### What is condition?

Rowe and Houle[14] referred to condition as the pool of resources available for utilization. This definition of condition corresponds to residual reproductive value or state in life history models and accounts for a large proportion of fitness[14]. This definition means that condition cannot be measured directly. Therefore, we used the residual mass as an estimate of condition[24,25]. Intuitively, residual mass approximates well the resources that should be available for utilization and there is likely to be a relationship between the two, but we acknowledge that this is not exactly the same as condition as used by Rowe and Houle[14].

### Genetic variances and correlation

To estimate the genetic variance in male courtship rate and in male condition we used a standard half-sib breeding design[5,6]. We housed each of the 12 field-collected sires with three randomly selected $F_1$ laboratory-reared virgin dams. Dams did not differ in body size across sires. After five days, dams were set up individually to construct brood masses. As males of this species occasionally help in constructing the brood mass, non-genetic paternal effects may occur. This was taken into consideration in the experimental design by excluding males after mating so that females constructed brood masses alone. Thus, our experimental design excluded the possibility of non-genetic paternal effects.

It has also been suggested that females may differentially invest in their offspring depending on the attractiveness of the male[27–29]. Differential investment based on male attractiveness could result in non-genetic similarities between the offspring of dams allocated to the same sire. If there is differential investment, apparent genetic sire effects may be confounded by non-genetic maternal effects. This problem of interpretation is inherent in all half-sib breeding designs where female investment has not been measured. In our experiments we took this possibility into account by measuring the female investment in offspring. There is variation in the weight of brood masses constructed by females, which is known to have a strong effect on offspring size and development. Thus, we measured the female investment as the brood mass weight. We found evidence for differential investment in brood mass weight translating into differential investment in offspring size (unpublished data), but brood mass weight did not influence offspring condition ($r = -0.042$, $n = 167$, $P = 0.596$) or courtship rate ($r = -0.053$, $n = 228$, $P = 0.427$). Therefore, our results do not arise from differential investment by females. However, we did not measure the size of the egg itself in the brood mass. Nevertheless, offspring growth and development in dung beetles is almost entirely dependent on maternal investment in brood mass[30] so that relatively subtle differences in the allocation of resources into eggs, if they existed, are unlikely to contribute to the sire effects reported here.

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Correspondence and request for materials should be addressed to J.S.K. (e-mail: jkotiaho@cc.jyu.fi).

# Hyperacute directional hearing in a microscale auditory system

**Andrew C. Mason*, Michael L. Oshinsky† & Ron R. Hoy**

*Neurobiology and Behaviour, SG Mudd Hall, Cornell University, Ithaca, New York 14853, USA*

**The physics of sound propagation imposes fundamental constraints on sound localization: for a given frequency, the smaller the receiver, the smaller the available cues[1]. Thus, the creation of nanoscale acoustic microphones with directional sensitivity is very difficult. The fly *Ormia ochracea* possesses an unusual 'ear' that largely overcomes these physical constraints[2–5]; attempts to exploit principles derived from *O. ochracea* for improved hearing aids are now in progress[6]. Here we report that *O. ochracea* can behaviourally localize a salient sound source with a precision equal to that of humans[7]. Despite its small size and minuscule interaural cues, the fly localizes sound sources to within 2° azimuth. As the fly's eardrums are less than 0.5 mm apart, localization cues are around 50 ns. Directional information is represented in the auditory system by the relative timing of receptor responses in the two ears. Low-jitter, phasic receptor responses are pooled to achieve hyperacute timecoding[8,9]. These results demonstrate that nanoscale/microscale directional microphones patterned after *O. ochracea* have the potential for highly accurate directional sensitivity, independent of their size. Notably, in the fly itself this performance is dependent on a newly discovered set of specific coding strategies employed by the nervous system.**

*Ormia ochracea* (Diptera: Tachinidae) is a parasitoid fly[10,11]. Gravid female flies locate their hosts, male crickets, by homing in on their loud, persistent songs. Because of its small body size, *O. ochracea* must deal with extremely small interaural difference cues to guide directional hearing[3]. The host cricket's calling song is an amplitude-modulated 5 kHz tone (6.8 cm wavelength); however, the fly measures less than 1 cm in any aspect and the distance

* Present address: Division of Life Sciences, University of Toronto at Scarborough, 1265 Military Trail, Scarborough, Ontario M1C 1A4, Canada.
† Present address: Department of Neurology, Jefferson Headache Center, Thomas Jefferson University, Philadelphia, Pennsylvania 19107, USA.

