

Representation of Perceptual Dimensions of Insect Prey During Terminal Pursuit by Echolocating Bats

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Abstract. The echolocating big brown bat, *Eptesicus fuscus*, broadcasts brief frequency-modulated (FM) ultrasonic sounds and perceives objects from echoes of these sounds returning to its ears. *Eptesicus* is an insectivorous species that uses sonar to locate and track flying prey. Although the bat normally hunts in open areas, it nevertheless is capable of chasing insects into cluttered environments such as vegetation, where it completes interceptions in much the same manner as in the open except that it has to avoid the obstacles as well as catch the insect. During pursuit, the bat shortens its sonar signals and increases their rate of emission as it closes in to seize the target, and it keeps its head pointed at the insect throughout the maneuver. In the terminal stage of interception, the bat makes rapid adjustments in its flight-path and body posture to capture the insect, and these reactions occur whether the bat is pursuing its prey in the open or close to obstacles such as vegetation. Insects can be distinguished from other objects by the spectrum and phase of their echoes, and *Eptesicus* is very good at discriminating these acoustic features. To identify the insect in the open, but especially to distinguish which object is the insect in clutter, the bat must have some means for representing these features throughout the interception maneuver. Moreover, continuity for perception of these features is necessary to keep track of the prey in complex surroundings, so the nature of the auditory representations for the spectrum and phase of echoes has to be conserved across the approach, tracking, and terminal stages. The first problem is that representation of changes

in the phase of echoes requires neural responses in the bat's auditory system to have temporal precision in the microsecond range, which seems implausible from conventional single-unit studies in the bat's inferior colliculus, where the temporal jitter of responses typically is hundreds of microseconds. Another problem is that echoes do not explicitly evoke neural responses in the inferior colliculus distinct from responses evoked by the broadcast during the terminal stage because the delay of echoes is too short for responsiveness to recover from the emissions. In contrast, each emission and each echo evokes its own responses during the approach and tracking stages of pursuit. How does the bat consistently represent the phase of echoes in spite of these evident limitations in neural responses? Local multiunit responses recorded from the inferior colliculus of *Eptesicus* reveal a novel format for encoding the phase of echoes at all stages of interception. Changes in echo phase (0° or 180°) produce shifts in the latency of responses to the emission by hundreds of microseconds, an unexpected finding that demonstrates the existence of expanded time scales in neural responses representing the target at all stages of pursuit.

Introduction

Echolocating bats broadcast ultrasonic sounds and perceive objects from echoes that return to their ears (Griffin, 1958; Novick, 1977; Popper and Fay, 1995). Most species of echolocating bats are insectivorous and use their sonar to detect and locate flying prey as well as to locate and avoid obstacles (Fenton, 1995; Griffin, 1958; Neuweiler, 1990; Schnitzler and Henson, 1980; Simmons *et al.*, 1995a). During pursuit of prey, the bat transmits a series of sounds and perceives the insect and

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other objects as a series of representations or images that guide the interception maneuver to a successful capture. As the bat approaches the target, the delay of echoes shortens from one broadcast to the next. During the terminal stage of the interception maneuver, the bat approaches so close to the insect that the delay of echoes is too short for the auditory system to register each echo as a distinct sound arriving just after the broadcast. Nevertheless, the bat orients to the insect and reaches out with its tail membrane to seize the target in midair, exhibiting knowledge of the insect's location in the final moments before capture. How does the bat perceive the insect and distinguish it from other objects during the terminal stage of pursuit if echoes arrive too soon after the broadcasts to directly evoke neural responses on their own? We describe how the bat's auditory system represents echo phase—one of several parameters of echoes related to the target's shape and one that must be perceived to distinguish the insect from other objects. During the terminal stage, even though individual echoes from the insect do not seem to evoke neural discharges distinct from those discharges specifically evoked by the broadcast sounds, the pattern of responses evoked by broadcasts and echoes together encodes the phase of echoes in a stable format throughout the interception maneuver.

Interception of Flying Insects

The pursuit maneuver

Figure 1 shows the interception of a flying insect by the big brown bat, *Eptesicus fuscus*. This common North American bat uses its sonar to locate and track such prey as flying moths, mayflies, or beetles (Kurta and Baker, 1990). The big brown bat usually hunts for insects in open spaces several meters from obstacles such as trees, buildings, or the ground. Under quiet conditions, *Eptesicus* can detect insect-sized targets at maximum ranges of 3–5 m (Kick, 1982), and the bat quickly approaches and captures its prey once detection has occurred. Figure 1 is a composite diagram made from photographic and video studies of individual pursuits in both laboratory and field conditions (Griffin, 1958; Saillant *et al.*, in prep.; Lee *et al.*, 1995). The bat is depicted as being in an open area with the insect initially about 1.5 m away. (Successive images of the bat and the insect are marked from #1 to #7 and show the locations of the bat and the insect at time intervals of about 100 ms.) The bat approaches the insect at a relatively constant velocity of about 3 to 4 m/s (Lee *et al.*, 1995), which leads to completion of the maneuver from Figure 1 in about half a second. During the pursuit, the bat emits a series of sonar sounds to guide its flight, changing these sounds progressively as it approaches nearer to the target. Interceptions

covering target distances from 1.5 m down to capture (as in Fig. 1) typically involve the production of roughly 30–40 separate sonar signals and reception of a corresponding number of echoes. Analysis of the bat's sounds and its behavior during the interception maneuver reveals a great deal about what the bat must perceive from the echoes it receives (Griffin, 1958; Kuc, 1994; Novick, 1977; Schnitzler and Henson, 1980; Simmons *et al.*, 1995a).

