone. The microphone was positioned above the animal's head and it was pointed towards the bat's heading direction.

To test how an acoustic interferer effects the echolocation behavior, an echolocation sequence (playback stimulus) was presented from a speaker, during the test trials. The speaker was positioned 20 cm in front and pointing towards the bat's head. The short distance between the speaker and the animal and the relatively tight fixation of the bat's head prevented situations in which the bat could reduce acoustic interference by motor responses like head "waggling" (33). Therefore, in our experimental paradigm, bats rely mostly on changes in call design or emission pattern to minimize signal interference. An echolocation call from the tested bat served as building block for the playback stimulus (see methods for details). Thus, for each animal and experimental day, a new "individualized" playback stimulus was constructed (for stimulus details see methods and Table 1). In total, the echolocation behavior in the presence of playback stimuli was characterized in ten bats (5 females and 5 males).

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Table 1 Call parameters of the playback stimuli. Each animal was stimulated with one of its own echolocation calls to ensure a high probability of acoustic interference. Since some call parameters change across days within an individual, a new jamming stimulus was generated each day. BW = bandwidth; p f = peak frequency

animal (day)	call duration [ms]	intensity rms [dB]	p f start [kHz]	p f end [kHz]	p f centre [kHz]	p f max [kHz]	p f mean [kHz]	BW5 [kHz]	BW10 [kHz]	sweep rate [kHz/ms]
f8 (1)	1,57	80,13	68,8	68,1	67,3	68,1	68,1	4,3	20,5	-0,446
f8 (2)	1,62	83,77	82	82	82,7	82	82	9,5	12,4	0,000
f9 (1)	1,94	87,02	61,5	82	82	82	82,7	27	30	10,567
f9 (2)	1,64	78,8	80,5	90,8	87,1	87,1	87,1	11,7	27,8	6,280
f10 (1)	1,85	85,86	68,1	85,6	82,7	86,4	85,6	16,8	28,5	9,459
f11 (1)	2,34	84,9	74,7	76,9	82	82	82	21,2	29,2	0,940
f11 (2)	2	78,13	69,5	79,8	85,6	86,4	86,4	7,3	13,1	5,150
f12 (1)	1,96	85,6	74,7	79,1	79,1	85,6	79,1	19	24,1	2,245
f12 (2)	2,15	80,25	80,5	82	82,7	87,1	82,7	10,2	27	0,698
m9 (1)	2,04	87,08	79,1	84,2	82,7	71	71	33,6	38,8	2,500
m9 (2)	2,3	83,95	78,3	82,7	82,7	82,7	82,7	5,1	22,7	1,913
m10 (1)	2,21	86,72	71	80,5	80,5	81,2	80,5	5,8	10,2	4,299
m10 (2)	1,62	82,25	67,3	84,9	82	87,1	82,7	9,5	32,9	10,864
m11 (1)	1,68	81,53	70,3	81,2	82	82	82,7	5,1	10,9	6,488
m12 (1)	1,4	83,57	79,1	66,6	61,5	79,1	67,3	23,4	24,9	-8,929
m12 (2)	1,53	77,23	79,8	89,3	87,8	87,8	87,8	4,3	27,8	6,209
m13 (1)	2,64	84,92	72,5	82	82,7	85,6	82,7	7,3	11,7	3,598
m13 (2)	2	76,35	67,3	81,2	80,5	82	80,5	10,9	33,6	6,950

The echolocation behavior recorded in the presence of the playback stimuli was compared with the behavior recorded during an initial control trial in which no stimulus was played back. Since bats adjust the call design and emission pattern with distance to obstacles, we pooled the calls into two groups, namely “long delay calls” and “short delay calls”. Echolocation calls that were broadcasted as the bat was farther than 1 m away from the acrylic glass wall were defined as “long delay calls”. Here, the echoes are delayed by more than 6 ms from the calls. Accordingly, echolocation calls that were emitted when the bat was closer than 1 m from the acrylic glass wall were defined as “short delay calls” (echo delays equal to or shorter than 6 ms).

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When echolocating in the presence of the playback stimulus, bats adapted their echolocation behavior in an individual dependent manner (Table 2). Four bats (female/F11; F12; male/M9; M12) increased the tendency of grouping their call emissions (exemplarily shown for F11 in Figure 2A; Figure 2E). Three bats (F8, M9, M13) increased the call intensity during the test trials (Table 2; Figure 2B). One bat (M11) decreased the call intensity of the "long delay calls". Five bats changed their call duration, two shortened (F8, M11), two lengthened (M9, M10) and one shortened the "short delay calls" and lengthened the "long delay calls" (F9, Figure 3B; Table 2). The adaptation in call duration of F9 demonstrates that some bats differently adapt "long delay calls", and "short delay calls" in response to the playback stimulus. Changes in the call spectra were sometimes prominent (Figure 2C and 2D) but also variable when comparing across animals (Table 2). Calls shown in figure 2C and 2D were recorded as the bat had approximately the same distance from the acrylic glass wall (~2 m). Changes in the call sweep rate varied less across animals. Seven out of eight bats that changed the sweep rate of the calls decreased the sweep rate. In other words, the call frequency changed more slowly during the test than during control trials (Table 2). Changes in the sweep rate could either derive from changes in the frequency range that the call covers or by changing the call duration. Since lowering the sweep rate was not associated with lengthening the call, the sweep rate was mainly affected by changes in the frequency range. Eight animals (80%) changed either the BW5 or BW10 of the calls in the test trials. These changes could either be a BW decrease (shown by 40% of the bats tested; F8, F10, M11, M13) or an increase (shown by 40%; F9, F11, F12, M9). Detailed data from three animals (A: F8; B: F9; C: M9) are plotted as boxplots in figure 3A-3C. For reasons of visualization, only parameters that changed statistically during the test trials are shown. Data from the remaining animals are presented in figure S1. In summary, each animal changed at least one call parameter in response to the playback stimuli. Only, M11 did not change the call design of the short delay calls during the test trials. The changes were shown in different combinations and directions, meaning that there was no single common behavioral adaptation induced by the playback stimuli.