between its eardrums is about 0.5 mm. This means that 5-kHz sound waves are not diffracted by the fly's body and generate no interaural intensity difference; indeed, none can be measured[3]. The interaural time difference (ITD) is frequency-independent and depends only on the speed of sound and the distance between the two ears. The maximal ITD in *O. ochracea* at 90° azimuth is 1.5 μs, and decreases to zero for a sound source on the midline axis (0° azimuth). This minuscule ITD is the only physical cue available for computation of source direction; yet *O. ochracea* can reliably localize cricket song both in nature and in the laboratory[10–12]. The principal evolutionary innovation responsible for the ability of *O. ochracea* to overcome its unfavourable auditory physics is a pair of anatomically and functionally coupled eardrums[3,4]. The mechanical resonance of *O. ochracea*'s peripheral auditory apparatus in a directional sound field transforms the minuscule time delay in the free field into two cues that can be used by its nervous system. First, the interaural time delay between the ipsilateral and contralateral eardrums is increased from a maximum of 1.5 μs to about 55 μs. Second, the vibration amplitudes of the ipsilateral eardrum are up to 10 dB greater than those of the contralateral, for sound sources at 45–90° azimuth. Thus, minute ITDs in the sound field are converted by the tympanal mechanics to interaural differences that are processed neurally, as described below.

To measure the auditory directional acuity of *O. ochracea*, we tethered females on a spherical treadmill (see Methods). The treadmill was attached to a moveable speaker, which could be positioned around the fly with 0.5° accuracy (Fig. 1). The flies walked in response to simulated cricket chirps broadcast from the speaker, and their movements were recorded by computer. Flies tracked changes in speaker location and altered their walking trajectory accordingly (Fig. 1b, c). Response latency was consistent (mean ± s.d.; 46.6 ± 4.9 ms), and similar to freely walking conditions (49 ± 22 ms). The duration of walking responses exceeded the stimulus duration (200 ms), and in most cases flies continued to walk with a constant velocity throughout the 1.2-s recording interval. Flies reliably turned in the direction of the speaker (Figs. 1c, 2a) and the turns were graded: larger turns in response to larger speaker angles up to 20–30° (Fig. 2b), the maximal response.

We measured the directional sensitivity of flies in two ways. First, by repeatedly presenting stimuli from speaker positions of the same angular displacement on either side of flies, we were able to measure their accuracy in lateralizing the sound source as a function of angle of incidence (that is, simply discriminating rightward from leftward speaker locations). Second, we compared the mean angular headings for different speaker locations on the same side as a measure of the flies' ability to truly localize the sound source (see Methods). Flies were extremely sensitive to changes in the location of the speaker by both measures. Overall, flies showed significant discrimination of sound angles as small as ± 2°, and some individuals were able to discriminate speaker angles of ± 1° from the midline (Fig. 2c, d). In the localization task, mean walking paths for individual flies and pooled responses of seven flies were significantly different, even for speaker locations on the same side of the midline differing by only 1–2° (Fig. 2e, f). Thus, flies are not only able to lateralize a sound source lying very close to the midline axis, but can also truly localize the source by making very precise turning movements. As the fly's two eardrums are separated by only 0.5 mm, a 1° angle of incidence represents an ITD cue at the tympanal membranes of a mere 25 ns. Similarly, a change in speaker location from 1° to 2° azimuth corresponds to a change in ITD from 25 ns to 50 ns. These minute time differences are the only directional cues available to the auditory system of the fly.

What are the neurosensory mechanisms that underlie the flies' behavioural ability to localize sound with such remarkable accuracy? We recorded the responses of individual auditory receptors. Each of the fly's ears contains about 100 receptor neurons[5,13]. Auditory receptors varied in their absolute sensitivity to sound level, with single unit thresholds at 5 kHz ranging from 55–95 dB sound pressure level (SPL) (mean ± s.d.; 77.0 ± 8.3 dB SPL, $n = 28$). Three characteristics of receptor physiology suggest that auditory directionality is based on a spike time code at the receptor

