

## **The eyes and ears both have it: Frames of reference in the auditory pathway**

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The ability to localize sounds is critical to survival -- predators and prey alike use sound to detect friend and foe. The location of a sound source can be deduced from differences in sound arrival time and pressure level across the two ears (for review see Blauert, 1997). Brain areas involved in sound localization have been assumed to use a head- (or ears)-centered frame of reference derived from these cues. However, only a few studies have actually addressed the frame of reference of auditory signals in the brain, and those that did have found evidence that auditory signals are ultimately encoded in a frame of reference anchored to the positions of the eyes. The superior colliculi of primates and cats contain neurons whose auditory receptive fields move when the eyes move, even though the head and ears are stationary (Hartline et al., 1995; Jay and Sparks, 1984; Jay and Sparks, 1987; Peck et al., 1995). In primate frontal eye fields, motor activity related to saccades to auditory stimuli depends on the position of the sound with respect to the eyes (Russo and Bruce, 1994). In lateral intraparietal cortex, memory activity for sounds is affected by the position of the eyes in the orbits (Stricanne et al., 1996).

Because this eye-centered frame of reference for sound location was discovered in oculomotor areas, it has been presumed to relate specifically to eye movements. However, an eye centered reference frame for sounds could be valuable for a variety of reasons. Perceptual comparison with visual information (e.g. visual capture and the ventriloquism effect) would be well served by an eye-centered reference frame, as would guidance of any behavior that can be governed by both visual and auditory stimuli (e.g. Cohen and Andersen, 2000). If an eye-centered reference frame for sound has broad utility, then sound locations may be encoded in an eye-centered reference frame beginning much earlier in the auditory pathway than has previously been imagined.

We investigated the frame of reference at an early point in the ascending auditory pathway, namely the inferior colliculus (IC). The IC is situated above the convergence of binaural signals in the superior olivary complex (for review see Ehret, 1997), and nearly all input to all higher areas passes through it. Lesions of the IC can cause deficits in sound localization behavior (Kelly and Kavanagh, 1994; Wagner, 1993; Zrull and Coleman, 1997). Neurons sensitive to the locations of sounds in space have been reported by a variety of studies using free field acoustic stimuli in cats, owls, and guinea pigs (Aitkin and Martin, 1990; Aitkin et al., 1984; Aitkin and Martin, 1987; Aitkin et al., 1985; Binns et al., 1992; Bock and Webster, 1974; Calford et al., 1986; Knudsen and Konishi, 1978; Semple and Aitkin, 1979; Semple et al., 1983; Volman and

Konishi, 1989; Wagner et al., 1987), but little is known about the spatial response properties in monkeys (Jay and Sparks, 1987). In addition to having a strategic location, the IC shows some intriguing multisensory properties, receiving visual input (to the pericentral nucleus: Itaya and Van Hoesen, 1982; cats: Mascetti and Strozzi, 1988) and somatosensory input (to the external nucleus: Aitkin et al., 1978; Aitkin et al., 1981; Paloff and Usunoff, 1992; Schroeder and Jane, 1976) in addition to auditory input. It has also been implicated in visually guided recalibration of auditory spatial processing in barn owls (Brainard and Knudsen, 1993a; Brainard and Knudsen, 1993b; Feldman et al., 1996)

We found that eye position modulates the responses of about 33% of IC neurons to sound. An example is shown here:

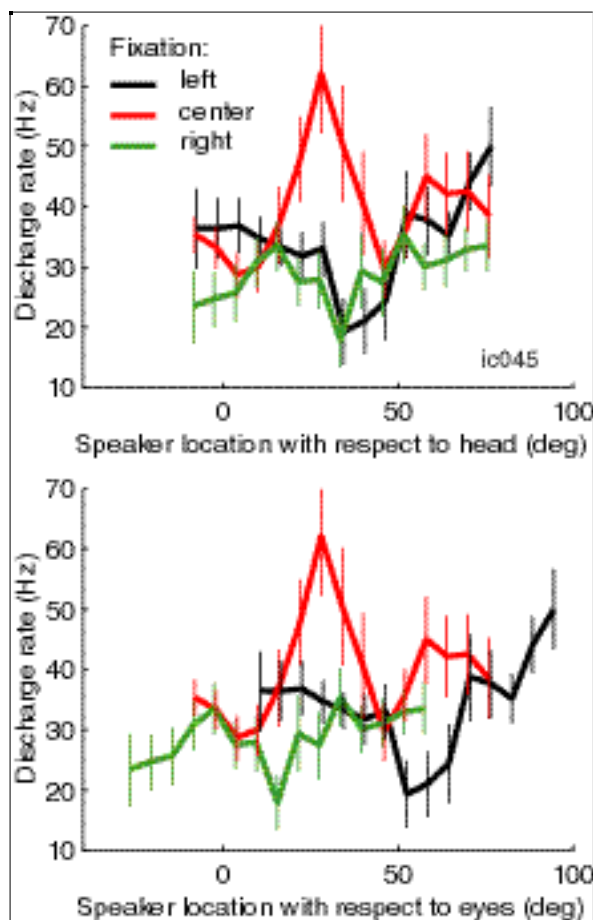


Figure 1. Response of an inferior colliculus neuron to sounds at different locations as a function of eye position. The top graph shows the responses to sounds at various locations with respect to the head. The three traces represent responses measured at each of the three eye fixation positions ( $18^\circ$  left, center, and  $18^\circ$  right). The bottom graph realigns the data to show the responses as a function of sound location with respect to the eyes. This cell was recorded from the left IC. Negative values on the abscissa indicate leftward (ipsilateral) speaker locations.