Characteristics of sonar sounds during pursuit

Eptesicus broadcasts frequency-modulated (FM) sonar sounds that are relatively brief (Hartley, 1992; Simmons, 1989). Figure 2 shows the bat's sonar broadcasts (solid spectrograms) and the echoes (dashed spectrograms) that the bat's ears would receive during a pursuit similar to that in Figure 1. (The sequence of numbers from #1 to #7 shows the approximate relation between the sounds in Fig. 2 and the numbered images of the bat and the insect in Fig. 1.) The spectrograms making up this "pursuit sequence" illustrate the general pattern of auditory stimulation that occurs during echolocation. (Fig. 2 also illustrates the general pattern of neural responses evoked by FM broadcasts and echoes; see below.) The bat's FM emissions and the echoes they produce contain first and second harmonics that together span the frequency range from roughly 20 kHz to 100 kHz (FM₁ sweeps from 55–60 kHz down to 24 kHz; FM₂ sweeps from 100–105 kHz down to 48 kHz). As the bat flies closer to the insect (Fig. 1), the delay of echoes shortens because the path-length traveled by the sound is reduced, and the bat reacts by shortening its sounds proportionally and increasing the rate of its emissions (Fig. 2).

In Figure 1, the length of the emitted sound as it propagates through the air at each numbered point in the interception (#1–#7) is shown by a grey line from the bat through the insect (34 cm of "sound-length" per millisecond of duration). The first broadcast signal in Figure 2 is about 8 ms in duration (at image #1 in Fig. 1), and succeeding signals shorten progressively from 8 ms down to about 1–2 ms during the approach and tracking stages (image #1 to image #5 in Fig. 1, corresponding to the first two-thirds of Fig. 2). At the beginning of the terminal stage the duration of the broadcasts is about 1 ms, and the duration rapidly shortens to 0.5 ms for the remainder of the flight (image #5–image #7, beginning at arrow alongside bat's flight-path in Fig. 1, corresponding to the latter one-third of Fig. 2), until the bat seizes the prey in its tail membrane (image #7 in Fig. 1). The interval between successive broadcasts also shortens, from about 50 ms at the start of Figures 1 and 2 to about 7 ms at the end, presumably because the bat takes advantage of the

steadily declining echo delay to squeeze in more sounds for more rapid updates of the sonar images (Griffin, 1958; Hartley, 1992; Novick, 1977; Schnitzler and Henson, 1980; see model of interception by Kuc, 1994).

Perception of Targets

Echo delay and target range

Each broadcast sound illuminates, or *ensonifies*, the target for only a few milliseconds, followed by a silent interval during which echoes are received (Fig. 2). During the interval following each broadcast, echoes return from objects at different distances according to the velocity of sound until echoes become so weak that they can no longer be detected (Griffin, 1958; Lawrence and Simmons, 1982). In air, the delay of echoes is 5.8 ms per meter of target range. Because *Eptesicus* has a maximum effective operating range of about 5 m for its sonar system, the bat can be expected to experience delays up to about 30 ms (Kick and Simmons, 1984) and routinely must cope with delays from less than 1 ms to 15–20 ms during its nightly activities (Griffin, 1958). In Figure 2, the first echo has a delay of about 10 ms. Successive echoes decrease in delay as the bat flies nearer to the target until delays become as short as 0.3–0.5 ms

just prior to the moment of capture when the insect is only about 5–10 cm from the bat's mouth. The bat regulates the duration of its broadcasts using knowledge of echo delay from one broadcast to the next; at the moment of capture the bat positions its tail membrane to seize the insect (Schnitzler and Henson, 1980; Simmons, 1989).

The bat perceives the target's direction and distance from the echo received after each broadcast and updates the images from one broadcast to the next to follow the target's changing position. When the insect flies near branches and leaves (several kinds of night-flying insects take such evasive action upon hearing the attacking bat—see Fenton, 1995), the bat must perceive the direction and distance of the vegetation, too, because it chases the insect while also avoiding collisions with these other objects (Simmons *et al.*, 1995a). To be precise, the bat must be able to perceive the locations of multiple targets while at the same time perceiving which target is the insect and which targets are part of the background. During the terminal stage, the bat makes last-minute adjustments in its flight-path and its posture to swing its tail membrane up behind the target, seize the target, and bring it to the mouth. If the insect has flown into vegetation, background objects are avoided as well; pho-

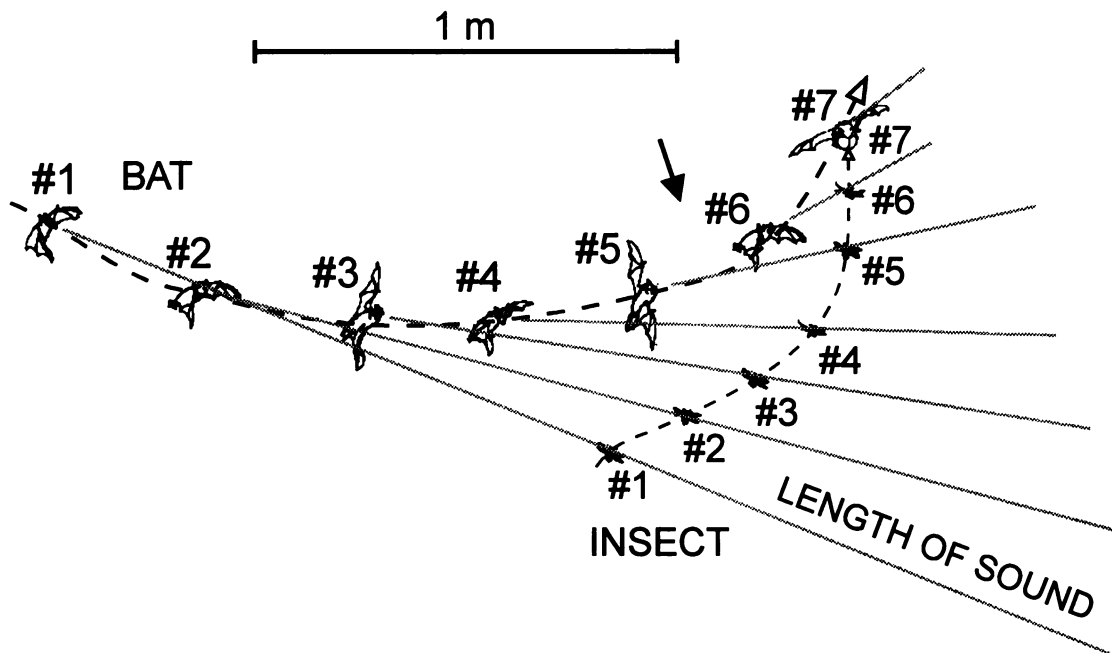


Figure 1. Diagram of an echolocating big brown bat intercepting a flying insect. Images numbered #1–#7 show locations of the bat and the insect at intervals of approximately 100 ms in this composite of numerous flights recorded in different studies. The bat emits sonar sounds throughout the maneuver (see Fig. 2), and the spatial extent of the broadcast sounds at points corresponding to the numbered images is shown by grey lines from the bat through the insect. The arrow near bat image #6 marks the location of the transition to the terminal stage of pursuit and locates the region of interest below.

tographs and video recordings reveal the bat's impressive agility during these maneuvers (see fig. 4.8 in Simmons *et al.*, 1995a). To achieve continuity in perception of the rapidly changing target scene, the bat somehow must carry information about the insect from one image to the next to avoid losing the insect in the background. We represent this continuity by a wide horizontal grey bar (labeled as perceived image) extending along the whole series of emissions and echoes in Figure 2.