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Table 2 Changes of the call parameters induced by the presence of playback stimuli. + = higher values for test than for control trials (+ = p < 0.05; ++ p < 0.01; +++ p < 0.001); - = lower values for test than for control trials (- = p < 0.05; -- p < 0.01; --- p < 0.001); F = female; M = male; l = long delay calls; p f = peak frequency; s = short delay calls

Animal ID	F8		F9		F10		F11		F12		M9		M10		M11		M12		M13	
Delay	l	s	l	s	l	s	l	s	l	s	l	s	l	s	l	s	l	s	l	s
Interval	++	+++			+	++	--		--				++	+			+		--	
Duration	-		+++	---							+		+		--					
Intensity		+++									++				--					++
P F start			-	---			+		+		---									
Sweep rate		---	---		--	-		-	+		--		--				-			
P F end		+++			+								---	-	---		--			
P F max			---	--	--			-		-			--				++			
P F mean			---	--				--		--										
BW5	---			++								+								
BW10	---			+++	---		++		++			+			--				-	

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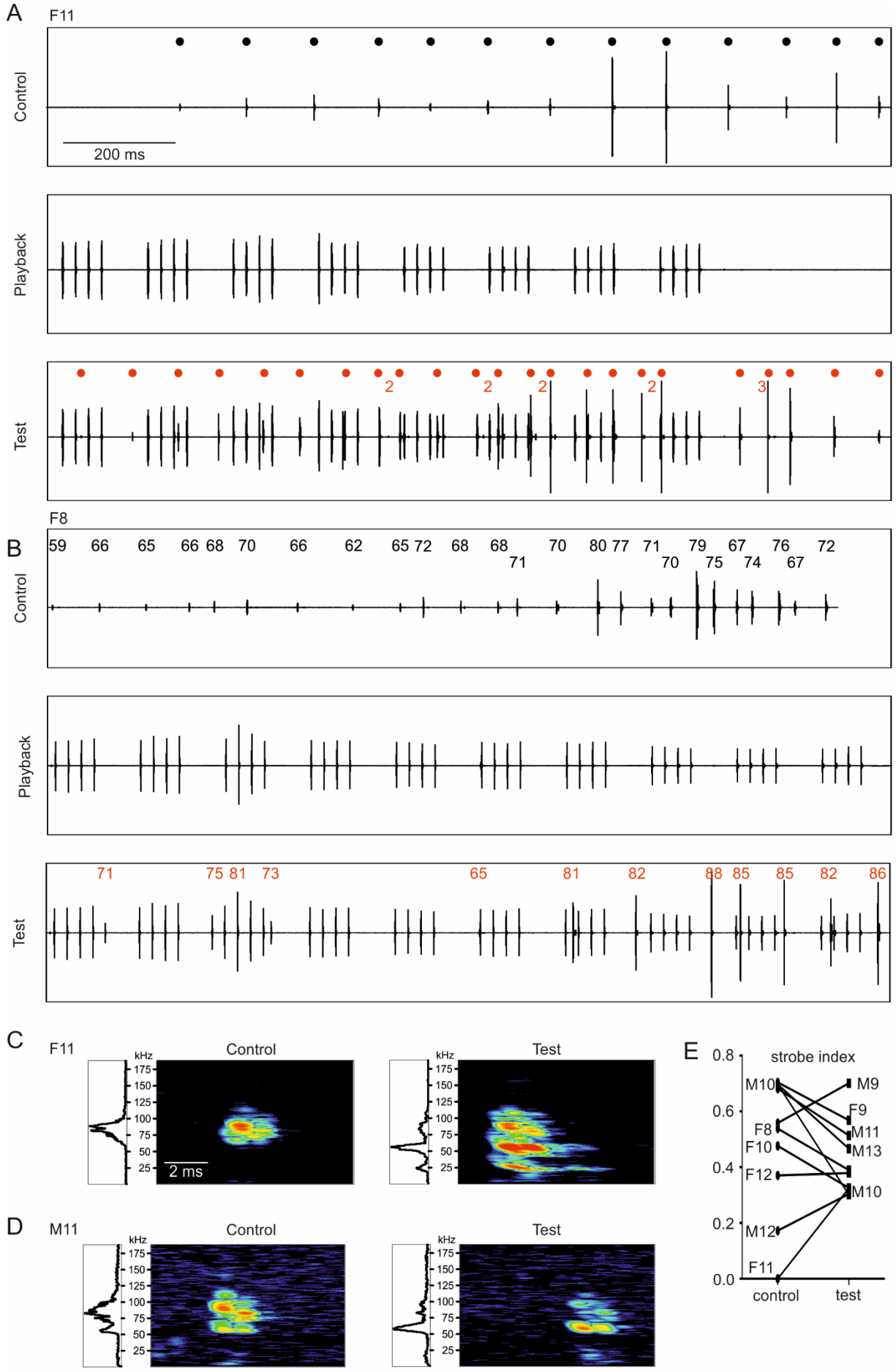

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Fig. 2 Exemplary adaptations of the echolocation behavior in response to the playback stimuli

(A) Oscillograms of one control trial (top), the playback stimulus (middle), and one test trial (bottom) from female 11 (F11). Time points of call emissions are indicated by black or red dots above each oscillogram. During the control trial, the bat did not emit echolocation call groups. During the test trial, the bat grouped some calls into doublets (indicated by the number 2) or triplets (indicated by a "3"). Note that the jamming stimulus was recorded in addition to the echolocation calls of the test trial. Thus, oscillogram deflections without a dot represent signals coming from the playback stimulus. (B) Oscillogram of one control trial (top), the playback stimulus (middle) and one test trial (bottom) from female 8 (F8). In comparison to the calls emitted during the control trials, the call intensity of the calls was increased during the test trials. Numbers above each emitted call indicate the call intensity. (C-D) Power spectra (left) and spectrograms (right) of representative calls emitted during the control and test trial for two individuals (F11, M11). To exclude distance dependent changes in the call design, all four calls were recorded as the bat was ~2 meters away from the acrylic wall. Both bats decreased the bandwidth and mean peak frequency of the calls during the test trials when compared with the calls recorded during the control trials. (E) Tendency of emitting grouped calls (strobe index) under control and test conditions in all bats tested (n=10).

