

(MLTs, a family of chemoreceptors lacking an RBD [12]). Opsins are (at least at the time of writing) unknown in sponges, but opsin-like proteins that lack an RBD (referred to as placopsins [12]) have been identified in the Placozoa. Phylogenetic analyses showed that placopsins are the orthologs of the animal opsins [12,13]. As the emergence of the placopsins postdates the separation between MLTs and opsins, from an evolutionary perspective, placopsins are either opsins or their closest relatives [12]. Irrespective of that, placopsins lack an RBD and are thus unlikely to be light receptors. In addition, ancestral character reconstructions have shown that, similarly to the placopsins, ancestral opsins did not have an RBD [12] (Figure 1B). The results of Leung *et al.* [8] have now confirmed that not all opsins bind to retinal and respond to light, providing the first proof that opsins (including ancestral ones) could function as chemoreceptors.

Ancestral opsins might have indeed been chemoreceptors. As MLTs bind melatonin (a neurohormone) and are the closest relatives of opsins, it could be conjectured that ancestral opsins might have also been binding melatonin. Intriguingly, melatonin has been shown to play a role in the regulation of circadian vertical migrations in zooplankton, and the origin of light reception has been suggested to be linked to the same phenomenon [19]. However, whether ancestral opsins bound melatonin, a different chemical similar to melatonin (e.g. serotonin or another derivative of tryptophan), or a chemical radically different to melatonin and to the other indolamines, is still unknown and will certainly be the topic of future research. What is certain is that, at some point, an ancestral opsin acquired the ability to bind retinal, giving animals their first ‘taste of light’.

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Motion Perception: Auditory Motion Encoded in a Visual Motion Area

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The motion of a translating sound source is easily perceived, yet clear evidence of motion mechanisms in auditory cortex has proved elusive. A new study may explain why, revealing auditory motion is encoded in a motion-specialised region of visual cortex.

The perception of motion is a vital human brain function. As active beings in a dynamic world, we need to have

information of our own movements and the motion of relevant objects in the world. Motion perception is not only



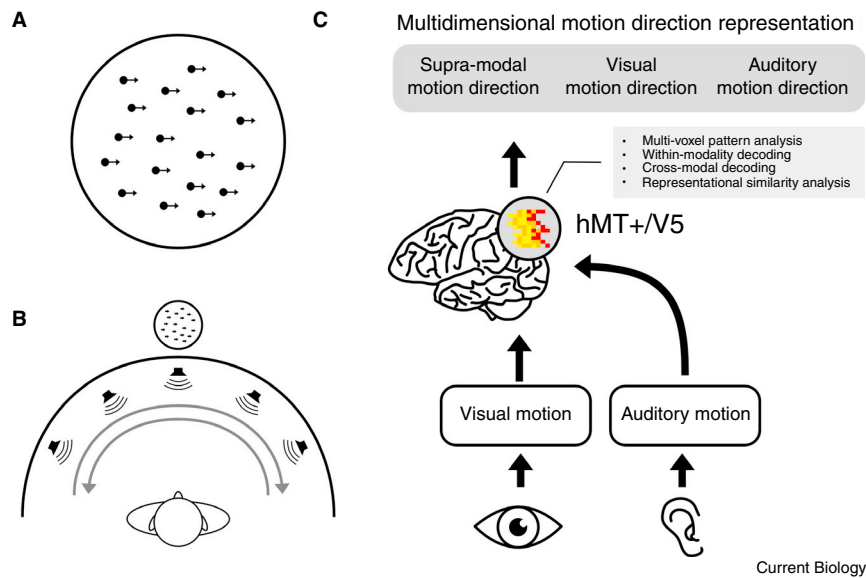


Figure 1. Auditory and visual motion research methods and key findings.

(A) Schematic depiction of a random-dot kinematogram stimulus used to evoke global motion brain responses in Rezk *et al.*'s study [11]. The motion signal was strong (100% motion coherence), dot lifetimes were limited to 200 ms and the speed was $4^\circ/\text{s}$. Stimulus duration was 1.2 s and the global motion signal translated 4.8° of visual angle during this time. (B) A schematic bird's-eye view of a speaker setup used to present auditory motion signals. The arrows indicate rightward and leftward motion and the motion path length was 120° . Rezk *et al.* made binaural, in-ear recordings for each participant in a semi-anechoic room from 31 speakers spanning the 120° path. The sounds were played back to participants in sequence through earphones while lying in the scanner, resulting in an externalised auditory motion percept comprising interaural timing and level cues, as well as monaural spectral cues. The auditory and visual spatial ranges were very different, as depicted by the relative size of the visual and auditory stimuli. (C) Visual and auditory motion signals evoke sensory-specific motion responses in sensory-specific cortical brain regions. In an fMRI study using a combination of multi-voxel pattern analysis and dissimilarity matrices, Rezk *et al.* were able to show that the visual motion-specific area hMT+/V5 contains independent auditory and visual motion direction representations, as well as an abstracted (supramodal) motion direction representation.

essential for navigating effectively through the environment, it also helps with figure/ground segregation and guides actions such as reaching and grasping [1]. Motion can also support form perception. In so-called 'biological motion', light points placed on the joints of a body moving in the dark give a strong percept of a moving person whose actions are easily identified [2]. Brain cells in a dorsal visual area called hMT+/V5 are highly specialized for detecting image motion, with cells tuned to direction and speed of motion. This area is centrally important to the perception of movement and lesions to this region leave an individual with a debilitating loss of visual motion perception [3–5]. This can, for example, result in difficulties with crossing a busy street or knowing when to stop pouring a cup of tea.