Target shape and echo spectra

Insects are not just single reflecting points; they are small objects with dimensions from a few millimeters up to a centimeter or two between their principal body parts (*e.g.*, the head, the wings, and the abdomen). A typical insect therefore returns not just one "echo" but several

reflections—a replica of the incident sonar sound from each prominent body part or *glint* (Kober and Schnitzler, 1990; Moss and Zagaeski, 1994; Simmons and Chen, 1989; Simmons *et al.*, 1995a). In sonar, the target's shape can be represented along the axis of range by the spacing of the glints, or by the time separation of the overlapping reflections, which might be up to about 100 μ s for insects of the sizes commonly pursued by *Eptesicus* (Simmons, 1989). The overlapping reflections interfere with each other to produce reinforcement and cancellation at different frequencies, which modifies the spectrum of the overall echo the bat receives from the insect relative to the spectrum of the sound that was originally transmitted. Interference also modifies the phase of echoes relative to the incident sound, and both the amplitude and the phase of echoes are potential cues for perception of target shape (Simmons, 1989).

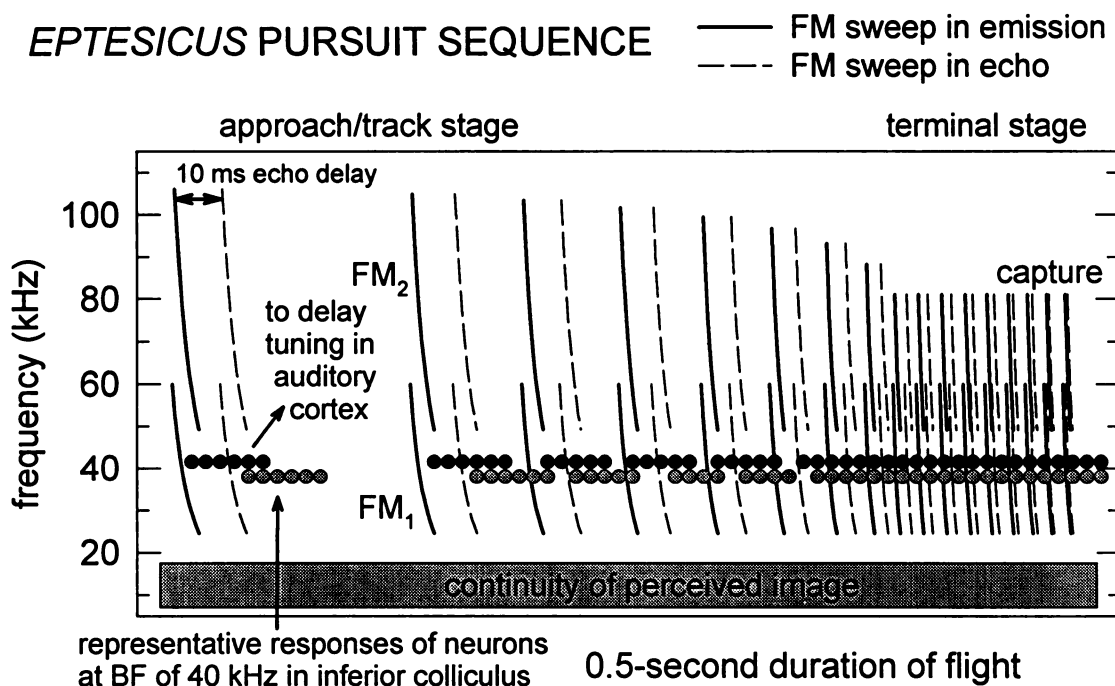


Figure 2. Diagram tracing general features of spectrograms for the bat's FM broadcast sounds (solid) and FM echoes (dashed) received from the insect during the pursuit in Figure 1. The numbers #1–#7 at top show the approximate relation between these sounds and the images of the bat and the insect in Figure 1. The arrow at #6 shows the transition to the terminal stage of pursuit. This diagram also shows the relation between occurrences of a specific frequency of 40 kHz in the FM sweeps and responses of single neurons in the inferior colliculus tuned to a best frequency (BF) of 40 kHz. Black dots show neural responses evoked by the broadcast sounds, and grey dots show responses evoked by echoes; these responses act as inputs to delay-tuned neurons at higher levels of processing (*e.g.*, auditory cortex). In the terminal stage (arrow), responses to the emissions and echoes run together, and the echoes themselves no longer evoke clear-cut responses separate from the emissions; instead, responses are triggered just by the emissions. Latencies of responses in the inferior colliculus are different for different neurons tuned to the same BF (*e.g.*, 40 kHz), and different neurons respond to different emissions or echoes at different points along the maneuver. As a result, the neural representation of the target cannot critically depend on which cells respond, apart from their BF and latency values. Continuity in the bat's perception of the insect throughout the flight is represented by the long horizontal grey bar.