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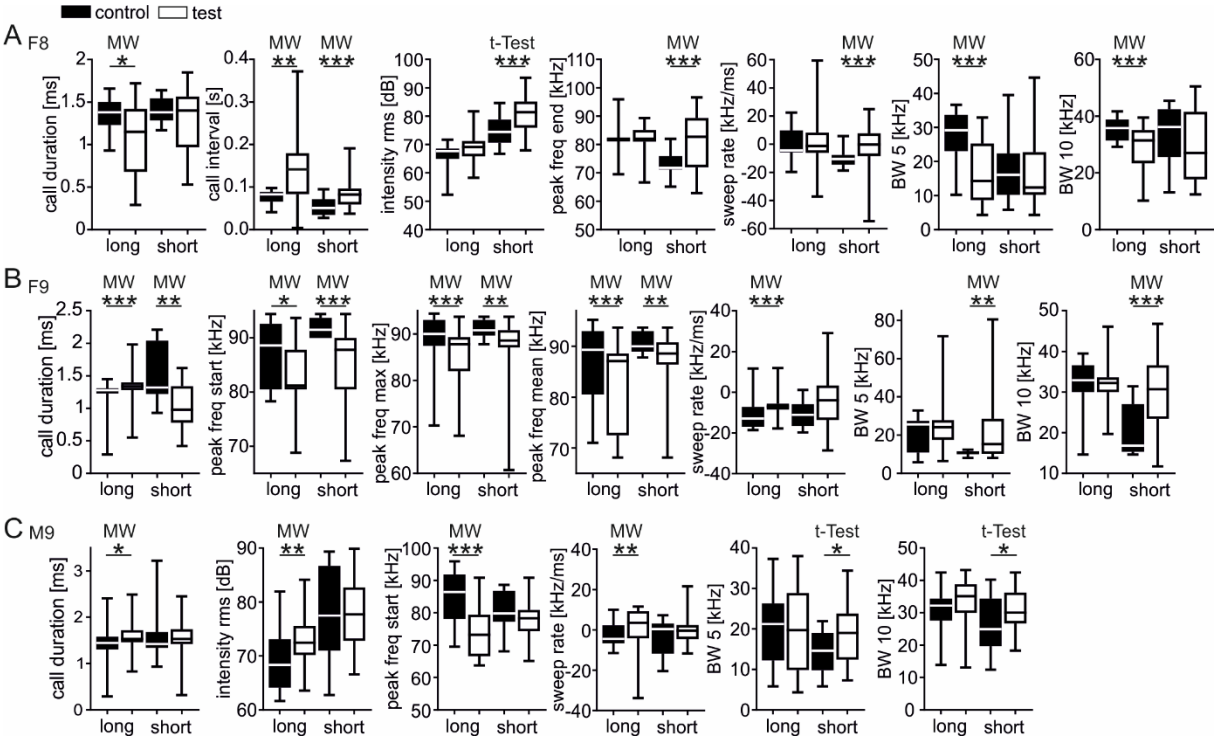

Fig. 3 Individual specific call adaptations in response to playback stimuli

(A-C) Boxplots from three individuals (female 8 = 1st row; female 9 = 2nd row; male 9 = 3rd row) showing the call parameters that the bats changed in response to the playback stimulus. Calls recorded under control conditions (absence of playback stimulus) are indicated by black boxplots, while white boxplots represent calls recorded under test conditions (presence of playback stimulus). Echolocation calls that are followed by an echo within 6 ms were grouped into "short delay calls". Echoes following a call by more than 6 ms were grouped into "long delay calls". Note that each bat changed different call parameters under test conditions. MW = mann-whitney test; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.0001$.

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Bats vary adaptation strategies across trials and days

To test for behavioral differences across days, eight bats were tested in two consecutive days. To do a trial-by-trial analysis and to gather enough data points for statistical analysis, we pooled data from long and short delay calls. During test trials, bats emitted slightly less calls than during the control trials (median n of calls: 16.5 control and 13 test; Mann-Whitney test: $p = 0.036$). By comparing the call parameters from F9 across days (Figure 4; Table 3) it becomes clear, that adjustments of call duration, starting, maximum, and mean peak frequency occurred exclusively on the first day (Figure 4). During the second test day, F9 mainly changed call intensity, terminal peak frequency, BW or sweep rate. Adaptation strategies did not only vary across days but also across subsequent trials during the same test day (Table 3). For example, F9 decreased the call sweep rate in three (trial 2, 3, and 4) out of five trials of the first test day (Figure 4, bottommost right panel). Changes of other call parameters varied less dramatically across trials of the same day. In all trials of the first day, F9 decreased its starting, maximum, and mean peak frequency. When comparing call adjustments across all trials, it becomes clear that all animals, except F11 for trials 6, 7, 8, and 12, changed at least one echolocation parameter, when confronted with the playback stimuli (Table 3). For detailed data from the remaining nine animals see figure S2-S10.

Table 3 Changes of the call parameters across trials. + = higher values for test than for control trials (+ = $p < 0.05$; ++ $p < 0.01$; +++ $p < 0.001$); - = lower values for test than for control trials (- = $p < 0.05$; -- $p < 0.01$; --- $p < 0.001$); F = female; M = male; l = long delay calls; p f = peak frequency; s = short delay calls

