

Cats exhibit the Franssen Effect illusion

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The Franssen Effect (FE) is a striking auditory illusion previously demonstrated only in humans. To elicit the FE, subjects are presented with two spatially-separated sounds; one a transient tone with an abrupt onset and immediate ramped offset and the other a sustained tone of the same frequency with a ramped onset which remains on for several hundred ms. The FE illusion occurs when listeners localize the tones at the location of the transient signal, even though that sound has ended and the sustained one is still present. The FE illusion occurs most readily in reverberant environments and with pure tones of $\sim 1-1.5$ kHz in humans, conditions where sound localization is difficult in humans. Here, we demonstrate this illusion in domestic cats using, for the first time, localization procedures. Previous studies in humans employed discrimination procedures, making it difficult to link the FE to sound localization mechanisms. The frequencies for eliciting the FE in cats were higher than in humans, corresponding to frequencies where cats have difficulty localizing pure tones. These findings strengthen the hypothesis that difficulty in accurately localizing sounds is the basis for the FE. © 2004 Acoustical Society of America. [DOI: 10.1121/1.1810136]

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I. INTRODUCTION

Experiments on the localization of acoustic stimuli have revealed a number of important features of sounds that increase localization accuracy, including broad bandwidths (Butler, 1986), rapid onsets (Rakerd and Hartmann, 1986), and anechoic environments (Hartmann, 1983). The Franssen Effect (FE) is an auditory illusion that emerges when listening conditions are less than ideal, and may be related to the well-studied precedence effect (Wallach *et al.*, 1949). The FE can be demonstrated by turning on a transient tone to one speaker with a sudden onset and slowly decaying offset while simultaneously turning on a second long-duration tone with a slowly rising onset to another speaker at a different location. In the FE, listeners are unable to discriminate these paired tones, located on either side of the listener's midline, from a single sustained tone with an abrupt onset presented from the location where the transient signal was presented (Franssen, 1962). The subjects apparently perceive the Franssen stimuli as only one fused stimulus coming from the location of the transient tone even though that tone is no longer physically present. The illusion occurs only for narrowband sounds (Yost *et al.*, 1997) in reverberant environments (Hartmann and Rakerd, 1989), but for sounds lasting indefinitely (Berkley, 1983).

The FE is thought to occur because listeners have difficulty localizing tones with no transient onset information (i.e., the sustained tone) in reverberant rooms, and because the signals are within a frequency range ($\sim 1.5-3.0$ kHz) where neither the interaural time or level difference cue is adequate for accurate localization (Hartmann and Rakerd, 1989; Stevens and Newman, 1936; Yost *et al.*, 1997). Listeners can localize the transient with its sudden onset, while

localization of the later steady-state sound poses more difficulty, especially in reverberant environments. In one hypothesis for the FE, when reflections are present they tend to corrupt localization cues from the sustained tone, resulting in cues that are “implausible” because they do not correspond to the frequency-specific interaural cues experienced naturally (Hartmann and Rakerd, 1989). Accurate localization is nearly impossible in this condition, particularly for frequencies where the cues are not reliable. Listeners apparently resolve this implausible situation by continuing to locate the sustained tone at the location of the transient.

The FE has never been demonstrated in any nonhuman animal, and human experiments have employed discrimination procedures rather than sound localization tasks. Hence, one of the hypothesized bases for the FE (negative relationship between absolute sound localization accuracy and the FE) has not been tested directly. The correlation between the frequency dependency of the FE and localization would be strengthened if similar effects were found in another species whose localization abilities differ from humans. We therefore tested cats, whose localization deficit occurs at a higher frequency than in humans. As in humans, localization in cats is good at low and high frequencies, but gradually worsens to the poorest performance at around 4 kHz instead of 1.5 kHz (Casseday and Neff, 1973; Martin and Webster, 1987; Populin and Yin, 1998). If the frequencies where the FE is effective are due to the inability to localize sounds, then the frequencies where the FE illusion succeeds in cats should be found at higher frequencies than in humans.

