

An Argument for Using Ethologically “Natural” Behaviors as Estimates of Unobservable Sensory Processes. Focus on “Sound Localization Performance in the Cat: The Effect of Restraining the Head”

David L. Sparks

Department of Neuroscience, Baylor College of Medicine, Houston, Texas

A major goal of systems neuroscience is to describe neural representations of the environment that mediate perception. An experimental strategy adopted by researchers involved in this effort is to obtain three-dimensional correlations between the physical properties of a stimulus, a psychophysical report of the subject, and measures of intervening neural events. Perception is, of course, a private event and objective indirect measures of the percept are obtained. Experiments related to the perceived location of a stimulus often ask subjects to point to the stimulus or to orient to it with an eye movement. Studies using orienting eye movements as the behavioral index of perceived location have become more common now that precise and accurate methods of measuring eye position are readily available. In this issue, Tollin et al. (p. 1223–1234) report that orienting movements of the eyes in head-restrained cats significantly underestimate the actual ability of the animals to localize auditory and visual targets.

The target paper compares two commonly used methods of measuring the accuracy and precision of the localization of visual and auditory targets in the cat: eye saccades in animals with their heads restrained and combined eye-head movements (gaze saccades) in animals without head restraint. The effects of stimulus duration were also examined. The shortest-duration stimuli were no longer present when the orienting movement began, and therefore the change in gaze position may have been based on a stored representation of the spatial location of the target. With long-duration stimuli, the stimuli were still present after the orienting movements began and dynamic sensory processing could influence movement accuracy. Target location varied in both azimuth and elevation. Because independent neural pathways that depend on different spatial cues are used to compute the azimuth and elevation of acoustic stimuli (see Zwiers et al. 2003 for a summary of relevant data), the effects of head restraint on localization were analyzed separately for azimuth and elevation.

Localization accuracy of both visual and auditory targets improved when measured using a combination of eye and head movements. The effects were not small. When brief stimuli were presented 9 and 18° along the azimuth from the central fixation target, head-restrained animals mislocalized visual and auditory targets by an average of 6.73 and 7.24°, respectively. When the head was not restrained, these values dropped to 1.21 and 0.15°. Improvement was greatest for the shortest-duration stimuli, not the longer duration stimuli that

allowed dynamic processing during the orienting movements.

Based on earlier studies (Populin and Yin 1998) using head-restrained animals as subjects, localization of auditory targets was thought to be less accurate than localization of visual targets and localization to be more accurate in azimuth than in elevation. But there is a striking improvement in the localization of auditory targets when the head is not restrained. Differences in localization of visual and auditory targets are small, and localization is very accurate in both azimuth and elevation. Interestingly, while the average mislocalization error (accuracy) was significantly reduced when the head was unrestrained, precision (variability around the average localization estimate) was not affected.

When used as a measure of localization, head-restrained eye movements significantly underestimate the ability of the animal to do so. It is interesting to speculate on why this is true even when subjects are reporting on the location of targets that do not require movements outside the oculomotor range. The authors point out that this underestimate of target location in space could still be a veridical report of what the animal perceives. They speculate that disruptions of the usual relationship between eye position and neck muscle activity produced by head restraint and the associated change in the pattern of proprioceptive and/or corollary discharge signals could produce illusory perceived locations. In this context, it should be remembered that sound localization behaviors are plastic. For example, modified visual-auditory experience induces changes in sound localization so that the localization of auditory targets conforms to modified visual representations, even when this requires an erroneous representation of the actual location of sound in space (see Zwiers et al. 2003 for more details). The authors offer a second possible explanation: the amplitudes of the eye saccades produced when the head is restrained may be reduced by the amount that the head would have contributed to the gaze saccade if the head had been free to move. Several lines of evidence summarized in DISCUSSION make the second explanation more plausible than it may seem to the nonexpert reader.

The goal of the experiment was to test the hypothesis that localization would be more accurate when the head was unrestrained. The authors (and others) had observed that cats usually use a combination of eye and head movements to orient to novel stimuli, even when the required change in the direction of gaze is small. Thus they expected the ethologically “natural” condition (head unrestrained) to pro-

Address for reprint requests and other correspondence: 1 Baylor Plaza, Baylor College of Medicine, Houston, TX 77030 (E-mail: sparks123@cox.net).

vide a better estimate of the ability of the animal to localize the stimuli, but I suspect that even the authors were surprised by the magnitude of the effects. In retrospect, however, the ethologically “unnatural” condition of measuring eye movements in head-restrained animals has been misleading in the past. The collicular motor maps currently being used in anatomical, physiological, pharmacological and computational studies were defined using microstimulation in head-restrained subjects and are grossly distorted (Sparks 1999).

REFERENCES

- Populin LC and Yin TC.** Behavioral studies of sound localization in the cat. *J Neurosci* 18: 2147–2160, 1998.
- Sparks DL.** Conceptual issues related to the role of the superior colliculus in the control of gaze. *Curr Opin Neurobiol* 9: 698–707, 1999.
- Tollin DJ, Populin LC, Moore JM, Ruhland JL, and Yin TCT.** Sound localization performance in the cat: the effect of restraining the head. *J Neurophysiol* 93: 1223–1234, 2004.
- Zwiers MP, Van Opstal AJ, and Paige GD.** Plasticity in human sound localization induced by compressed spatial vision. *Nat Neurosci* 6: 175–181, 2003.