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Animal ID	Trial (Day)	Intensity	Duration	Interval	Sweep rate	P F start	P F end	P F max	P F mean	BW5	BW10
F8	1 (1st)	++	---	+++	-		+++		+	--	---
	2 (1st)			+						-	
	3 (1st)			++						---	---
	4 (2nd)	+++			-		++				
	5 (2nd)										
	6 (2nd)			++							
F9	1 (1st)					--		-	--		
	2 (1st)	-	+		-	---		--	-		+
	3 (1st)		+		-	--	+	--	--		
	4 (1st)		++		-	---		---	---	++	++
	5 (1st)		+			---	--	--	--		
	6 (2nd)	+++					+++				
	7 (2nd)			++	---					-	-
	8 (2nd)	--		++	--		+++				
F10	1 (1st)	++	+	+	---		+	-			
	2 (1st)	++	+++		--			---	-		
	3 (1st)				--	--		-		-	
	4 (1st)	-		+	--	-	+	--	-		
	5 (1st)				-		++				
	6 (1st)			++							
F11	1 (1st)	+		---		-		--			
	2 (1st)		---								
	3 (1st)	+		--			--	--	---		
	4 (1st)			-				---	-		
	5 (2nd)			--						++	
	6 (2nd)										
	7 (2nd)										
	8 (2nd)										
	9 (2nd)	-		--						+	
	10 (2nd)	-									
	11 (2nd)			-							
	12 (2nd)										
F12	1 (1st)		+	+							
	2 (1st)			+++	--	-					+
	3 (1st)						-				
	4 (2nd)			---	+++	+++	--			+++	+++
	5 (2nd)			---	+++	+	--			++	++
	6 (2nd)			-	++	+	--			++	++
M9	1 (1st)	++	++		--	---					
	2 (1st)		+	++		--					
	3 (1st)	+++						++	++	---	
	4 (1st)				--	---					
	5 (2nd)			---	--	---				++	+++
	6 (2nd)									++	++
	7 (2nd)							-	-	+	+
M10	1 (1st)					-		--	-		
	2 (1st)					---		---		-	
	3 (2nd)						--				
	4 (2nd)	+++	+++	++							
	5 (2nd)		+++	+++			-				
	6 (2nd)		+++	+	+++	+++	--				
M11	1 (1st)	---					---	--	---		
	2 (1st)						--				-
	3 (1st)	-							--		
	4 (1st)	---	-					+		-	-
M12	1 (1st)						-				
	2 (1st)			+++	+					---	---
	3 (1st)			+	-						
	4 (1st)										
	5 (2nd)				+						
	6 (2nd)				++						
M13	1 (1st)	+++		---	---	+++					
	2 (1st)		+		-	+					
	3 (1st)		-	--	---	+++					
	4 (2nd)				---	---			-	--	
	5 (2nd)			--	---	-			-	-	
	6 (2nd)				-	---			-	--	--
	7 (2nd)	+	---	+++			+++	+	+		--
	8 (2nd)				--	-	++		-	-	

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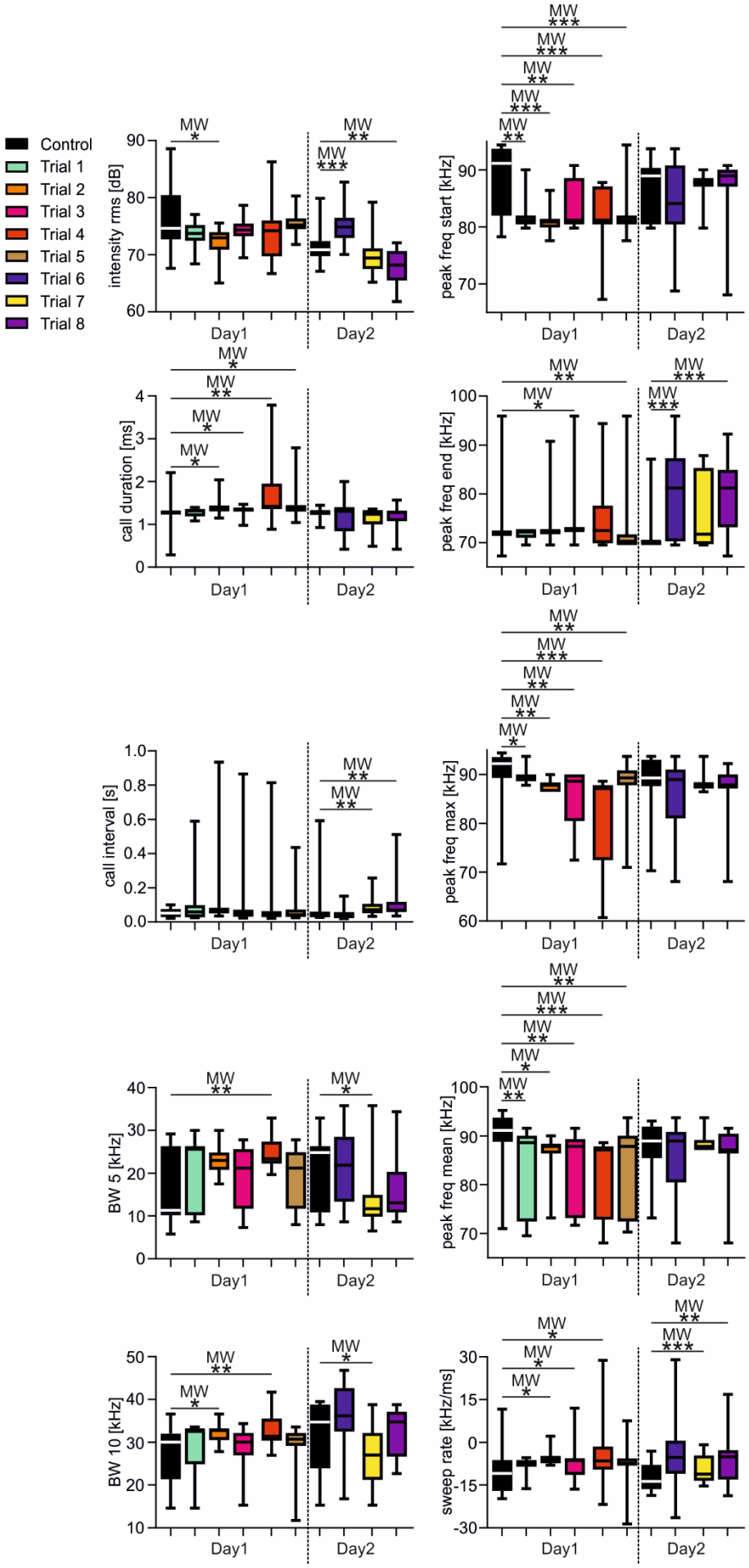

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Fig.4 Bats switch adaptation strategies across trials and days

