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Comment on Greene et al.: Spatial hearing ability of the pigmented Guinea pig (*Cavia porcellus*): Minimum audible angle and spatial release from masking in azimuth

The recent study of sound localization in Guinea pigs by Greene et al. (2018) addresses the relationship between the magnitude of the interaural cues generated by an animal's head and its sound-localization acuity. In doing so, they present a table of nine species showing that the larger an animal's head, the more accurately it can localize sound. They go on to say that “Heffner (2004) *postulates* [emphasis added] that animals with larger heads could potentially benefit from the availability of a larger range of acoustical ILDs [interaural level differences] and ITDs [interaural time differences] to use in determining the source azimuth”. However, although we have considered the possibility that head size, and the resulting magnitude of the binaural locus cues, determines sound-localization acuity, we have never found that to be true. We would like to comment on this.

Many years ago, we began studying hearing in large mammals, specifically horses, cattle, and an elephant. Although we were primarily interested in the upper frequency limits of their audiograms, we took advantage of this opportunity to study their sound-localization abilities as well. At the time, little was known about the variation in sound localization among mammals as only half a dozen species had been tested. We knew, as did others, that humans, with our comparatively large heads, had better acuity than monkeys and cats, which, in turn, had better acuity than smaller mammals such as rats and hedgehogs. Thus, we began the study expecting that large-headed animals would have better localization acuity than smaller mammals.

At first, the results were as expected, with the localization ability of the elephant being a little better than that of humans. However, the theory that head size was correlated with sound localization acuity collapsed when we tested horses and cattle. We can still recall our initial disbelief when we found that horses and cattle were much worse at localizing sound than rats. Believing that sound-localization acuity was determined by the distance between the ears, we continued to push for better performance, but were eventually forced to accept that horses and cattle have poorer sound-localization acuity than much smaller mammals. Consequently, by 1979, we had realized that a mammal's head size is not a good determinant of its sound-localization acuity. This led us to embark on two lines of research. The first was to acquire two additional horses for more detailed testing using a simpler behavioral procedure; their results replicated the initial findings of poor localization acuity in horses (Heffner and Heffner, 1984). The second line of research was to begin a survey of sound localization in mammals of widely varying sizes, lineages, and lifestyles.

Initially, we had no clear idea why sound-localization acuity should vary and we examined many potential explanatory factors, including trophic level (i.e., predator vs. prey), nocturnal vs. diurnal activity pattern, and three visual factors (maximum visual acuity, width of the binocular visual field, and width of the field of best vision). Of these variables, only the width of the field of best vision was closely correlated with sound-localization acuity, unconfounded by all the other factors. Specifically, the narrower an animal's field of best vision, the better its sound-localization acuity, with the correlation between these two factors hovering around $r = 0.90$—a value that was not significantly reduced in a multiple regression analysis. This suggested that the main purpose of sound localization is to direct an animal's gaze, its best acuity, to the source of a sound. For a detailed statistical analysis of these factors, see Heffner and Heffner, 1992; for the most recent description, see Heffner and Heffner, 2016.

With the addition of the Guinea pig sound-localization data presented by Greene et al. (2018), there are nearly forty species of mammals whose sound-localization acuity is known (for references to other species, see Heffner et al., 2014). Although Greene et al. restricted their comparison to small species, they left out small mammals, such as the least weasel and the dog-faced fruit bat, that have better sound-localization acuity than some larger mammals. Moreover, their focus allowed them to omit large mammals, such as horses and cattle that have poorer sound-localization acuity than many smaller species.

In summary, we argue that mammals are not under pressure to be as accurate or as sensitive as physically possible. Instead, they are under biological pressure to have sensory abilities adequate to survive and reproduce. This is why sound-localization acuity in mammals does not correspond with the magnitude of the physical locus cues available to them, but with the accuracy needed to direct their best vision to the source of a sound. Species such as mice, gerbils, horses and cattle which possess broad regions of best vision will require less accuracy to direct that vision than species that have a narrow fovea or area centralis, such as humans, macaques, cats, and pigs (Heffner and Heffner, 2018). Thus, not only is there no reason to expect different species to have similar binaural time and intensity thresholds, but it may be that few, if any, species push their binaural analyses to the physiological limit of their auditory systems.

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