II. METHODS

A. Subjects and materials

Three adult female cats were outfitted with head holders, eye coils, and coil connectors (Populin and Yin, 1998). All

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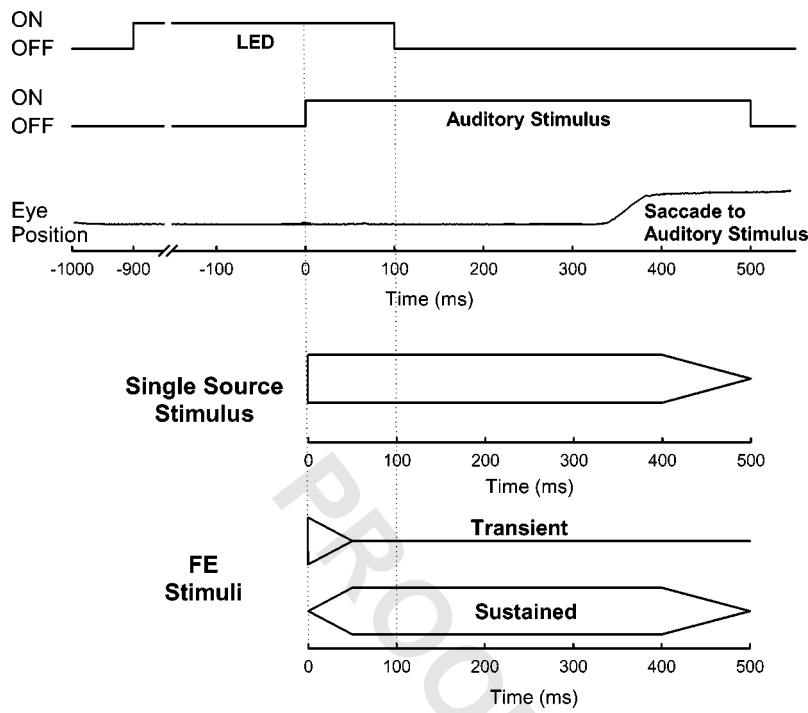


FIG. 1. Schematics of FE and SS stimulus conditions. Cats were required to fixate on an LED until its offset, after which a gaze shift was required to either a SS stimulus presented to one location ($\pm 30^\circ$) or the paired Franssen stimuli presented to both locations. In the Franssen condition, a transient tone burst with an immediate offset ramp is presented to one side while the same tone is presented simultaneously to the other side with a slow onset ramp (50 ms) and long sustained duration. The stimuli began 100 ms before the fixation LED was terminated so that the cue to make a saccade came only after the stimuli had been on for 100 ms and the transient stimulus was already OFF for 50 ms.

procedures were approved by the University of Wisconsin Animal Care and Use Committee and complied with NIH guidelines for animal use.

During experimental sessions, cats were placed in the center of a dark sound-attenuating chamber whose walls and major pieces of equipment were covered with sound-absorbent foam (10.2 cm Sonex; Ilbruck Co.). The cats were placed in a restraint bag with their heads free and faced a bank of 15 frequency-response matched loudspeakers (Morel Acoustics, Model MDT20). For this experiment, only two of the speakers at $\pm 30^\circ$ azimuth (0° elevation) were used to test for the FE though the other speakers were used for training and standard trials. The speakers were arranged horizontally and vertically along arcs 90 cm from the center of the head ranging from $\pm 80^\circ$. Speakers were hidden from view by a black translucent cloth. A 2.0-mm-diameter red LED was suspended over the center of each speaker. The gaze position (i.e., the position of the eyes in space resulting from combined head movement and eye saccades) was recorded using the scleral search coil technique.

Cats were tested under these echo-reduced conditions as well as under echoic conditions where the walls, ceilings, and floors of the testing booth were lined with heavy-duty plastic panels. The inner dimensions of the acoustic chamber were $2.2 \times 2.5 \times 2.5$ m. We used the method described by Yost *et al.* (1997) to demonstrate that these two conditions differed in their reverberation characteristics. For each room condition, the response to 50 presentations of a 100- μ s click was obtained, averaged, and then bandpass filtered between 500–12000 Hz. The microphone was placed where the center of the cats' head was during the experiments and the speaker was placed at ($0^\circ, 0^\circ$). The rms level of the averaged response for the first 5 ms of the recording, which contains the direct signal from the source (the acoustic delay from the speaker to the microphone was not included in the 5-ms window) was compared to the rms level of the recording for