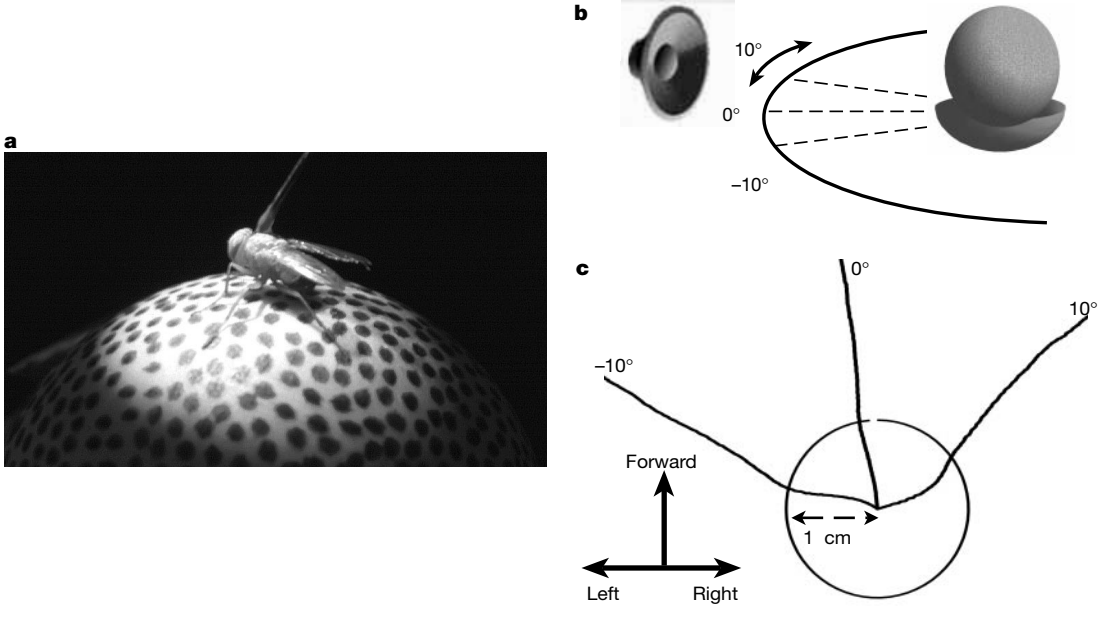


**Figure 1** Behavioural measurement of auditory directional acuity. **a**, Female *O. ochracea* tethered on a speckled spherical treadmill. **b**, Simulated cricket calls broadcast from a moveable speaker elicit phonotactic walking responses from the fly. The resulting rotation of the ball is detected by an optical sensor and recorded by computer. **c**, Virtual walking path of *O. ochracea* in response to stimuli from different directions. The forward direction (on the midline axis) is 0°. Negative angles represent speaker positions to the left of midline; positive angles to the right. The circle corresponds to a 1 cm radius of real walking distance.