To summarize the trend in coordinate frame across the whole population of cells, we computed a head-centered and an eye-centered mean response offset for each cell:

$$offset = \frac{\frac{\sum_{i=1}^n abs(\bar{R}_{e,i} - \bar{R}_{c,i})}{2n}}{abs(\bar{R})} * 100$$

where  $\bar{R}_{e,i}$  and  $\bar{R}_{c,i}$  are the average responses of the cell to a sound at speaker location  $i$  while the eyes fixated either eccentrically ( $e$ ) or at the center ( $c$ ). We only included speaker locations that existed for all three fixation positions in both head- and eye-centered frames of reference for this analysis;  $n$  corresponds to the number of speaker locations.  $\bar{R}$  is the average response across all stimulus conditions. In short, this metric represents the average difference between the responses for each eye position when plotted in head and eye-centered reference frames respectively, expressed as a percentage of the average auditory response overall. These metrics therefore summarize the agreement between the response curves for the three fixation positions in head- and eye-centered reference frames, respectively. A true head-centered frame of reference would have a head-centered mean response offset of 0, and a true eye-centered frame of reference would have an eye-centered mean response offset of 0.

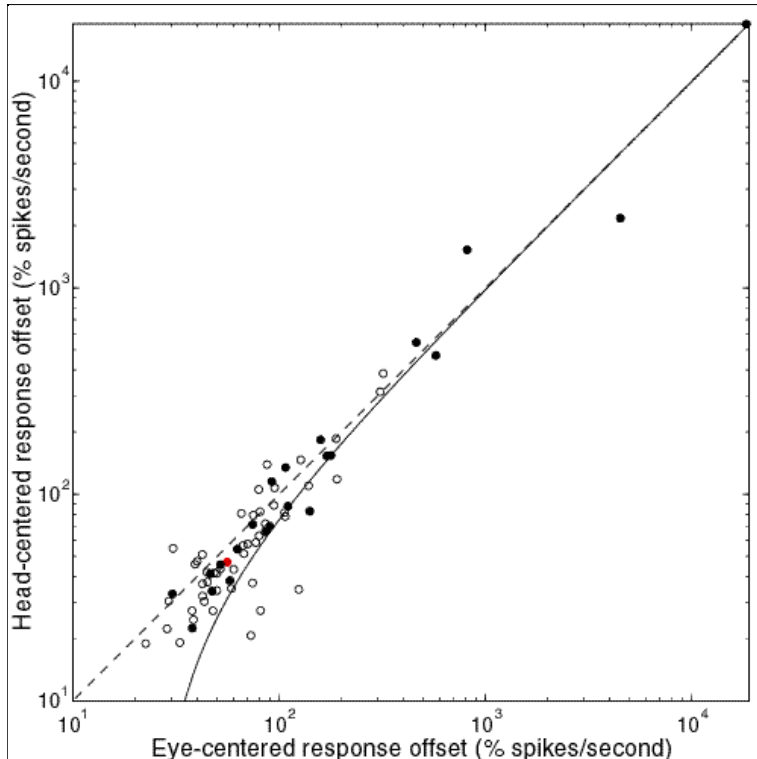


Figure 2. Average response offset due to fixation position in head-centered vs. eye-centered reference frames, expressed as percentage of the average response of each cell across all stimulus conditions. Points lying on the line of slope 1 (dashed trace) indicate responses that align equally well (or poorly) in head- and eye-centered reference frames. Points falling below the dashed line indicate responses that were better aligned in a head-centered reference frame; those above the line were better aligned in an eye-centered reference frame. Filled circles indicate cells that showed a significant main effect of eye position in the 2-way ANOVA; the red circle is the cell from Figure 1. The linear regression line (solid) had a slope of 1.00,  $r^2 = 0.98$ , ( $r = .99$ )  $p < 0.001$ . The line appears curved on this log-log plot due to its intercept at a value of -25.

In summary, cells in IC encode sound location in a distributed fashion that is intermediate between head- and eye-centered reference frames. A computational analysis of the signals present in IC suggests that the information they contain is sufficient for computing an eye-centered reference frame without requiring any additional information. These results suggest that the coordinate transformation of auditory signals from a head- to an eye-centered frame of reference is gradual, and that it has begun by an earlier point in auditory processing than has previously been appreciated.

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