Perception of target shape

Eptesicus perceives changes in the fine delay (glint) composition of echoes as well as their amplitude spectrum and phase (Menne *et al.*, 1989; Mogdans and Schnitzler, 1990; Moss and Schnitzler, 1995; Simmons, 1989; Simmons *et al.*, 1989; 1990a, b; 1995a). For example, in various discrimination tasks, *Eptesicus* readily can detect small changes in the frequency of spectral peaks and notches as well as shifts in echo phase (e.g., 0° to 180°, -90° to +90°, -45° to +45°). The bat's ability to perceive changes in the amplitude spectrum of echoes is not surprising: its auditory system represents ultrasonic frequencies topographically, thus creating a map of the acoustic spectrum in terms of activity levels in neurons tuned to different frequencies (Covey and Casseday, 1995; Kössl and Vater, 1995; Neuweiler, 1990; Pollak and Casseday, 1989). However, the ability to perceive ultrasonic echo phase-shifts is unexpected (Pollak, 1993; Schnitzler *et al.*, 1985): it requires that neural discharges in lower auditory centers exhibit some degree of synchronization to peaks and valleys in the cycles of ultrasonic sounds, and, furthermore, that discharges of individual higher-level neurons somehow preserve this information on a time scale of only a few microseconds. The main problem stems from the variability actually observed in the timing of neural discharges (in the bat's inferior colliculus; see below), which typically is hundreds of microseconds—much larger than the timing precision seemingly needed to record changes in echo phase (Pollak *et al.*, 1977; Schnitzler *et al.*, 1985). Nevertheless, several experiments show that the limit for detection of echo-delay or phase-related alternations in delay by *Eptesicus* is smaller than 0.5 μ s (Moss and Schnitzler, 1995; Simmons *et al.*, 1995a). The minimum threshold seems to be about 10–15 ns (Simmons *et al.*, 1990a). Until recently it has seemed physiologically impossible for bats to represent the phase of echoes, but in fact it is computationally feasible even with the known limitations inherent in neural responses recorded from the bat's auditory system (Saillant *et al.*, 1993; Simmons *et al.*, 1995b). How does the bat represent echo delay or phase so it can detect small changes (in the range of a fraction of a microsecond) in the timing of FM sweeps if the noisiness in neural responses amounts to hundreds of microseconds?

Auditory Representation of Sonar Emissions and Echoes

Transient, distributed character of single-unit responses to FM emissions and echoes

During echolocation, each of the bat's auditory receptors "looks at" the FM sweep in the broadcast sound or

in an echo for only that portion of the sweep that passes near its tuned frequency (Kössl and Vater, 1995). During the late approach and terminal stages of pursuit, the bat's FM signals are only about 0.5–3 ms long, which provides a very short (several hundred microseconds) effective duration for auditory stimulation at each frequency (Simmons *et al.*, 1989). On-responses marking the time of occurrence of successive frequencies in FM sweeps are passed from cell to cell upward along the bat's auditory pathway. These responses travel from the auditory nerve through the cochlear nucleus and other brain-stem sites to the inferior colliculus, which is a major auditory processing center in the bat's brain (Covey and Casseday, 1995; Pollak and Casseday, 1989; Simmons *et al.*, 1995b). The inferior colliculus is a good location in which to examine how responses might encode information about targets that the bat eventually perceives. This auditory processing center gathers responses from all auditory nuclei in the lower brain-stem and imposes some degree of integration before sending information to higher auditory centers and to motor centers (Casseday and Covey, in press; Covey and Casseday, 1995; Pollak and Park, 1995). Analysis of the timing of on-responses in neurons of the inferior colliculus to specific frequencies in FM sweeps indicates that the effective stimulus for echolocation (which is the occurrence of the specific frequency band or segment of the FM sweep that excites each neuron) indeed lasts for only a few hundred microseconds and leads, on the average, to just one spike for each stimulus presentation in each neuron (Bodenhamer and Pollak, 1981; Ferragamo, 1994).

Figure 2 illustrates schematically the timing of neural responses in the inferior colliculus of *Eptesicus* in relation to the FM sweeps in the bat's sonar emissions and the echoes received from a target corresponding to the insect in Figure 1. Each neuron is tuned to a specific frequency ("best" frequency, or BF) between 10 and 100 kHz, and each cell registers the time of occurrence of its best frequency in a short-duration FM sweep with a single spike at a specific latency (Casseday and Covey, 1992; Ferragamo, 1994; Haplea *et al.*, 1994; Jen and Schlegel, 1982; see Covey and Casseday, 1995). The diagram in Figure 2 shows rows of dots representing single-spike responses of individual neurons tuned to a best frequency of about 40 kHz on the vertical frequency axis (black dots for responses to emissions and grey dots for responses to echoes; each dot represents a different neuron). Although these neurons are all tuned to a frequency of 40 kHz, their responses nevertheless differ in latency. At any particular frequency there are neurons in the inferior colliculus with latencies ranging from about 3–4 ms to about 25–30 ms, with a scattering of longer latencies out to 40–50 ms or more. As the bat's pursuit of

the insect continues, the broadcast sounds and echoes come closer together and shorten in duration. Concomitantly in Figure 2, the bursts of responses these sounds evoke also come closer together and eventually merge into a more-or-less continuous series of spikes in different neurons (still one spike per neuron for each broadcast or echo, however). Even in the terminal stage, each broadcast is able to evoke responses in individual neurons of the inferior colliculus because the minimum interval between broadcasts is about 7 ms. Eventually, however, the echoes in the terminal stage arrive too soon to evoke responses separate from those occurring to the broadcast because the delay of echoes falls below the minimum recovery time of about 2 ms for the inferior colliculus. (In the terminal stage, the black dots and the grey dots in Fig. 2 are triggered by the solid spectrograms, with no dots triggered by the dashed spectrograms.) The problem therefore is that neural responses in the latter part of the pursuit are all evoked by the broadcast, none by the echo, while the target itself necessarily is represented only by the echo.