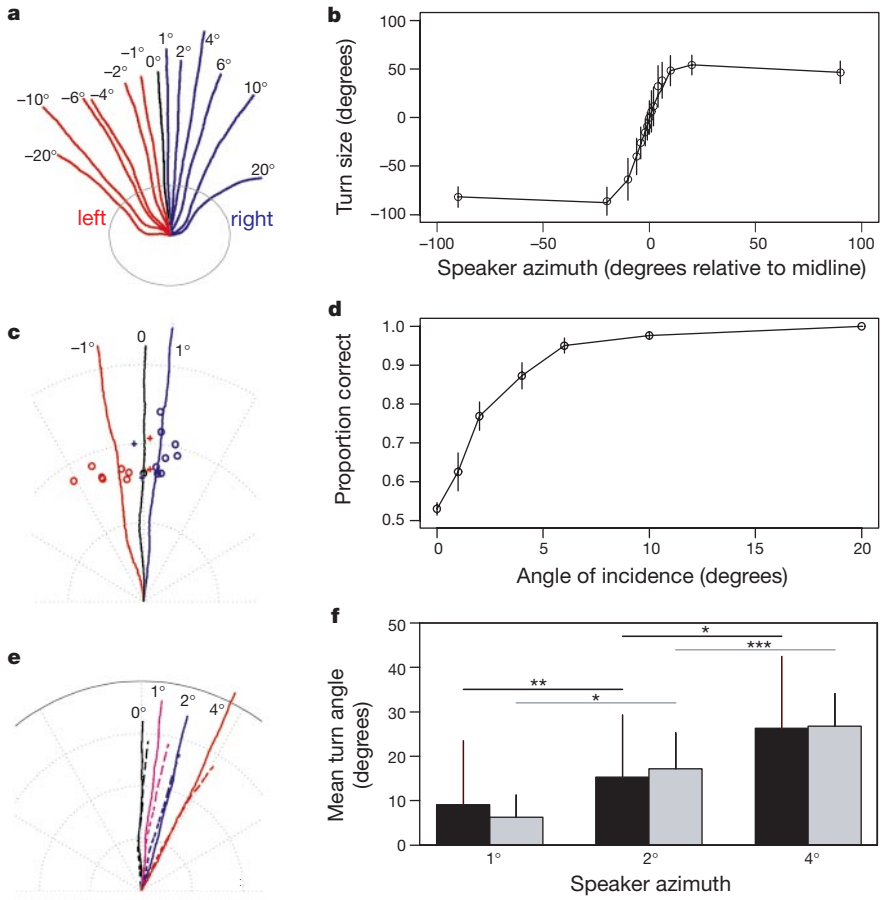


**Figure 2** Directional responses. **a**, Mean paths of one fly ($n = 10$ trials for each speaker position). **b**, Turn size (degrees of rotation relative to 0° path, mean ± circular s.d.), measured at midpoint of each run ($n = 7$ flies, 10 trials per fly per angle). **c**, Sound lateralization. Responses of a fly with mean paths significantly different at ± 1° ($n = 10$, mean path angles: left, –10.0 ± 11.0°, Rayleigh's $Z = 0.9566$; right , 11.1 ± 4.9°, $Z = 0.9962$; left versus zero, $F = 7.8442$, $P < 0.01$; right veursus zero, $F = 5.4731$, $P < 0.025$)[18]. Symbols indicate midpoints of individual runs. Individual runs for all flies and angles were scored (circles, correct; plus signs, incorrect) depending on whether they were displaced from the mean 0° run in the same direction as the speaker. **d**, Mean (± s.e.) proportion of correct turns for all speaker angles (right and left pooled, $n = 19$ flies, 20 turns per angle per fly). **e**, Sound localization. Mean paths ($n = 10$ runs per angle) for one fly (broken lines), and all flies pooled (solid lines, $n = 7$) are shown. **f**, Turn angles (mean ± s.d.) for individual (black) and pooled (grey) responses varied with speaker azimuth. Asterisk, $P < 0.05$; double asterisk, $P < 0.01$; triple asterisk, $P < 0.001$).

level. First, we found that most receptors responded to a sound pulse with only a single spike, independently of sound level or duration (Fig. 3a); they never produced additional spikes with increasing sound level. Second, increases in stimulus intensity were instead coded by response latency—the mean latency for a given receptor systematically decreased as stimulus intensity increased (Fig. 3d). Third, at a given sound level the response latency was very consistent, with an average jitter (s.d. of the latency) of 70 μs (Fig. 3b). This may be compared with jitter at the millisecond level in primate cortical neurons[14], but only 30 μs for the specialized time-coding receptors in the electric fish *Eigenmannia*[15]. The individual auditory receptors in *O. ochracea* fire with highly consistent latency, the value of which is a function of stimulus intensity (Fig. 3d) resembling the situation in electric fish. It is important to realize that differences in sound direction at the auditory periphery cause a difference in the relative amplitude at which the eardrums vibrate[3]—equivalent to interaural differences in stimulus intensity. Thus, sound direction can be represented by the relative timing of receptor spikes in the left and right auditory channels.

To verify the effects of sound direction on the timing of afferent auditory responses at the population level, we made simultaneous extracellular recordings from the two auditory nerves while changing the location of a sound source. The time course of the auditory summed action potentials (SAPs) matched the timing and threshold characteristics of individual receptors (Fig. 3b, c). Notably, the dependence of SAP latencies on stimulus intensity matched the latency/intensity relationship shown by individual receptors. In fact, overall population response latencies reflected those of individual receptors over the full range of intensities tested (Fig. 3c, d). Direct measurement of the mean interaural latency differences in auditory responses as a function of sound direction showed that they varied with angle of incidence for angles up to 20–30° but saturated for higher angles, mirroring the fly's behavioural responses (Figs 2b, 3e). Thus, interaural latency differences can encode the position of a sound source because the time-preserving characteristics at the single-unit level confer sufficient temporal coherence to the afferent population comprising each auditory channel.