the next 25 ms, which contains the acoustic reflections. Following Yost *et al.* (1997), we took the $20 \log_{10}$ of the ratio of these two levels to determine how much lower the reflections were compared to the initial click. For the echo-reduced chamber, the last 25 ms was down 24.9 dB from the initial 5 ms, and for the echoic condition the ratio was lowered by only 18.4 dB. Hence there was a 6.5 dB difference in room conditions, which was smaller than the 13.2 dB difference obtained in the Yost *et al.* (1997) study. The differences between our echoic and echo-reduced rooms were also evident in the magnitude spectrum of the averaged click recordings. The additional reflections in our echoic room would be expected to introduce prominent peaks and valleys into the spectrum due to comb-filtering effects. To quantify this, we computed the standard deviation of the spectrum (from 500–12000 Hz), which was 7.8 dB for the echo-reduced room and increased to 10.3 dB for the echoic room. In summary, our treatment of the echo-reduced room with plastic panels changed the characteristics of the listening condition at the position of the cats' head, albeit not as much as that described by Yost *et al.* (1997).

B. Stimuli and procedures

On each day of testing, the cats were presented with a wide range of different auditory and visual stimuli from all possible locations. Schematics of the stimuli of interest for these experiments are depicted in Fig. 1. The stimuli were either broadband noises or pure tones from 250 to 9000 Hz and were presented from either $+30^\circ$ or -30° on the horizontal plane. The single source (SS) stimuli had a total duration of 500 ms, which was comprised of an immediate onset, a 400-ms sustained portion, and a 100-ms linear ramp offset. The FE stimuli consisted of two signals presented simultaneously, one to the -30° and one to the $+30^\circ$ locations, or *vice versa*. The transient signal had an immediate

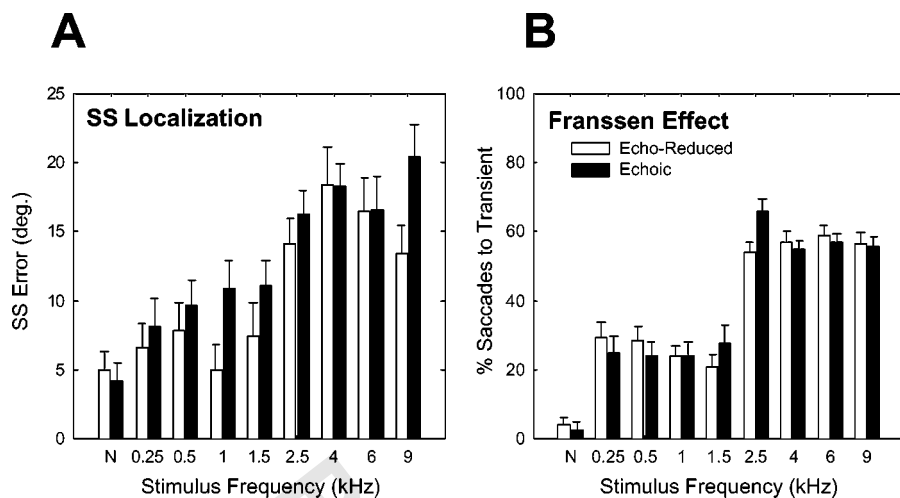


FIG. 2. Mean horizontal error in localizing SS stimuli as a function of stimulus frequency (a) and mean percent saccades to transient stimulus location during Franssen stimuli (b) as a function of stimulus frequency for three cats. For both graphs, echo-reduced conditions are the white bars and echoic conditions are the black bars. Data are averaged across the left and right stimulus conditions. Error bars represent between-subject standard errors.

onset, followed by a 50-ms linear ramp offset, for a total duration of 50 ms. The sustained signal had a 50-ms linear ramp onset, a 350-ms sustained portion, and a 100-ms linear ramp offset, for a total duration of 500 ms. The stimuli were presented such that the maximum amplitudes of their envelopes were the same as the maximum amplitude of the corresponding sustained stimulus that produced a level of 60 dB SPL. The stimuli were roved by ± 10 dB across trials.