Early in the pursuit maneuver, when the repetition interval between the broadcasts is long (>50 ms between successive sounds) and the delay of echoes is long (>10 ms), neurons in the bat's inferior colliculus are able to respond separately to each emitted sound and then to each echo. This response is possible because the limiting recovery times for the neurons to respond to the second of two transient stimuli are shorter than the intervals between successive sounds and their echoes. However, as the repetition rate of emissions increases and the delay of echoes decreases, the acoustic stimuli encroach on limitations in the rate at which different neurons can follow rapid sequences of sounds or recover their responsiveness in time to respond to the echo as well as the emission (Casseday and Covey, in press; Casseday *et al.*, 1994; Condon *et al.*, 1994; Covey and Casseday, 1995; Haplea *et al.*, 1994; Jen *et al.*, 1993; Moriyama *et al.*, 1994; Pinheiro *et al.*, 1991). Some neurons that might respond to the first emission, to the first echo, and then to the second emission thus will "drop out" when the second echo occurs, to be replaced by other cells with more favorable response characteristics (they prefer faster rates or shorter delays). Consequently, throughout the approach and tracking stages of interception, as echo delay and the interval between emissions both become shorter, different subpopulations of neurons appear and then disappear from the overall active population of cells. The already distributed nature of these responses is carried even further in the terminal stage by the fact that no neurons appear to respond directly to the echoes at all during the terminal stage. Instead, responses that convey information specifically about the echoes are merged or "dis-

tributed" into responses to the emission. How does the bat achieve some continuity in its images throughout pursuit if different neurons are used at different points in the sequence and if echoes also fail to elicit discernible responses of their own during the terminal stage?

Neural display of target range

The bat's auditory system uses the timing of neural responses in the inferior colliculus to create a higher-level representation of echo delay that ultimately displays target range in the midbrain and auditory cortex (Dear and Suga, 1995; Dear *et al.*, 1993a, b; O'Neill, 1995; Suga, 1990; Suga *et al.*, 1995). Broadly spread latencies in the inferior colliculus amount to physiological delays imposed on responses to systematically retard and disperse the registration of each frequency by different neurons. Shorter latencies (*e.g.*, <4–5 ms) probably are due to the time required for responses to travel up to the inferior colliculus along different pathways, but longer latencies (>5 ms) appear to be caused by periods of inhibition with different lengths, which produce the delays themselves, followed by brief bursts of excitation to trigger responses at the end of the inhibitory delay window (Casseday *et al.*, 1994; Saitoh and Suga, 1995). The dispersal of latencies shown in Figure 2 creates physiological delay lines whose delay "taps" correspond to individual neurons responding at their characteristic latencies to the emission (black dots) or to the echo (grey dots). These delayed neural responses leave the inferior colliculus and travel upward to the medial geniculate (auditory thalamus) and auditory cortex, where higher-level neurons are placed to receive inputs from both the emission and the echo. These receiving cells are *coincidence-detectors* that each produce a spike when, and only when, their inputs from the emission and the echo arrive simultaneously (Carr, 1993). By detecting the coincidence, or simultaneity, of its inputs, the coincidence-detector becomes tuned to the time difference between the response latencies to the emission and the echo, or echo delay (O'Neill, 1995; Suga, 1990; Suga *et al.*, 1995). In *Eptesicus*, coincidence-detectors in the auditory cortex are tuned to echo delays from 2–3 ms to 28 ms, with different neurons having different best delays (Dear *et al.*, 1993a, b). The delay-tuning curves of these neurons represent target ranges from about 0.3–0.5 m to about 5 m, which covers most of the operating range of the big brown bat's sonar (Kick, 1982; Kick and Simmons, 1984). The accuracy with which delay-tuning curves represent target range is limited, however: the width of delay tuning in *Eptesicus* is no better than about 0.5–1 ms even in the most sharply tuned neurons and typically is several milliseconds for each cell (Dear *et al.*, 1993a, b).

The bat as a whole has an echo-delay acuity of a microsecond or less (Moss and Schnitzler, 1995). The width of delay-tuning curves in *Eptesicus* appears to be more closely related to the coarse scale of delay acuity associated with discrimination of differences in target range (50–100 μ s; Moss and Schnitzler, 1995; Simmons, 1973) than to the fine delay acuity associated with perception of phase and glints (0.01–1 μ s; Simmons *et al.*, 1990a, b).

Interestingly, the only portion of the bat's sonar operating range not covered by cortical delay-tuned neurons is the short end from about 0.5 ms to 2 ms which the bat encounters during the terminal stage of pursuit, when it has come within about 0.3–0.5 m of the insect. Such short ranges also are encountered when the bat flies to a landing site (see Lee *et al.*, 1995) or examines any objects closer than 0.3–0.5 m. This is the region where neurons in the bat's inferior colliculus can no longer produce separate responses to echoes and thus can deliver no echo inputs to drive delay-tuned coincidence-detectors. Nevertheless, the bat perceives the range to the insect during the terminal stage, including such details about range as are provided by the spectrum and phase of echoes. During the terminal stage, how does the bat represent target range, including the fine delay information implicit in its ability to perceive changes in echo phase as changes in delay? For that matter, how does the bat perceive echoes at all during the terminal stage?

Overcoming the distributed character of the neural representation for targets

On the average, each neuron in the bat's inferior colliculus discharges only once and thus participates in actively representing an echo for only the brief duration of its spike. Other neurons discharging at other times carry the representation in the inferior colliculus over the entire epoch of roughly 30–35 ms during which the echo from the target is processed, which lasts more or less until the next broadcast sound is emitted (Simmons *et al.*, 1995b; see Fig. 2). The same is true for delay-tuned neurons in the bat's auditory cortex; each delay-tuned cell registers an emission-echo coincidence with, on the average, a single spike and thus only very briefly contributes to the representation of echo delay. Other delay-tuned neurons responding at later times carry the representation across the whole epoch of 30–35 ms associated with processing echoes from each broadcast sound (Dear *et al.*, 1993a, b). The distributed character of the representation of targets is not occasioned solely by the occurrence of an average of only one spike in each neuron. Additional distribution occurs because the same neurons do not follow the emission or the echo throughout the entire pursuit. Both in the inferior colliculus and in the

auditory cortex, different neurons will respond to emission-echo pairs at different stages of the pursuit maneuver because these cells differ in their preferences for the duration, repetition rate, and other temporal features of the train of stimuli. Toward the end of the flight, responses to echoes are distributed even further in the sense that no obvious responses are triggered at all by echoes in the terminal stage. This is the essence of the distributed character of the bat's auditory code for echo delay. To achieve some degree of continuity in its images of the target, the bat must have a means for integrating responses across multiple neurons to overcome the distributed character of the neural representation for each target. Recordings made in the inferior colliculus from local groups of neurons discharging together for each stimulus provide a means to bypass the dispersion of responses observed one cell at a time and achieve the desired integration of information about the target in actual experiments (see Simmons *et al.*, 1995b). These multiunit responses, recorded directly from neighboring cells in a small volume of tissue, show how groups of cells share the work of representing emissions and echoes.