Call parameters are shown as boxplots for each trial (8 test trials and 2 control trials) across two days from one bat. For visualization purposes, each trial is color coded. Since some call parameters change in a day dependent manner and independently from the behavioral context (compare intensity values of the two control trials), it was necessary to compare the test trials with the control trial of the corresponding day. Note that the bat changes some call parameters only at day 1 (e.g. peak freq start; call duration; peak freq max) and not at day 2. MW = mann-whitney test; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.0001$

Bats dynamically switch adaptation strategies within trials

After demonstrating that the bats can change adaptation strategies across days and trials, we were interested in assessing if the bats also vary the strategies within trials. Therefore, we directly compared the emitted call parameters with the call parameters of the playback stimuli. The upper color maps in figure 5A and 5B exemplarily show the relative differences between the call parameters and the playback parameters (note that the playback stimuli consisted in repetitions of the same call) for two trials coming from two different bats (M9 and F12). The calls are indicated as columns where the leftmost column represents the call with the longest echo delay and the rightmost column represents the call with the shortest delay of the trial. Each line represents the relative difference of an emitted call and the call of the playback stimulus with respect to a specific parameter. The relative difference was calculated by subtracting the playback parameters from the call parameters. This difference was normalized against its absolute maximal difference of the considered parameter. So, for each parameter, there was at least one maximal difference represented by a value of either +1 (red cell = parameter of the call is higher than the one of the playback) or -1 (blue cell = parameter of the call is lower than the one of the playback). The darker the red and the darker the blue patches are, the more positive and negative are the call parameters in comparison to the playback stimulus, respectively. Looking at the trial from M9, it becomes clear that the bat initially emitted calls with lower starting peak frequencies (peak start) and call intensities than the playback stimulus. At an echo delay of about

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3 ms (between the 12th and 13th call, white dashed line in Fig. 5A), the bat abruptly switched the strategy and increased the maximum and mean peak frequency and decreased the BW of subsequent calls. To visualize abrupt changes, we calculated the differences of the parameters of subsequent calls and plotted the values in the bottom color maps shown in figure 5A and 5B. We defined an abrupt change when the considered parameter varies by more than 50% between subsequent calls. For example, according to figure 5A, the terminal (peak end), maximum peak frequency (peak max), and the sweep rate of call 13, are more than 50% higher than the ones of call 12. This is indicated by red cells at the corresponding column (white dashed line) in the lower color map of figure 5A.

Sudden changes in call design were also visible in other trials, like the one of F12 shown in figure 5B. Here, the abrupt changes occurred at around 2.5 ms echo delay (white dashed line) by decreasing the call intensity, starting (peak start), and terminal frequency (peak end) while the maximum peak frequency (peak max) as well as the call bandwidths (BW 5 and BW10) were abruptly increased. When comparing all analyzed calls (889 calls from 69 trials and 10 animals), about three quarters of the calls (74.24%) show sudden changes in at least one call parameter (Figure 5C). About half of the calls (50.84%) showed abrupt changes in more than one call parameter. We were interested in knowing if the bats predominantly change particular call parameters or if all parameters were equally often changed during the trials. The pie chart plotted in figure 5D shows that the bats do not focus on changing a particular call parameter but they rather change most of the parameters with equal probability. Only call intensity and call duration were least (7.24%) abruptly changed within the trials. Abrupt changes were more often detected for spectral parameters.

When taking a closer look on the pattern of call changes over subsequent calls (color maps at the bottom of figure 5B), it becomes obvious that the bats sometimes change the call parameters in an alternating manner. During the second half of the trial, the bat alternates between high and low terminal (peak end) and maximum peak frequencies (peak max), indicated by gray and black arrowheads, respectively. Before analyzing the alternations in more detail, we wondered how often the bats change a particular call parameter during the trial. The bar plot in figure 5E shows that the bats changed spectral parameters more often per trial (mean of peak start = 2.85 ± 2.39; mean of peak end = 2.96 ± 1.59; mean of peak max = 2.8 ± 2.29; mean of BW5 = 2.84 ± 1.75; mean of BW10 = 3.26 ±

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2.39; mean of sweep rate = 2.51 ± 1.82) than the call intensity (mean = 1.91 ± 1.57) and the call duration (mean = 1.73 ± 1.46) ($p < 10^{-5}$ Kruskal-Wallis test). Since spectral parameters varied more often during the trials, alternations occurred with a higher probability in spectral than in non-spectral (call intensity and call duration) parameters (Figure 5F). Across the spectral parameters, the probability of alternations did not differ significantly ($p = 0.91$ Kruskal-Wallis test), indicating that alternations could equally occur in each of the analyzed call parameters.

