continuously decrease in intensity that the terminal loudness is less than it would be if that final intensity were presented alone. Such decreasing loudness may signal decreasing environmental importance, because it is consistent with the departure of a sound source. So, viewing their findings in environmental terms, the endpoint of a downward-sweeping sound (or departing source) might be less important (and less loud) than the endpoint presented alone, which could signal a new source.

An analogous effect occurs in vision where an unimportant background in a visual scene can appear to be darker than a more important figure, despite the two having equal luminance[5]. More experiments on the perception of both loudness and loudness change are called for, but for the moment the evolutionary position seems able to accommodate both sets of data.

John G. Neuhoff
Department of Psychology, Lafayette College, Easton, Pennsylvania 18042-1781, USA
e-mail: neuhoffj@lafayette.edu

1. Neuhoff, J. G. *Nature* **395,** 123–124 (1998).
2. Shaw, B. K., McGowan, R. S. & Turvey, M. T. *Ecol. Psychol.* **3,** 253–261 (1991).
3. Schiff, W. & Oldak, R. *J. Exp. Psychol. Hum. Percept. Perform.* **16,** 303–316 (1990).
4. Rosenblum, L. D., Wuestefeld, A. P. & Saldana, H. M. *Perception* **22,** 1467–1482 (1993).
5. Kanizsa, G. *Organization in Vision: Essays on Gestalt Psychology* (Praeger, New York, 1979).

Movement of motor and cargo along cilia

Intraflagellar transport (IFT)[1] is important in the formation and maintenance of many cilia, such as the motile cilia that drive the swimming of cells and embryos[2], the nodal cilia that generate left–right asymmetry in vertebrate embryos[3], and the sensory cilia that detect sensory stimuli in some animals[4]. The heterotrimeric kinesin-II motor protein drives the anterograde transport of macromolecular complexes, called rafts, along microtubule tracks from the base of the cilium to its distal tip[5], whereas cytoplasmic dynein moves the rafts back in the retrograde direction[6]. We have used fluorescence microscopy to visualize for the first time the intracellular transport of a motor and its cargo *in vivo*. We observed the anterograde movement of green fluorescent protein (GFP)-labelled kinesin-II motors and IFT rafts within sensory cilia on chemosensory neurons in living *Caenorhabditis elegans*.

The anterograde IFT motor, heterotrimeric kinesin-II[7], consists of two heterodimerized kinesin-related motor subunits and one accessory subunit (KAP)[8]. To observe kinesin-II-driven IFT within chemosensory cilia, we used transgenic lines of *C. elegans* expressing GFP fused to the kinesin-II KAP and to a presumptive cargo molecule, OSM-6, a component of IFT rafts that has an essential role in chemosensory ciliary function[5,9].