Multiunit responses in the bat's inferior colliculus

Figure 3 illustrates a series of local multiunit responses recorded with a high-impedance single-unit electrode positioned "between cells"—that is, without having spikes from a single neuron dominate the signal. Each time a stimulus is delivered to the bat's ears, the electrode picks up clusters of spikes mixed together at similar amplitudes from different cells rather than the spikes of just one cell at a very high amplitude. The waveform being recorded is an analog signal made up from a combination of spikes in different cells; the stimulus is repeated numerous times and the response is averaged across these multiple presentations to reveal the presence of synchrony between any of the spikes and the stimulus. Each peak in the response trace in Figure 3 thus shows the simultaneous occurrence of spikes in a group of cells at a fixed latency following the stimulus, and different peaks represent groups of neurons responding synchronously at different latencies. The responses shown in Figure 3 were evoked by presenting the bat with a series of 54 electronically simulated sonar emissions and echoes that mimic a whole pursuit sequence, and then averaging the set of analog responses over 64 independent occurrences of the entire sequence of sounds. Note that these sounds only *simulate* 54 emissions and echoes because the bat is not actually vocalizing the broadcasts; instead, the bat's ears receive stimulation that corresponds roughly to what they would receive if the bat did produce these sonar sounds while approaching a target. The spe-

A IC MULTI-UNIT RESPONSE TO PURSUIT SEQUENCE

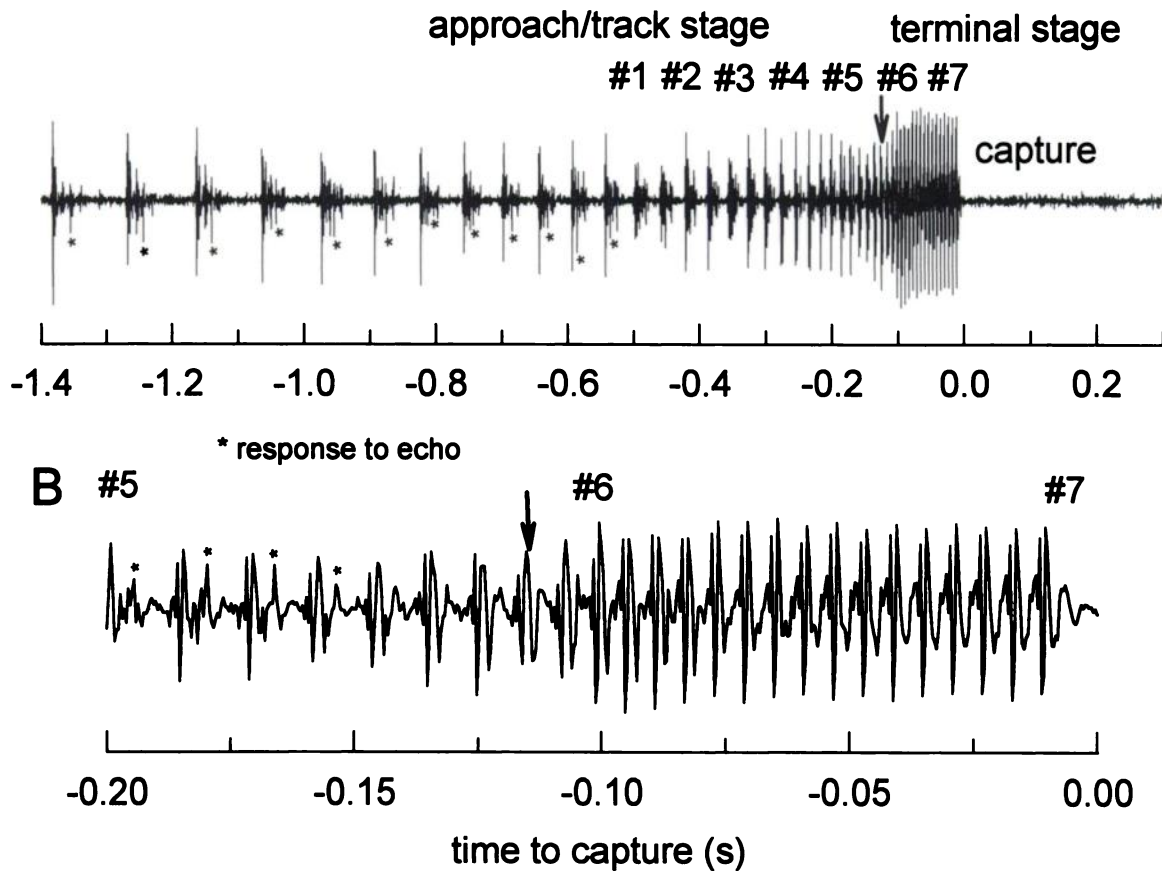


Figure 3. Multiunit responses recorded in the inferior colliculus of *Eptesicus* for a series of acoustic stimuli simulating an entire pursuit sequence of emissions and echoes (whole sequence in A; final 0.2 second of sequence in B). The segment of this stimulus/response sequence that corresponds to Figure 1 and 2 is shown by #1–#7 for the numbered images in Figure 1. The arrow marks the transition into the terminal stage. Asterisks show approximate locations of responses just to the *echoes* at those points where they are visible in the trace (first 12 visible at scale of A; first 33 visible at scale of B); at other points responses to echoes are either obscured by multi-peaked structure of responses to emissions (at -0.5 s to -0.15 s in A) or else specific responses to echoes are absent due to neural recovery times being slower than echo delay (at -0.15 s to 0 in B, which includes the terminal stage).

cific segment of the artificial pursuit sequence used to generate the responses in Figure 3 that corresponds to the maneuver shown in Figures 1 and 2 is marked with numbers from #1 to #7; these give the approximate locations of the numbered images of the bat and the insect in Figure 1 alongside the multiunit response trace.