Nevertheless, difference cues at the receptor level remain extremely small. Interaural latency differences are about 3.5 μs per degree over a range of 30° azimuth on either side of the midline. Therefore, for the smallest sound angles consistently discriminated by *O. ochracea* (2°), the overall latency difference is about 7 μs. The variability of receptor-spike timing (70 μs jitter for individual receptors) is much greater. Hence, reliable detection of a mean latency difference of 7 μs can only be achieved by pooling the responses of a population

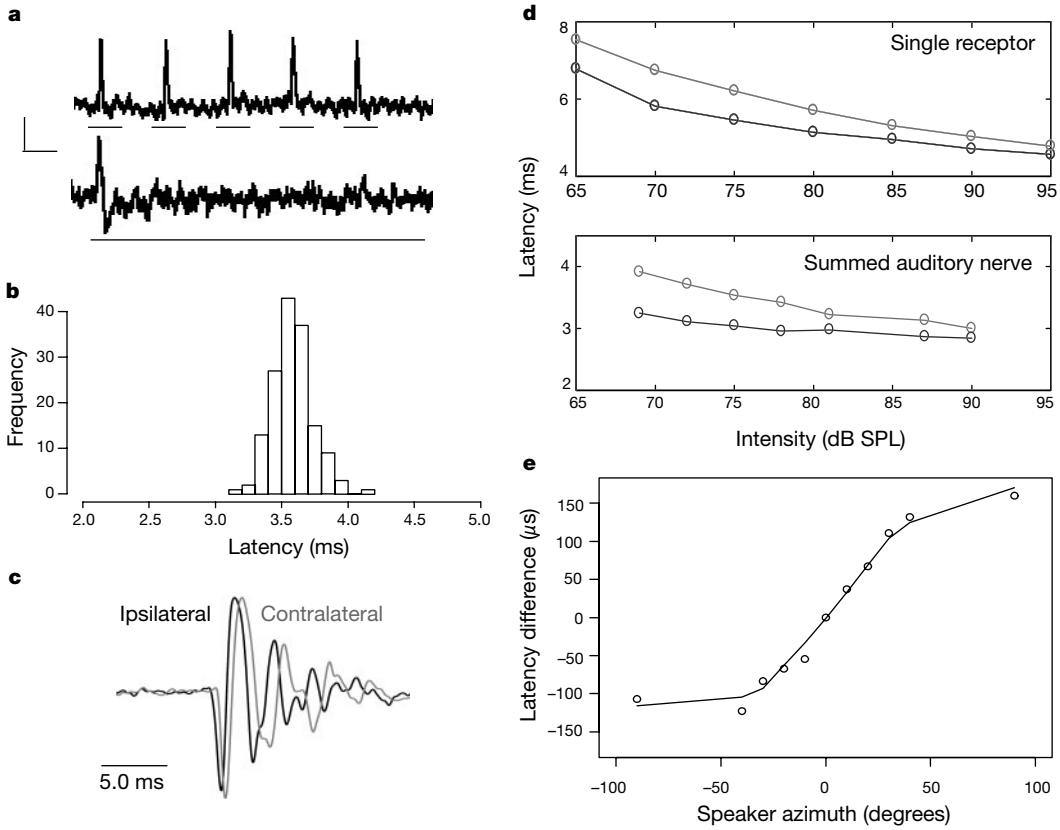


**Figure 3** Characteristics of auditory receptors. **a**, Most receptors respond with only a single spike at stimulus onset, independently of duration. Responses are shown for a simulated cricket chirp (top) and continuous tone (bottom). Lines indicate stimulus timing (5 kHz, 85 dB SPL). Scales: horizontal, 10 ms; vertical, 2 mV. **b**, Spike latency for a single receptor. **c**, Summed action potentials recorded in the left (black) and right (grey) auditory nerves in response to speaker at –90° (50 sweeps averaged). The effect of direction on response latency is apparent (ipsilateral response leads). **d**, Latency versus stimulus intensity in single receptors (upper, speakers at ±90°) and summed action potentials (lower, speaker at –90°). Responses shown are for –90° speaker location. Latency declines with increasing intensity in both ipsilateral (black) and contralateral (grey) responses, but ipsilateral latencies are shorter at all intensities. **e**, Mean latency difference in auditory nerve responses (left – right, $n = 11$) versus speaker position. Latencies in the left auditory nerve are shorter than those of the right nerve for leftward sound source locations, but are longer for rightward locations.

of receptors with lower individual timing accuracy—a phenomenon termed temporal hyperacuity[8,9]. Consistently, the fly auditory system seems to be specialized for timing information, with frequency discrimination accomplished primarily through peripheral filtering mechanisms[4]. If receptor neurons are pooled solely to improve timing information, such a system only requires the accurate preservation of the relative timing of inputs from the two ears at subsequent stages of processing[16]. Through this economy of coding, the relatively simple nervous system of the fly can show hyperacute sensitivity.

