

cleaning behaviour to test models of non-kin cooperation.

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Perception of changes in loudness

Neuhoff¹ reported that “rising level tones... change (in loudness) more than falling level tones despite having the same actual change in level... indicating that direction of change is an important (and previously unaddressed) factor in the perception of dynamic loudness change”, and speculated that: “In a natural environment this over-estimation could provide a selective advantage, because rising intensity can signal movement of the source towards an organism.” Leaving aside the question of why it may not be as important for survival to detect the movement of a sound source away from an organism, we dispute the assertion that there is no prior evidence about the influence of direction of change on the degree of change in perceived loudness. This evidence does exist and shows, in contrast to the result reported by Neuhoff¹, that declining signal intensity covers a greater range of loudness than does rising signal intensity.

Twelve years earlier it was reported² that tones continuously decreasing in intensity from moderate to very low levels follow a course of accelerated “softening” until the end of the downsweep, when the loudness is very much less than it would be if that final intensity had been presented alone. The underlying mechanism for this phenomenon, which was subsequently named “de-recruitment”³, is unknown, but arguments have been made for both central and peripheral factors. For example, it was later shown⁴ that at least some part of the effect occurs at the receptor site, as a test in the contralateral ear at the end of the downsweep showed little or no de-recruitment.

In these earlier studies, the loudness of sounds sweeping up, instead of down, over the same ranges of intensity yielded some

evidence for loudness enhancement (or “up-cruitment”) at the end of the sweep. However, the effect, where it occurs at all, is much smaller than the accelerated softening in downsweeps. It should be noted that the earlier work concerned sweep durations much longer than the 1.8 seconds used by Neuhoff. A more recent study^{5,6} has shown that, although de-recruitment is diminished when duration is as short as one second, a 30-decibel downsweep for 1- and 2.5-second durations covers a bigger range of loudness than the comparable upsweep.

It would therefore be prudent to limit Neuhoff’s conclusions to his own test conditions and method of measuring loudness change: the larger loudness change recorded earlier for downsweeps under a range of conditions and with a variety of measurement techniques contrasts with Neuhoff’s finding based on a single duration, a single intensity range, and a single measurement procedure.

How can this apparent conflict be explained? Perhaps, as Neuhoff argues, direct judgement of “perceived change” taps a fundamentally different process from judgements of loudness obtained at the beginning and end of a sweep. But listeners have been known to make their own decisions about what to attend to in an experimental setting: although Neuhoff cautioned his subjects to avoid making a judgement of overall loudness, they may have done so; the direction of change may have an effect on such judgements that is quite different from its effect on loudness judgements made at discrete stages of a sweep. Close attention should also be paid to procedural differences that may turn out to be decisive.

Neuhoff’s results are of great interest but, in our view, they need to be considered in the context of what is already known about loudness perception for signals that are continuously changing in intensity. It remains to be seen whether his finding is of sufficient generality to warrant speculation about its role in the process of evolutionary selection.

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Neuhoff replies — Canévet and his colleagues suggest that their findings address dynamic loudness change and are inconsistent with my recent discovery of a bias for rising intensity tones¹. However, the two sets of experiments address fundamentally different questions. Canévet *et al.*’s listeners were asked to make judgements about loudness, whereas my listeners were asked to make judgements about the amount of dynamic change. Essentially, their listeners answered the question “How loud is it now?” by assigning a number to the loudness of a changing intensity sound at various times throughout the stimulus duration. This provided a discrete measure of loudness at various snapshots in time. Listeners in my experiments were specifically asked to ignore the overall loudness of the sounds and to make summary judgements about the amount of loudness change, essentially answering the question “How much did it change in loudness?”

From static judgements of loudness at discrete points in time, Canévet and his colleagues infer the perceived amount of dynamic loudness change. But they do not measure perceived dynamic change directly. There can be inherent shortcomings in inferring characteristics of dynamic perception by extrapolating from static judgements. Their experiments are important and have implications in areas from physiology to auditory display. However, once the difference between the perception of loudness and the perception of dynamic loudness change is made clear, perhaps the discrepancy between our results is not so unexpected.

Judgements of dynamic change may be mediated by different mechanisms from static judgements of loudness. Because intensity change is the important factor in specifying the arrival time of a source², a direct judgement about the amount of change might be more useful for localizing a source than a series of snapshot judgements of loudness. A bias for rising intensity when judging loudness change is consistent with studies that show that listeners systematically err on the side of safety when estimating the arrival time of a sound source^{3,4}. The bias for rising intensity may therefore provide a selective advantage.

Canévet *et al.* suggest that their findings undermine this claim. However, keeping in mind the differences between loudness and loudness change, their work is not necessarily inconsistent with the evolutionary position. They have shown for tones that

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 luminance⁵. 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.

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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 embryos², the nodal cilia that generate left–right asymmetry in vertebrate embryos³, and the sensory cilia that detect sensory stimuli in some animals⁴. 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 tip⁵, whereas cytoplasmic dynein moves the rafts back in the retrograde direction⁶. 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-II⁷, consists of two heterodimerized kinesin-related motor subunits and one accessory subunit (KAP)⁸. To observe kinesin-II-driven IFT within

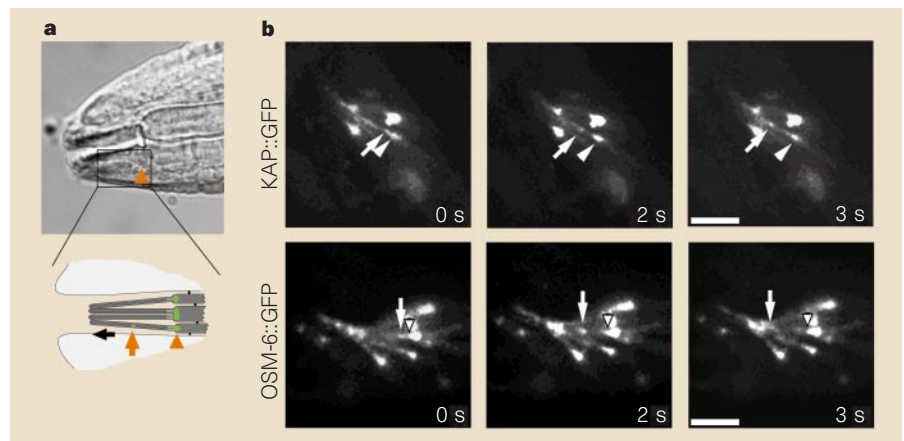


Figure 1 Visualization of intraflagellar transport (IFT). **a**, Schematic diagram of *Caenorhabditis elegans* chemosensory cilia. Top, a differential interference contrast light micrograph of the head of an adult worm orientated to the left. The boxed region shows the position of an amphid channel containing 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.

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}.

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 systems⁵ (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 ($0.65 \pm 0.11 \mu\text{m s}^{-1}$ ($n=50$) for the KAP compared with $0.65 \pm 0.10 \mu\text{m s}^{-1}$ ($n=50$) for OSM-6), which is similar to the velocity of microtubule motility driven by purified heterotrimeric kinesin-II in a motility assay⁷. In contrast, the sensory ciliary transmembrane receptor ODR-10 moved at a faster rate ($1.59 \pm 0.28 \mu\text{m s}^{-1}$ ($n=10$)), 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 IFT⁵. 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 system¹⁰, 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.

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