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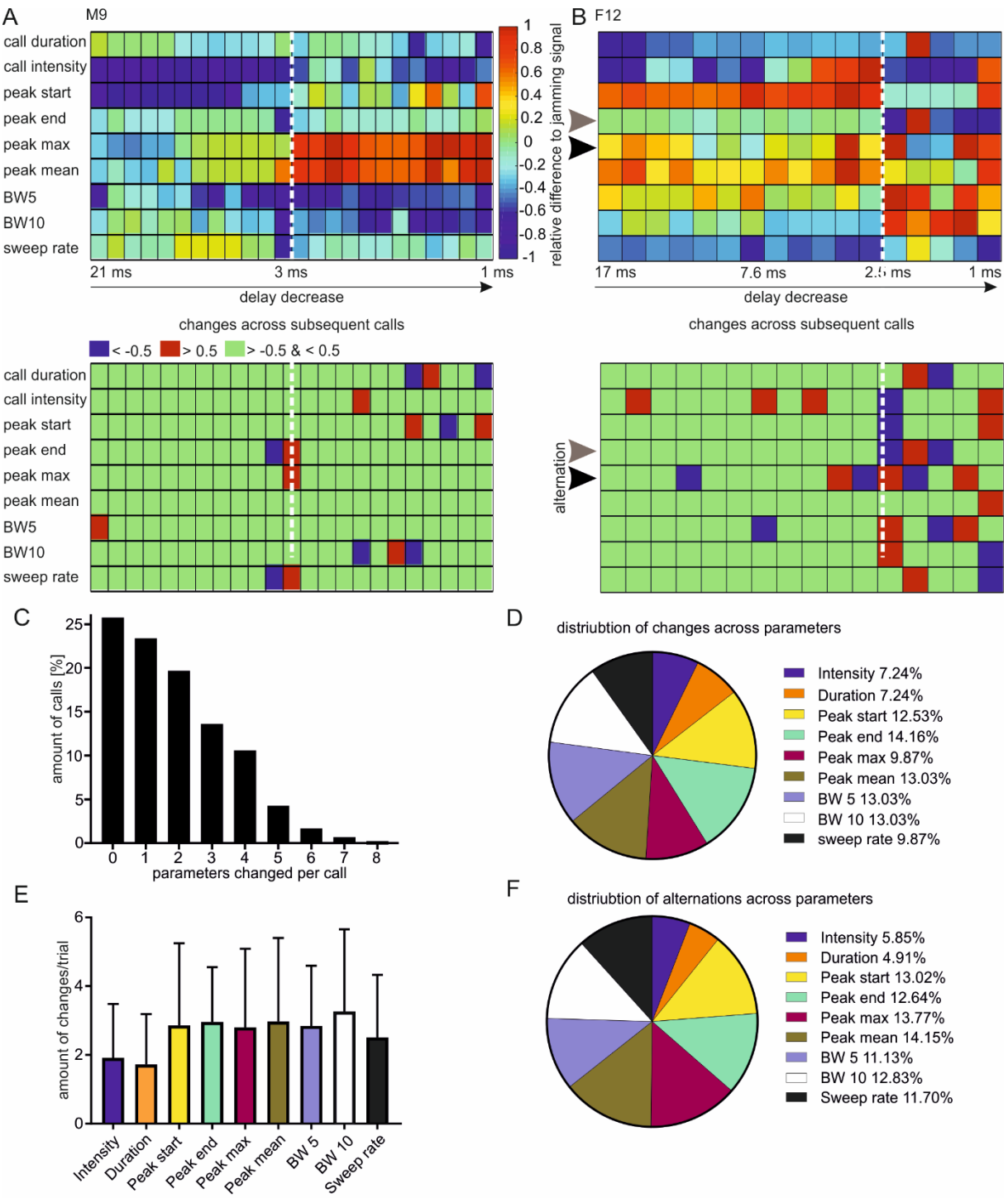

Fig.5 Bats switch adaptation strategies within trials

(A-B upper graphs) Color maps from two representative test trials (M9 in (A) and F12 in (B)) illustrating the differences between the calls and the playback stimuli in a call-wise manner. Along the x-axis, the calls are ordered according to their emission order during the trial. The echo delay value from some call-echo pairs are indicated in the x-axis. Along the y-axis, normalized call parameter differences are color coded. The differences were normalized to their absolute maximum value at the

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corresponding parameter for the specific trial. The differences of the following call parameters were considered: call duration, call intensity, peak frequency at the beginning, end and maximum of the call, mean peak frequency of the call, bandwidth 5 (BW5), bandwidth 10 (BW10), and sweep rate. In some trials a clear transition of the adaptation strategies can be detected (white vertical dashed lines). In some cases, the bats alternate call values, as exemplarily shown for F12 for the terminal and maximum peak frequency indicated by a gray and black arrowhead, respectively. (A-B lower graphs) Colormaps illustrating abrupt changes of call parameters across subsequent calls. Abrupt changes occurred when a call parameter between two consecutive calls varied by more than 50% (blue and red cells represent reductions or increases of the corresponding call parameter). Changes of the call parameters that are below 50% were not abrupt enough to be defined as a change (green cells). Transitions between adaptation strategies and alternations between call parameter values can more easily be seen in the lower colormaps. (C) Histogram showing the amount of parameters that are abruptly changed per call for all investigated calls (n = 889). Note that almost 75% of the calls show at least one abrupt change. (D) Pie chart illustrating the distribution of abrupt changes over the call parameters. Abrupt changes did mainly occur in the call spectrum and less often for the intensity or duration. (E) The mean values of the amount of changes per trial are plotted against the call parameter. Spectral parameters did vary more often across trials than non-spectral ones (duration and intensity). (F) Pie chart representing the relative distribution of alternations across different call parameters.

Discussion

The present study characterizes adaptations of the echolocation behavior of the fruit-eating bat *C. perspicillata* when the bat echolocated in the presence of playback stimuli. These playback stimuli potentially interfered with the bat's biosonar signals making signal extraction for the bat challenging. Adjustments of the echolocation behavior do not only occur in the presence of acoustic interferer but also when the bats approach obstacles or transiting between different environments. Thus, it is crucial to test the influence of acoustic interference on the echolocation behavior under an invariant

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behavioral context. The pendulum paradigm fulfills these requirements because the behavioral scenario of an approach flight can be repetitively mimicked.

Our results demonstrate that *C. perspicillata* varies different call parameters and the emission pattern when echolocating in the presence of the playback stimuli. Instead of relying on one adaptation strategy, the bats use different adaptation strategies (Table 2 and Figure 3). To our surprise, bats could switch between different strategies across (Table 3, Figure 4) and even within trials (Figure 5). This makes the adaptation of the echolocation behavior in the presence of acoustic interferers highly dynamic and unique across different individuals and time points. With this flexibility, the animals create unique echolocation streams that can be distinguished from interfering signals.

Coping with signal interference

Signal interference is a problem that every animal and sensory system must cope with. Each species must extract ethologically relevant stimuli out of the mass of stimuli that it encounters daily. The more the signal resembles the background, the more challenging is signal extraction. To facilitate signal processing, animals employ different behavioral adaptations (1, 2) like orienting the sensory organs towards the signal (34-40). Bats increase head waggles and the inter-pinna distance when orienting under challenging conditions (33). This putatively improves the localization of the echo source (33). Additionally, adjustments of the pinna's shape and orientation may increase the directionality of hearing (41). In the present study, head waggles were avoided by tightly positioning the bats on a platform in the pendulum mass. Moreover, by adjusting the jamming source close to the animals' head motor responses may barely facilitate signal extraction under these conditions.