The cats were trained using operant conditioning to indicate via gaze shifts the apparent two-dimensional location of various auditory and visual targets. During testing, FE trials were interspersed within experimental sessions of standard trials at a 10–15% rate. A delayed saccade paradigm was used to measure responses to these stimuli (as well as for the SS stimuli). Here, the cats fixate (within $\pm 4^\circ$) a LED at the midline ($0^\circ, 0^\circ$) for a variable time period (~ 1000 ms) and then make gaze shifts to the sound source upon termination of the LED. In these trials, the acoustic stimuli began 100 ms before termination of the LED, but cats were required to maintain fixation until the LED was gated off. The delayed saccade task was purposely used so that, for the FE stimuli, the transient signal had been terminated for 50 ms while the sustained signal remained on when the trigger (LED offset) was given to make the saccade. When the FE is experienced, the cats will look towards the location of the transient and not towards the location of the ongoing sustained sound. If the FE is not operating, the cats will look towards the sustained sound's location because at the time of LED offset it is the only sound on.

Responses to the SS stimuli were required to be within an electronic acceptance window centered on the target (± 8 – 15°) for ~ 750 ms for a food reward of a puree of cat food. The reward contingency for the FE stimuli differed from our usual criteria; since these stimuli are illusory and have no “correct” response, the cats were rewarded on all trials in which they attempted this task.

C. Data analysis

The dependent variable in these experiments was the final two-dimensional gaze position after the gaze shift to the apparent location of the acoustic target. We used a velocity criterion (Populin and Yin, 1998) to determine when the eye

movements began and ended by determining the time when the magnitude of the velocity of the eye movement exceeded 2 SD of the mean velocity computed during the fixation of the initial LED. All trials were used in the analysis of the data even if the cat had not been rewarded, ensuring that the accuracy of the responses reported here was not confounded by the size of the acceptance window. Each data point for each cat in the SS conditions was based on at least 40 trials while data points in the FE conditions were based on at least 20 trials. Horizontal errors in localizing the stimuli were reported as a function of stimulus frequency. Errors were computed separately for each trial as the difference in degrees between the actual stimulus source and the final eye position of the cat. For the FE stimuli, the trials in which the cats made gaze shifts greater than 5° away from the midline towards the side of the transient signal location were considered to exhibit the FE.

III. RESULTS

Three domestic cats were trained on a delayed saccade task using operant conditioning procedures with a food reward to make gaze shifts to either a stimulus presented from a single source location (SS) or from pairs of locations (FE), schematics of which are shown in Fig. 1. For the FE trials, the fixation LED was on during the transient signal and remained on for at least 50 ms after it was turned off. When the LED turned off (the signal to make the gaze shift to the target), the sustained signal continued. The mean saccade latency was 230 ms (S.D. = 97 ms) for the FE stimuli so that by the time of the gaze shift, the transient signal had been off for 280 ms, on average. In this experiment, a gaze shift to the transient signal location during presentation of the FE stimuli is indicative that the FE was elicited. That is, the cats were looking towards an illusory signal location after that signal had been turned off for almost 300 ms despite the presence of the sustained signal at the other speaker.

Mean results from three cats are shown in Fig. 2. Errors for localizing the SS stimuli (A) were low (5 – 10°) for broadband noises and pure tones from 0.25 to 1.5 kHz. For tone frequencies of 2.5 to 9 kHz errors were much higher (15 – 20°). These results are similar to previous studies on the localization of pure tones by cats (Casseday and Neff,