Our results provide a neuroethological analysis of a remarkable behavioural ability that links both applied and theoretical studies of sensory systems. These results have significant implications for efforts to develop artificial acoustic devices based on the design principles of *O. ochracea* ears[6]. The acoustic orientation behaviour of *O. ochracea* demonstrates that such devices have the potential for very high sensitivity and accuracy. However, the flies' performance is not based solely on biomechanics (that is, the inherent directional properties of its eardrums). The associated neural apparatus is also highly specialized for this singular task. Directional information, initially encoded by *O. ochracea*'s tympanal mechanics, is represented by a population latency code at the receptor level, and then translated into behavioural output with high efficiency and accuracy. *Ormia ochracea* is an ideal system for investigating the statistics of neural information processing[17]. Its behavioural output is tightly linked to sensory input by the primary receptors, and receptor coding is accessible to detailed study at both single-cell and population levels. Although subsequent processing in the fly's central nervous system and motor system is necessary to generate the act of steered locomotion, our results show that for the task of sound localization, the afferent code is simple and well defined. The fly's specializations in auditory processing are as remarkable as its unusual tympanal apparatus. □

## Methods

### Behavioural measurements

We measured auditory directionality using phonotactic walking responses (*O. ochracea* make their final approach to a singing cricket by walking). Flies were fixed to a wire with low-melting-point wax, and this wire was attached to a micromanipulator. Under red light, mounted flies were then placed in a normal walking position on a spherical treadmill. The treadmill consisted of an optically actuated computer-pointing device (Logitech Marble Mouse) that was modified to hold a table-tennis ball floating on an air stream. A random dot pattern on the table-tennis ball activated the optical sensor when the ball was rotated by the walking movements of the tethered fly (for a video clip of the fly's response see www.scar.utoronto.ca/~amason/Movie/flyball2.mpg). The fly's virtual trajectory was recorded by computer, using custom software that captured coordinates at 0.5 ms intervals. The treadmill was located at the centre of rotation of a speaker (Sony MDR-ED228LP, ~1 cm diameter in a 3 cm baffle) that was attached to a movable arm at a distance of 12 cm from the position of the fly. The speaker could be rotated in 0.5° measurable increments through 40° on either side of the midline axis of the fly. We synthesized acoustic stimuli using Tucker-Davis Technologies (TDT) System II hardware and custom software. Stimuli consisted of a train of 5-kHz, 10-ms tone pulses delivered at a rate of 50 pulses $s^{-1}$ with 10 pulses per train for a total stimulus duration of 200 ms. Stimuli were amplified (Harman Kardon PM655), passed through a computer-controlled attenuator (TDT PA-4) and then sent to the speaker. Stimulus timing and amplitude were

controlled by computer.

For comparison of response latencies, freely walking flies were recorded using a Redlake Motionscope high-speed video recorder at 1,000 frames $s^{-1}$. Stimulus generation was as described above.

### Localization and lateralization tasks

Stimulus duration was constant across all presentations, and the response of the fly did not modify the stimulus in any way (that is, the task was open loop). Unlike closed-loop stimulus conditions, in which the directional stimulus would decrease as the fly approached the angle of the speaker, here the angle of the speaker relative to the fly was fixed, and the fly received a constant turn signal throughout the stimulus. Therefore the fly's movements that generate the measured turn angles in these experiments could not bring them to face the direction of the speaker (turn angles should overshoot the actual speaker position). If the flies were simply lateralizing the stimulus source they would receive a constant turn signal (right or left) for the duration of the stimulus, and the angle of the flies' paths relative to the midline axis should be similar for all speaker positions. If the flies were truly localizing the sound source then paths for different speaker positions should be consistently different from one another and turn angle should increase with speaker angle.