For some behaviors - like communication, electrolocation, or echolocation - the animals produce the signals which allows them to directly control the signal's discriminability from the background. The latter becomes clear when considering a cocktail party (42). In a noisy environment, we can focus on our communication partner by carefully listening to him/her and improve the signal-to-noise ratio by increasing our voice intensity ((22, 43), an adaptation known as the Lombard-effect). Signal extraction may not only be improved by changing the signal intensity but also by reducing the spectral overlap between signal and background. This adaptation has originally been described in

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electrolocating fish (31, 32). When encountering animals whose signal frequencies overlap with the fish's own signal frequency, the animals shift the signal frequencies away from each other. This behavior has been circumscribed as jamming avoidance response (JAR) and it reduces the signal interference with signals coming from conspecifics. JAR has also been demonstrated in different bat species ((7, 11-14, 16-20) and present study). However, in contrast to weakly electric fish - that try to occupy an individual specific frequency band - bats dynamically adjust their call spectra in various situations. Bats adjust their calls when approaching an obstacle or when transiting between different environments (24, 26, 28, 44-54). Since frequency adjustments occur frequently and under various conditions, an adaptation that purely focuses on a JAR may not be efficient enough to orient collision-free in the presence of signal interferer. Note that some studies reported that bats do not shift their frequency in response to acoustic interference (55) or that the frequency shifts are purely correlated with the object distance (15). Since we compared echolocation calls that were emitted roughly at similar distances between the bat and the object, we can exclude that the frequency shifts, presented in our study reflect distance dependent changes of the call design.

Repertoire of behavioral adaptations in response to interfering signals and their possible neural correlates

Fine adjustments of the call design and/or emission pattern may sufficiently simplify the discrimination between relevant biosonar signals and the playback stimulus. For example, adjustments in call bandwidth could minimize acoustic interference, since decreasing the bandwidth restricts the population of neurons that process echo information. On the contrary, increasing the call bandwidth activates auditory neurons that are not responding to the playback stimulus. Thus, neurons that do not respond to the playback stimulus could "selectively" process frequencies that are unique to the biosonar signals but are not present in the interferers.

Bats also increase the signal-to-noise ratio by increasing call intensity (18-22, 24, 56). Unexpectedly, in the present study, sometimes the bats decreased their call intensity when they echolocated in the presence of interfering signals. Although, this decreases the signal-to-noise ratio, it could be still useful from a neuronal perspective. Many auditory neurons respond more strongly and

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selectively to low than to high sound levels resulting into non-monotonic intensity rate functions (57-61). This makes some neurons highly selective to faint biosonar signals while being insensitive to intense background stimuli.

Some studies reported that bats lengthen their calls when flying in noisy environments (20, 21, 23, 56, 62). In the present study, we observed that some bats lengthened, and others shortened their calls. Both adaptations putatively minimize acoustic interference. Shortening the calls decreases the chance of a temporal overlap between signal and background. Lengthening the calls increases the risk of temporal overlap but it could still be useful if only a small portion of the echo needs to be detected to gain enough spatial information.

Not only the call design, but also the emission pattern is adjusted to reduce or even avoid signal interference. Some bat species alternate between two call designs that differ in the frequency spectrum (25-27). This adaptation allows a higher call rate by emitting a pair of calls before receiving an echo from the first call of the pair (63, 64). The arising echoes differ in their frequency spectra which makes their discrimination feasible (28). Alternation of spectral call parameters have also been observed in the present study. However, these alternations occurred occasionally and not throughout the entire trial. Thus, the behavioral importance of alternating call parameters in *C. perspicillata* needs to be further assessed.

Some bats reduce their call rate (29) and temporally even cease to emit calls (30). This adaptation may be beneficial if the bats eavesdrop on echolocation signals from conspecifics and use the signals for orientation (65-68). Although, *C. perspicillata* emitted less calls during the test than during the control trials, we cannot assess with the pendulum paradigm if the bats eavesdropped on the echolocation signals coming from the speaker.

Lastly, some individuals increase their rate of grouping calls when orienting in noisy environments ((22, 26, 69, 70) and present study). Grouping the calls may improve echolocation performance in different ways. First, a defined periodicity of echo arrivals allows echo identification based on prediction (8, 33, 44, 49). Second, grouping the calls could create an information redundancy allowing the bats to rely only on a small portion of the call group (69).

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Bats show different combinations of adaptations when echolocating in the presence of acoustic interferer

Instead of relying on one of the behavioral adaptations, our results indicate that bats have a toolkit of different combinable adaptations to potentially minimize acoustic interference (19, 22). The dynamics and variability of the strategies are important factors for explaining the high diversity of behavioral adaptations reported in former studies. We must keep in mind that the discriminability of a signal from the background is dictated by the difference of the physical parameters between the signal and the background. Hereby, it is unimportant which physical parameter is adjusted, as long as the signal has its own physical identity providing a high discriminability from the background. For call-echo assignment, it has been discussed that bats keep an "internal copy" of their broadcasted calls and compare the copy with the received echoes (4). This idea goes in line with behavioral results showing that correct call-echo assignment is decreased when spectro-temporal properties of the echo are manipulated (71-73) or when echoes are replaced by noise bursts (74). Because of missing behavioral data in *C. perspicillata*, it remains speculative to what extent the echolocation calls need to differ from the playback stimuli so that bats can still extract the signals. When comparing different call parameters against the playback stimuli used in the present study, it becomes clear that some echolocation calls emitted during the trials differed pronouncedly from the playback stimuli (Figure S11). Although having no detection thresholds from *C. perspicillata*, there are some behavioral and electrophysiological results from other bat species that use similar call designs as *C. perspicillata* (*Eptesicus fuscus*: (75, 76); *Tadarida brasilienisis*: (77), *Antrozous pallidus* (78)). Based on these studies, we may speculate that *C. perspicillata* can extract signals that differ for one of the following parameters by more than 10 dB in intensity, by at least 0.7 ms in duration, by more than 5 kHz in the peak frequency, by more than 12 kHz in the bandwidth, and by more than 6 kHz in the sweep rate from the playback stimuli. By considering these thresholds, *C. perspicillata* may be able to extract about 94% of the calls from the playback stimuli. Only 5.96% of the calls did not reach our hypothetical detection thresholds for any of the investigated call parameters. Note that the emission pattern could not be considered for a call-by-call analysis. Thus, it is still probable that the remaining 5.96% of the call's echoes could be detected by the fact of anticipation of the echo pattern. This could

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be accomplished by grouping the calls (Figure 2A, (69)). In the present study, four out of ten bats increased the tendency of grouping the calls (Figure 3D). Electrophysiologically, we showed that auditory neurons of the midbrain and the cortex of *C. perspicillata* can still extract relevant spatial information when the bats are stimulated by high call rates can still be processed by (69, 79-81).