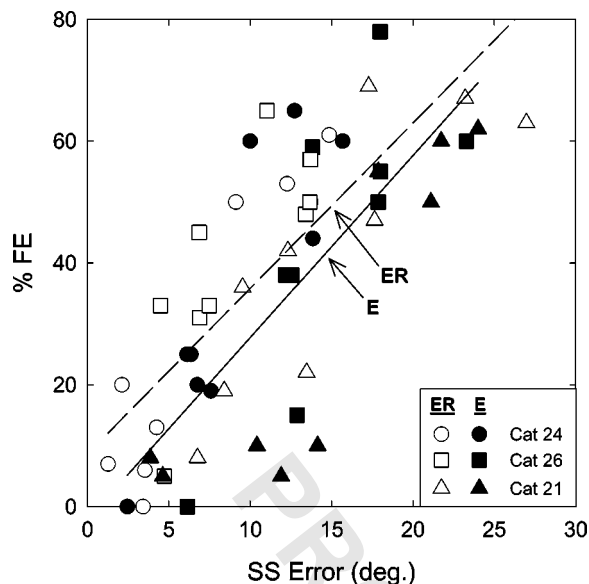


FIG. 3. Percent of trials where the FE is elicited as a function of error in localizing SS stimuli across all frequencies tested. Data shown separately for each cat (symbol type) and room condition (E=echoic, black symbols; ER=echo-reduced, white symbols). Mean regression lines are also shown for all three cats in the ER (dashed line) and E conditions (solid line).

1973; Martin and Webster, 1987; Populin and Yin, 1998). In Fig. 2(b), the incidence of the FE illusion is depicted as the percent of responses towards the transients. When the stimuli were broadband noises, the cats rarely (<5% of all trials) made saccades to the transient, choosing to almost exclusively look towards the sustained sound. When the stimuli were pure tones ranging from 0.25 to 1.5 kHz, the cats looked at the transient on a higher proportion (~25% of trials, and in the remainder of the trials looked towards the sustained sound. At higher frequencies, the cats very often (>50%) looked towards the transient signal location rather than to the sustained sound. Both the localization of SS stimuli and the occurrence of the FE illusion were equally prevalent in the echo-reduced and echoic conditions. These results suggest that for pure tones, especially at higher frequencies, the cats are experiencing a phantom sound located at the transient signal's location even though that sound had been extinguished for some time, similar to the FE illusion found in humans.

To test the hypothesis that the FE is experienced most readily for stimuli that are difficult to localize on their own, Fig. 3 shows the percentage of trials where the FE was elicited against the mean error in localizing SS stimuli across all frequencies. Supporting this hypothesis, for all cat correlations [r -values ranged from +0.76 to +0.93 across cats, mean echo-reduced (ER) $r=0.79$, mean echoic (E) $r=0.75$] and slopes (mean ER=2.72; mean E=2.99) were high. Thus, the correlation between sound localization difficulty and the incidence of the FE illusion is high for cats, in agreement with the data from humans (Yost *et al.*, 1997). Furthermore, consistent with expectations, the FE in cats was not elicited at the same frequencies as in humans, but rather was more pronounced at higher frequencies where SS localization is difficult for cats.

Since we used localization procedures, we also calcu-

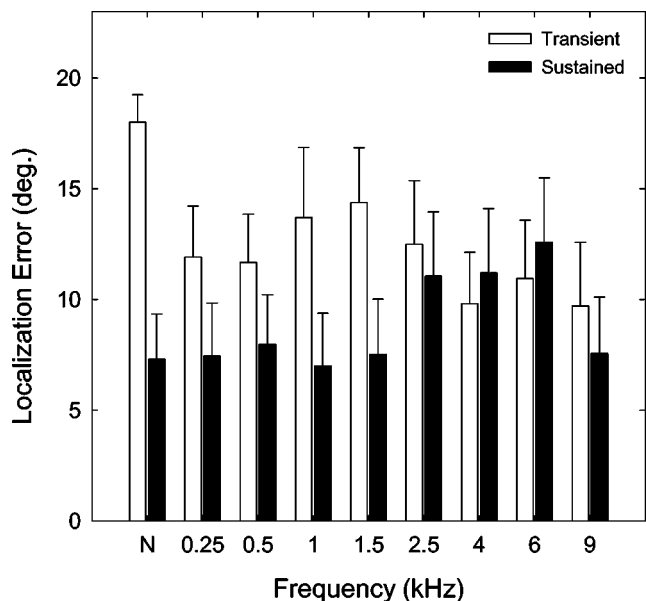


FIG. 4. The mean horizontal error in localizing the transient (white bars) and sustained (black bars) FE stimuli as a function of stimulus frequency for three cats. Data are averaged across the left and right stimulus conditions and across the echo-reduced and echoic room conditions. Error bars represent between-subject standard errors.

lated mean errors for localizing FE stimuli when the cats indicated the transient or sustained FE stimuli (Fig. 4). Localization errors for the transients were high for broadband noise and slightly higher for low-frequency pure tones than for high-frequency tones. Errors were fairly constant for the sustained signals across all frequencies, increasing slightly at higher frequencies, mirroring the same trend for SS trials (Fig. 2). Thus, at the lowest frequencies where the FE is operating on only a small percentage of the trials, the illusion is not only not as prevalent, but it is also not as robust since the cats are not looking accurately at the transient's location.