In detail, the series of averaged multiunit responses shown in Figure 3 consists of bursts of peaks triggered by each broadcast and its associated echo, with each burst lasting for up to about 30–40 ms. Usually there are “silent intervals” between bursts of responses when no sounds are occurring. However, as the repetition rate of the artificial broadcasts increases, the silent interval be-

tween bursts shortens until, about at the arrow in Figure 3, the bursts of responses run together to form a continuous sequence of peaks. The response trace in Figure 3 contains well-defined peaks that register the reception of each of the 54 simulated sonar broadcasts, followed by several lower-amplitude peaks that correspond, first, to the wide spread of response latencies seen in the inferior colliculus for the emitted sound and, second, to responses for the simulated echoes as well as the broadcasts. In Figure 3, virtually every simulated broadcast produces a response (beginning with the largest peak in each burst of peaks), and most of the echoes produce a response, too (echo responses that are readily visible in

the traces shown in Figure 3A–B have been marked with *). The presence of distinguishable responses to the broadcast and then to the echo is maintained up to the transition between the approach or tracking stages of pursuit and the terminal stage in the artificial pursuit sequence (at arrow in Fig. 3B).

Although the responses in Figure 3 are composed chiefly of spikes that emerge from the averaging process due to their synchronization with the stimulus at different latencies, individual response peaks are not derived from the same neurons at all positions in the sequence. Different neurons contribute to the multiunit response peaks at different stages in the sequence because neurons in the bat's inferior colliculus vary in their preferences for duration, repetition rate, and echo delay. Interestingly, the total number of neurons and level of synchrony making up the responses to the individual emissions appear relatively stable across different emission-echo pairs in Fig. 3A–B because the peaks are roughly of the same height (amplitude variability is less than 50%) and width throughout the whole sequence. Separate peaks occur in response to the echoes (*) for about the first 33 emission-echo pairs in Figure 3, but these echo responses are more difficult to discern because they are lower in height and because they also are mixed with multiple peaks in the response to the emission alone. These multiple peaks correspond to the spread of response latencies for different neurons tuned to the same frequency (e.g., at 40 kHz in Fig. 2). During the terminal stage (starting at arrow in Fig. 3), the disappearance of any obviously separate response peak to each echo is virtually guaranteed because hardly any neurons in the bat's inferior colliculus have recovery times shorter than 1–2 ms. Thus, the general appearance of multiunit responses in the bat's inferior colliculus to simulated sonar broadcasts and echoes appears largely predictable from the results of single-unit studies.

Representation of delay and phase in multiunit responses

The multiunit responses in Figure 3 are analog waveforms obtained by averaging spikes from clusters of neurons over multiple presentations of the artificial pursuit sequence. Individual neurons will either appear in the averages or drop out according to each cell's sensitivity to frequency, amplitude, duration, delay, and repetition rate. Consequently, there is no straightforward way to interpret each multiunit response peak in relation to responses of individual neurons to these stimulus parameters if that is the goal. But what if the bat's brain is not just trying to assemble a rate-coded feature-by-feature description of emissions and echoes during pursuit?

What if the bat's brain instead seeks to reconstruct aspects of the acoustic signals as *time-series* events, perhaps even with scant regard for which neurons produce the responses that make them up (Simmons, 1996; Simmons and Dear, 1991)?

Averaged multiunit responses are not only averaged synchronized spikes from multiple neurons, they are also time-series signals with their own properties of amplitude, peak height, and phase. The neurons whose spikes make up different peaks in the averaged waveform in Figure 3 may respond to only a portion of the pursuit sequence—perhaps to a few of the emissions or the echoes out of the whole series of emission-echo pairs, but the parameters of the multiunit responses appear not to depend critically on this fact because all the emissions and many of the echoes evoke specific peaks in these responses. What would happen to the multiunit responses *as signals* if echo delay or phase were changed by a few microseconds? Figure 4 illustrates just one example of the surprising dependence of local averaged multiunit responses from the inferior colliculus of *Eptesicus* on fine temporal features of emissions and echoes (Simmons *et al.*, 1995b). The figure shows the positive-negative-positive series of peaks in the multiunit response evoked at a latency of 4.4–5.2 ms by one of the emissions taking place early in the terminal stage (at arrow in Fig. 3), when the delay of echoes is about 1 ms—too short for the echo on its own to evoke strong responses in the inferior colliculus. (The horizontal time scale in Fig. 4 is expanded relative to Fig. 3 and has its origin shifted to the onset of the specific emission-echo pair #37 designated by the arrow in Fig. 3. Consequently, time values in Fig. 4 are latencies relative to the artificial emitted sound.)

All the emissions and the echoes used to produce the responses shown in Figure 3 are set to be *normal in phase* relative to each other and at the same time *inverted in phase* relative to an arbitrary, external phase standard (180° phase, or I,I in the terms used in the legend for Fig. 4). Figure 4 shows what happens to a representative peak from Figure 3 when the phase of the emitted sound or the echo is altered from this initial 180°/180° (I,I) condition. (The solid line in Fig. 4 is labeled I,I for “inverted” or 180°/180° phase of the emission and the echo together.) The five curves in Figure 4 then show different phase conditions for the emission and the echo (I,I for 180°/180°; N,N for 0°/0°; I,N for 180°/0°; N,I for 0°/180°; and I,I for a repeat of 180°/180°). The chief effect of these changes in phase for the emission and echo is that the response peaks in Figure 4 slide sideways over a time interval of up to several hundred microseconds according to the phase of the emission in relation to the echo. This effect is not restricted to the particular response peak selected for Figure

Response to terminal-stage emission-echo pair for different combinations of emission and echo phase