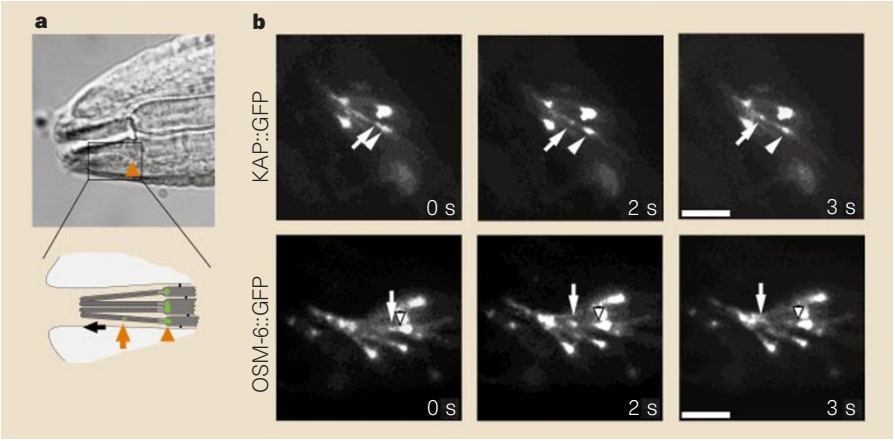

Figure 1 Visualization of intraflagellar transport (IFT). **a,** Schematic diagram of *Caenorhabditis elegans* chemosensory cilia. Top, a differential interference contrast light micrograph of the head of an adult worm orientated to the left. The boxed region shows the position of an amphid channel containing sensory cilia. This region is represented in the diagram (bottom), which shows a close-up of sensory cilia orientated with their distal endings facing left, and contacting the external environment through openings in the cuticle. Green indicates fluorescent kinesin-II or OSM-6, which accumulate at the transition zone at the base of the cilia (orange arrowhead) and move (black arrow) as dots (orange arrow) to the distal endings of the cilia. **b,** Fluorescence micrographs of sensory cilia in GFP transgenic worms as represented by the boxed region and the diagram in **a**. Fluorescent kinesin-II motors and fluorescent OSM-6 subunits of IFT rafts accumulate at the base of the transition zones where they appear as large dots (arrowheads). Arrows indicate position of dots of fluorescent kinesin-II and fluorescent OSM-6 as they travel to the distal tip of the sensory cilium (left, as in **a**). A movie of this process can be seen at http://www.mcb.ucdavis.edu/faculty-labs/scholey/. Details of the methods are available on request from J. M. S.

With a fluorescence microscope, we observed that KAP::GFP and OSM-6::GFP polypeptides accumulate in the region of the transition zone at the base of the sensory cilia. This is consistent with previous immunofluorescence data on IFT motors and raft polypeptides in other systems[5] (Fig. 1). We observed small fluorescent dots corresponding to the kinesin-II KAP and the OSM-6 cargo emerging from these regions and moving out towards the distal tip of the sensory cilia. Both the motor and its presumptive cargo moved anterogradely at identical rates (0.65 ± 0.11 μm s^{-1} ($n = 50$) for the KAP compared with 0.65 ± 0.10 μm s^{-1} ($n = 50$) for OSM-6), which is similar to the velocity of microtubule motility driven by purified heterotrimeric kinesin-II in a motility assay[7]. In contrast, the sensory ciliary transmembrane receptor ODR-10 moved at a faster rate (1.59 ± 0.28 μm s^{-1} ($n = 10$)), confirming that the identical velocities displayed by KAP::GFP and OSM-6::GFP are not an artefact of the recording technique.

This direct viewing of the intracellular transport of a motor and its cargo *in vivo* provides strong support for the hypothesis that heterotrimeric kinesin-II is the motor protein that drives anterograde IFT[5]. In chemosensory neurons of *C. elegans*, it is likely that kinesin-II-driven IFT delivers structural components of sensory ciliary axonemes and components of the sensory signalling machinery that are concentrated in these cilia.

Genetic studies have identified 25 genes, including *osm-6*, that are essential for ciliary function in this system[10], and the ability to view IFT in organisms carrying mutations in these genes will make it possible to determine which of the corresponding gene products are linked to the kinesin-II transport pathway. In a broader context, our approach should allow the direct observation of motor and cargo molecules participating in IFT in a broad range of cilia and flagella.

Jose T. Orozco, Karen P. Wedaman, Dawn Signor, Heather Brown, Lesilee Rose, Jonathan M. Scholey
Section of Molecular and Cellular Biology, University of California, Davis, California 95616, USA
e-mail: jmscholey@ucdavis.edu

1. Rosenbaum, J. L., Cole, D. G. & Diener, D. *J. Cell Biol.* **144,** 385–388 (1999).
2. Morris, R. L. & Scholey, J. M. *J. Cell Biol.* **138,** 1009–1022 (1997).
3. Nonaka, S. *et al. Cell* **95,** 829–837 (1998).
4. Perkins, L. A., Hedgecock, E. M., Thompson, J. N. & Culotti, J. G. *Dev. Biol.* **117,** 456–487 (1986).
5. Cole, D. G. *et al. J. Cell Biol.* **141,** 993–1008 (1998).
6. Pazour, G. J., Wilkerson, C. G. & Witman, G. B. *J. Cell Biol.* **141,** 979–992 (1998).
7. Cole, D. G. *et al. Nature* **366,** 268–270 (1993).
8. Signor, D., Wedaman, K. P., Rose, L. S. & Scholey, J. M. *Mol. Biol. Cell* **10,** 345–360 (1999).
9. Collet, J., Spike, C. A., Lundquist, E. A., Shaw, J. E. & Herman, R. K. *Genetics* **148,** 187–200 (1998).
10. Starich, T. A. *et al. Genetics* **139,** 171–188 (1995).