IV. DISCUSSION

These experiments demonstrate, for the first time, that a nonhuman animal experiences the auditory Franssen Effect illusion. Although there is always some uncertainty in determining whether an animal is experiencing an illusion such as the FE in the same way a human does, our methodology of first training cats to look to the apparent locations of simple stimuli that can be accurately localized (e.g., broadband noise) for a food reward and then interspersing, on a small percentage of trials, stimuli expected to elicit the illusion (and for which we do not define a "correct" response) is one way to determine objectively how cats perceive complex illusory stimuli. We have also used this technique successfully to demonstrate that cats experience the precedence effect (Populin and Yin, 1998; Tollin and Yin, 2003).

In our experiments, cats localize FE stimuli towards the location of the transient, ignoring the much longer steady-state sound, predominantly at high frequencies. The fact that this happens at the high frequencies where cats have trouble localizing single source stimuli and not at low frequencies or with broadband noise stimuli, which cats localize more accurately, supports the hypothesis that cats experience this

auditory illusion. An alternative explanation for the findings, that the cats simply look towards the first stimulus (i.e., the transient), is not supported by our data since there were many stimulus conditions where the cats almost never looked towards the transient (e.g., broadband noise).

Although our localization methodology differed significantly from the discrimination methods used in previous studies of the FE in humans, the correlations between poor sound localization ability for SS tones and the incidence of the FE were quite similar across species. There were differences, however, in the prevalence of the FE between cats and humans. In Yost *et al.* (1997), when humans were asked to discriminate the paired FE signals from the SS signal at the transient's location, the FE was evoked on $\sim 2\%$ of trials for broadband noises, similar to the cats. However, the FE reached a maximum of only $\sim 35\%$ of trials for 1.5 kHz tones. Our cats showed a more pervasive FE, indicating the auditory image at the transient's location in 44–78% of all trials for all frequencies above 2.5 kHz. This difference is likely seen because the cats were actively localizing the sounds while the human observers only had to discriminate a difference between SS and FE stimuli, a difference which need not be based on apparent location. Until similar localization experiments are completed on humans, a direct comparison of the prevalence of the FE in cats and humans cannot be made.

Another difference between our results and those from humans was that we found little dependence on room conditions. The cats exhibited errors in localizing SS stimuli and also showed the FE equally under echo-reduced and echoic room conditions (see regression lines in Fig. 3). This difference might be due to either excessive acoustic reflections from the equipment necessary to conduct these experiments under our echo-reduced conditions, or from the less-reflective echoic conditions presented to our cats compared to the humans. Our acoustic measurements of the testing chamber under echoic and echo-reduced conditions suggest the latter explanation, but since the previous experiments on the FE illusion in humans used discrimination rather than localization procedures, we do not know whether the higher incidence and independence of the acoustic environment of the FE in cats are due to species differences or differences in methodology.

The FE is thought to be related to the precedence effect (PE), another auditory illusion where the initial acoustic stimulus location dominates over any later occurring stimulus locations (Wallach *et al.*, 1949). Although the PE illusion has been demonstrated in a number of animal species (Dent

and Dooling, 2003; Keller and Takahashi, 1996; Kelly, 1974; Tollin and Yin, 2003), this is the first demonstration of the Franssen illusion in nonhumans and the first to show it using a localization, rather than a discrimination, task. Mechanisms for the PE, which occur for time periods $< \sim 100$ ms, are likely to be different from those involved in this illusion because of the long-lasting nature of the suppression of the directional information from the sustained stimulus, which has been shown to last indefinitely in humans (Berkley, 1983). Now that the illusion has been demonstrated in cats, we can seek its underlying neural correlates.

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