In summary, our results emphasize that bats may profit not only from one but rather from many behavioral adaptations to reduce the risk of signal interference. The bats dynamically adjust and switch their adaptation strategies across subsequent calls. Future studies investigating jamming avoidance behavior should carefully take into account the vast repertoire of behavioral adaptations that animals may use to escape sensory interference.

Materials and methods

Animals

Experiments were conducted in 10 bats (5 females and 5 males) of the species *Carollia perspicillata*. The bats were bred and kept in a colony at the Institute for Cell Biology and Neuroscience (Goethe-University Frankfurt). The experiments comply with all current German laws on animal experimentation and they are in accordance with the Declaration of Helsinki. All experimental protocols were approved by the Regierungspräsidium Darmstadt (experimental permit # #FU-1126).

Pendulum paradigm and audio recordings

For controlling the behavioral context, the bats were positioned in the mass of a pendulum and they were repetitively swung towards an acrylic glass wall (50 × 150 cm, Figure 1A) (80-83). The smooth surface of the acrylic glass wall ensured call reflection without producing prominent spectral notches in the echoes. During the swing, the bats emitted echolocation sequences that were recorded, together with their echoes, by an ultrasound sensitive microphone (CM16/CMPA, Avisoft Bioacoustics, Germany). The microphone had a sensitivity of 50 mV/Pa and an input-referred self-noise level of 18 dB SPL, as reported by the manufacturer. The frequency response curve was flat (± 3 dB, as specified by the manufacturer) in the range from 30-130 kHz. The microphone travelled with the mass of the pendulum and it was medially positioned above the bat's head. The membrane of the microphone was

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adjusted as closely as possible to the bat's ears (~ 4 cm). The microphone was connected to a sound acquisition system (Ultra Sound Gate 116Hm mobile recording interface, + Recorder Software, Avisoft Bioacoustics, Germany). To test the influence of acoustic interference on the echolocation behavior, bats were swung in the pendulum while they were acoustically stimulated with a playback stimulus (see below). We compared the echolocation behavior recorded in the absence of playback stimuli (control trials) with the one shown in the presence of playback (test trials). Our reasoning was that since the behavioral context was invariant during control and test trials, except for the occurrence of the playback stimulus, we could correlate adaptations in the echolocation behavior with the presence/absence of the playback.

Initially, the bats were tested in a control trial followed by test trials where an echolocation call recorded during the forward swing of the control trial was selected to construct an individual-specific playback stimulus. The playback stimulus consists of an echolocation call that was presented as quartets with a call interval of 25 ms and the quartets were repeated with an inter-quartet interval between 130 and 150 ms. The intensity of the playback stimulus was adjusted to rms values (of single calls) between 80 and 90 dB SPL for all animals. We reasoned that using an echolocation call of the tested animal as playback stimulus could be the most effective way of achieving acoustic jamming. The latter is supported by the fact that subtle inter-individual differences in call design could be detected by the animals, which reduces signal interference (84). During test trials, the playback stimulus was presented from an ultrasound speaker (MK 103.1 Microtech Gefell Microphone Capsule used as speaker) that was flat in the range from 5 to 120 kHz (mean level in calibration curve 84 ± 3 dB SPL, the speaker's protection cap was replaced with a self-made cap to prevent energy loss at high frequencies). The speaker was placed pointing towards the bat's head at a distance of 20 cm. Eight out of ten bats were tested on two consecutive days, but with different, day-specific, playback stimuli. The latter should exclude that changes of the call design that may occur across days might bias our analysis. An overview of the call parameters used for constructing playback stimuli is shown in Table 1.

Analyzed echolocation parameters

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Since the time pattern of the playback stimuli was kept constant, we could discriminate between biosonar signals emitted by the bat and the playback stimuli. The call emissions were manually tagged in the software Avisoft SAS Lab Pro (Avisoft Bioacoustics, Germany). To characterize the echolocation calls, different call parameters were measured in Avisoft SAS Lab Pro. The present study focused on call level, call duration, peak frequency at different call time points (start, end, maximum amplitude, and mean), bandwidth 5 (BW5), BW10, and sweep rate (Figure 1B). Regarding the call spectra, we considered only the peak frequencies (frequencies with the maximum energy at particular time points of the call or on average of a call) because the peak frequencies might be the most salient spectral information of the echo that would suffer least from reflective attenuation. BW5 and BW10 represents frequency ranges at 5 and 10 dB below the mean peak frequency (Figure 1B). The sweep rate was calculated by subtracting the initial peak frequency from the terminal peak frequency and by dividing by the call duration.

The call emission pattern was characterized by measuring the call intervals and the tendency of grouping the calls. Analysis of the call groups was done using custom-written scripts in Matlab 2014 (MathWorks, USA). Call groups were defined according to two criteria (47, 69). An “island criterion” defines call groups that are isolated in time. An isolation was fulfilled as soon as the preceding and following call intervals of a call group were 20% longer than the call intervals within call groups. If the “island criterion” is fulfilled, a second criterion, the so called “stability criterion”, defines the size of the call groups indicated by the number of calls belonging to a group. The stability criterion is fulfilled if the call intervals within call groups are stable with a 5% tolerance. Next, we calculated a strobe index for each animal and each condition (control and test trial). The strobe index represents the relative amount of calls that were emitted as groups.

Statistics

For statistical analysis, we used the software GraphPad Prism 7 (GraphPad Software, USA; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.0001$). Since the echolocation behavior in two conditions (control versus test trials) were compared to each other, statistical tests were either based on nonparametric Mann-

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Whitney tests (MW; in case of non-Gaussian distribution) or on parametric t-Tests (in case of Gaussian distribution).

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