### Neurophysiology

Intracellular recordings were obtained from single auditory receptors using glass microelectodes (borosilicate, thin-walled 1.0 mm o.d., 70–120 MΩ). Receptors were recorded in the pterothoracic ganglion near the point of entry of the frontal nerve, which carries the auditory axons. After recordings, cells were injected with Lucifer Yellow and visualized under fluorescence microscopy to confirm that recordings were from primary receptors. Amplified (AM Systems Model 1600) neural responses were recorded by computer (100-kHz sampling rate) using an analogue-to-digital interface (TDT AD1). Stimuli were tone pulses of varying frequency and duration generated using the same system as in the behavioural experiments, but delivered through a different speaker (Realistic Horn Tweeter).

We obtained auditory nerve recordings using tungsten wire electrodes (AM Systems, 0.25 mm). Amplified (AM Systems Model 1800), summed action potentials from both nerves were recorded by computer (100-kHz sampling rate). We carried out recording and stimulation as described above. For these recordings, the preparation was mounted in the same apparatus that was used for the treadmill experiments, and responses from the two auditory nerves were recorded simultaneously for stimuli delivered from different angles of incidence. As the sampling rate of our acquisition system was limited to 100 kHz, the smallest angle of incidence measured in these experiments was 10°.

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Correspondence and requests for materials should be addressed to A.C.M. (e-mail: amason@scar.utoronto.ca).

# Motion direction, speed and orientation in binocular matching

**Raymond van Ee*† & Barton L. Anderson***

** MIT Deparment of Brain and Cognitive Sciences, Cambridge, Massachusetts 02139, USA*
*† Utrecht University, Helmholtz Institute, Princeton Plein 5, 3584CC, Utrecht, The Netherlands*

**The spatial differences between the images seen by the two eyes, called binocular disparities, can be used to recover the volumetric (three-dimensional) aspects of a scene. The computation of disparity depends upon the correct identification of corresponding features in the two images. Understanding what image features are used by the brain to solve this matching problem is one of the main issues in stereoscopic vision[1]. Many cortical neurons in visual areas V1 (ref. 2), MT (refs 3, 4) and MST (refs 5, 6) that are tuned to binocular disparity are also tuned to orientation, motion direction and speed. Although psychophysical work has shown that motion direction[7] can facilitate binocular matching, the psychophysical literature on the role of orientation is mixed[8,9], and it has been argued that speed differences are ineffective in aiding correspondence[7]. Here we use a different psychophysical paradigm to show that the visual system uses similarities in orientation, motion direction and speed to achieve binocular correspondence. These results indicate that cells that multiplex orientation, motion direction, speed and**

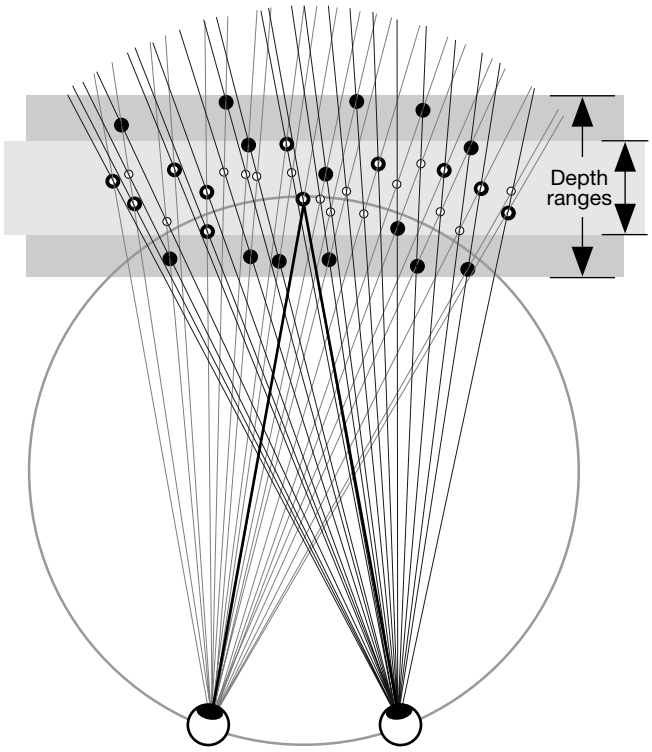


**Figure 1** Top view of the geometry of the binocular matching problem. The intersections of the visual lines indicate the locations of possible matches. The drawing is schematic; contours in three dimensions introduce another dimension of ambiguity (namely, determining how correspondence between portions of the contours in the two eyes should be defined). One configuration represents a large depth range (black dots), the other a small depth range (white dots). The two configurations create identical sets of visual lines.