N = normal (0°) phase, I = inverted (180°) phase

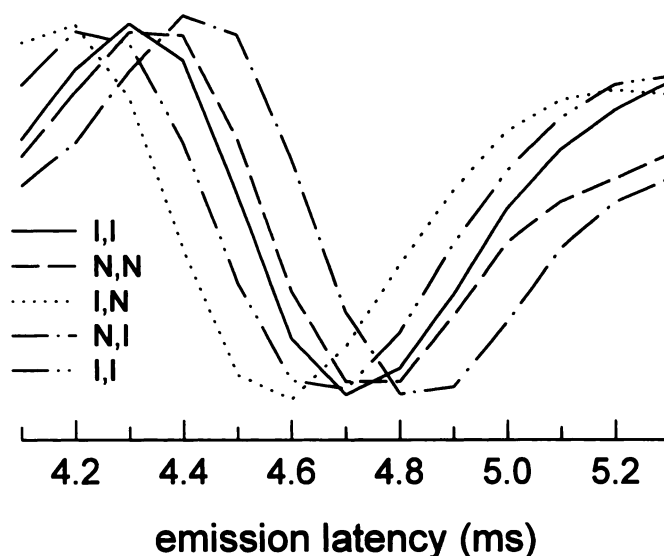


Figure 4. Waveform of the peaks in the multiunit response marked by the arrow in Figure 3B (see also arrows in Figs. 1 and 2). The first response peak shown here has a latency of about 4.4 ms and originates from within the inferior colliculus; nominally it is a response to an emission from the terminal stage, when responses specifically associated with the echoes no longer are visible by themselves. Although there is no clear response peak associated with the echo at this stage, the latency of the illustrated response peak for the emission nevertheless shifts according to the phase of both the emission and the echo ($N = 0^\circ$; $I = 180^\circ$; see text). The responses to the emissions in Figure 3, at latencies of 4–5 ms after each emission, all show large latency shifts of 100–200 μ s associated with 0° and 180° phase shifts in these simulated emissions and echoes. Evidently the responses to each “emission” in fact are responses to a complex of sounds that must include at the very least the previous echo along with the current emission. The phase of the echo is represented consistently throughout the pursuit maneuver, but this information resides in an unexpected place—in the latencies of peaks in what would nominally be considered the response to the emission.

4; all of the peaks in the multiunit responses evoked by the emissions in Figure 3 slide the same way with changes in emission or echo phase as shown in Figure 4. This effect can only mean that latencies of the neural spikes making up the peaks in the multiunit responses to the emissions have somehow become consistently dependent on the phase of the original ultrasonic emissions, echoes, or both. The magnitude of the latency shifts associated with the 180° phase shifts is especially interesting: For the stimulus, a phase shift of 180° in the ultrasonic signal moves the cycle-by-cycle structure of the acoustic waveform by only about 5 to 20 μ s (half the ultrasonic period) depending on the frequency at each point in the FM sweeps, yet for the responses, the peaks in Figure 4 slide in latency by 50–200 μ s.

Magnification of microsecond stimulus time scale in multiunit neural responses

Two significant aspects of the phase-shift effect in multiunit responses from the bat's inferior colliculus deserve comment. First, the size of the latency shift in the response is as much as 100–200 μ s for some combinations of emission and echo phase. This is roughly 10 times greater than the changes in timing for the cycles of the sound associated with the phase shifts. For this effect to appear at higher auditory processing centers (*e.g.*, inferior colliculus), there must be some mechanism for magnifying or expanding small differences that occur on a scale of a few microseconds in the timing of neural responses at lower auditory processing centers. In the infe-

rior colliculus, the time-scale magnification is roughly a factor of 10 for 0°/180° phase changes in emissions or echoes. We have observed time-scale magnifications of roughly 10–100 for various other delay changes in echoes (Ferragamo, 1994; Simmons *et al.*, 1995b). This phenomenon appears robust and ubiquitous in the inferior colliculus and auditory cortex of *Eptesicus*. Moreover, for a given recording site, the same size of time magnification affects all the responses in the pursuit sequence in the same manner, providing a stable, consistent representation of the detailed structure of emissions and echoes without requiring any individual neurons to respond consistently. The locally recorded analog multiunit response thus carries information necessary to explain the bat's performance without this information manifesting itself in conventional single-unit recordings.

The second significant aspect of the phase-shift effect is that the magnitude and direction of the latency shifts depend not only upon the current stimulus phase conditions but also on the previous phase conditions. Notice that the latencies of response peaks in Figure 4 for the second occurrence of the I,I or 180°/180° phase conditions do not match latencies for the first occurrence of this condition. That is, when the original (I,I) stimulus condition is restored, the multiunit responses do not shift back to their original latencies; instead, they are offset, in this example by about 40 μ s. We have observed many similar examples of latency offsets in responses to phase shifts and other stimulus parameters that appear to depend on the stimulus conditions previously presented (Simmons *et al.*, 1995b). In general, the time-scale magnification of latencies does not register just the absolute phase of emissions or echoes by itself (*e.g.*, 0° or 180° for either sound) but instead registers their relative phase coupled with a reference latency that depends upon the stimulus conditions that occurred previously.

It thus seems as though at least part of the basis for continuity in the neural representation of echo phase, and therefore perception of target shape, across the pursuit sequence may reside in the latencies of responses to emissions distributed across multiple neurons on a magnified time scale. The apparent absence of responses to echoes in the terminal stage (due to neural recovery times that are too short) may not be a problem for the bat, because information about echoes (*e.g.*, echo phase) actually resides in responses nominally associated with the emissions, not with echoes. The relatively large variability of latencies for individual neurons in the inferior colliculus (which typically is in the range of hundreds of microseconds and which should obscure the presence of the much smaller time shifts of a few microseconds associated with stimulus phase) also may not be a problem for microsecond-scale perception of echo delay. By plac-

ing fine timing information in response latencies on stretched time scales, the bat overcomes the problem. In effect, the bat can “read” echo delay and phase information from neural responses as though the observed latency variability were reduced by the time-magnification factor associated with the responses. The observed latency variability of hundreds of microseconds thus may be only a few microseconds as far as the bat is concerned. Because all the multiunit responses to the emission in Figure 3 exhibit a time shift of the same size (Fig. 4) in spite of the failure of the same neurons to respond consistently across all the sounds in the sequence, these responses call into question the whole idea that rate-tuned responses of single units are the minimal computational elements used by the brain to create images for perception (Simmons, 1996). Instead, vital aspects of perception appear to be manifested in the timing of responses irrespective of which neurons are doing the responding. We have observed a whole family of similar magnified multiunit response-latency shifts caused by changes in the phase of the emission or the echo, the interaural delay difference of the echo, and the time separation of overlapping reflections from target glints (see Simmons *et al.*, 1995b). In each case, the latency of peaks in the multiunit response changes by a larger amount than the stimulus—typically 10 to 100 times greater. The use of multiple time scales in neural responses is itself a novel observation that raises questions about how to interpret responses in relation to representation of stimuli.

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