Although the visual domain has taken centre stage in studies of motion

perception, humans also rely on other senses to perceive the motion of objects. Think about biking through a busy city centre. The view of your surroundings is restricted to what is in front of you. You cannot see a car approaching from behind, but you can hear it getting nearer [6]. Indeed, most of us would readily agree from experience that with our eyes closed we could recognise the speed and trajectory of a moving sound. It seems trivially easy, yet curiously, it is far from trivial for the brain's auditory system. Despite several decades of searching for motion detectors in auditory cortex, there is only very scant evidence that such detectors exist at all [7]. There are certainly none in the form of the 'Reichardt detector' commonly used to model visual motion by comparing two locations with one signal delayed relative to the other [8–10].

It is an enduring puzzle that motion is so easily perceived in both audition and vision, yet only the visual system has yielded clear neural evidence for motion mechanisms. A new study by Rezk *et al.* reported in a recent issue of *Current Biology* sheds light on this enigma [11]. They used functional magnetic resonance imaging (fMRI) to reveal the brain regions responsive to auditory or visual motion, localising those responses to the planum temporale (PT) for audition and hMT+/V5 for vision. Then, using various analyses such as multi-voxel pattern analysis (MVPA) and dissimilarity matrices (DSM), the authors were able to test whether each region was sensitive to motion in the other sensory domain. Here, the authors found an interesting asymmetry: activity patterns in the visual motion region right hMT+/V5 represented the direction not only of visual motion, but also of auditory motion. The converse, however, was not found: auditory area PT did not encode visual motion direction.

The finding that the key visual area for motion processing, hMT+/V5, also responds to auditory motion is fascinating but must be interpreted carefully. It would be tempting to conclude that right hMT+/V5 responds to motion in a supramodal way only: encoding the direction of spatial change over time regardless of whether motion was heard or seen. However, the authors show this is not the case. Within right hMT+/V5, the responses evoked by auditory and visual motion showed opposite patterns of activity, indicating that information about auditory and visual motion direction was separately available by being represented in a different way. However, when the authors investigated whether the pattern of brain activity in right hMT+/V5 could be best explained by independent processing of auditory and visual input or by a multisensory model combining auditory and visual input from hearing and vision, their analyses supported a multisensory model. Auditory and visual motion signals not only independently activate hMT+/V5 but the region also contains enough supramodal motion information to decode motion direction independent of sensory origin (Figure 1C). In sum, these findings reveal a multidimensional representation of motion.

A relevant point here is that the auditory and visual motion speeds and path

lengths differed greatly. The motion duration was 1.2 s for both, but due to the restricted field of view in the fMRI scanner, the visual paths were just 4.8° of visual angle long. There was no restriction for auditory motion (presented through earphones) and the sound swept around the participant through 120° of angle (Figure 1A,B). Would matching the auditory and visual motions in speed and length enhance the reported effects? Because spatial congruence is a key principle for multisensory integration [12,13], matched audiovisual motion stimulation might reveal a stronger pattern of multisensory responses [14]. Unfortunately, in an MRI scanner, that would mean reducing the auditory sound path length to match vision, and auditory motion is not very salient over short spatial ranges. A strong aspect of the sounds used is that they were custom-made for each individual participant using a ‘virtual auditory space’ approach [15]. This ensured that participants heard externalised, ecologically valid sounds sweeping around them with appropriate binaural difference and monaural spectral cues.

Given the absence of Reichardt-like detectors for auditory motion, one idea is that a series of static sound locations is detected and motion is inferred between them. This ‘snap-shot’ model is very similar to what visual motion researchers call long-range apparent motion [16]. Perhaps hMT+/V5 provides the auditory motion inference based on static locations received from the auditory system. After all, area MT neurons respond very well to a sequence of displaced static visual images [17] and may potentially do so to a sequence of sound locations. It would certainly be efficient to do it that way, and given the multisensory component in Rezk *et al.*'s data [11], it is a viable possibility. There have been reports of motion-related activity in auditory cortical areas, although it is not clear whether these are motion responses *per se* or responses to dynamic changes in spatial cues [7]. Perhaps these areas receive motion signals that originate from MT or MTa, the area just anterior to hMT+/V5 found by Rezk *et al.* to encode auditory motion [11]. The puzzle of auditory motion is far from solved but the notion

that visual area MT could provide a motion percept from auditory locations would be very efficient: it would avoid duplicated motion systems for each sense, and we know that the brain is, above all, efficiently designed.

An outstanding question concerns the reference frames of motion information obtained via different senses. In early brain areas, visual spatial information is encoded in retinal coordinates (eye centered) whereas auditory spatial information is encoded in head-centered coordinates [18,19]. How motion information from different senses could be spatially mapped onto each other in a visual motion-sensitive brain area (hMT+/V5) is still unknown. Some neurons in hMT+/V5 take eye position into account when encoding visual motion to produce a spatiotopic representation [20], as demonstrated by neurons that respond differently to the same retinal stimulus when eye position changes. Whether the final reference frame in hMT+/V5 is spatiotopic or eye-centered, it is unclear how the head-centered coordinates of audition could correspond to either reference frame in hMT+/V5. The problem is solvable provided eye, neck, and trunk position are known. Such information is employed in other neural contexts to achieve a common reference frame, but the specifics of reference-frame transformations for cross-modal motion remain to be worked out.

Other questions to be addressed include how auditory motion in elevation and azimuth is combined, given that each dimension depends on different auditory processes (monaural spectral vs binaural difference cues, respectively). A further question concerns the asymmetry of hMT+/V5 representing auditory motion, but PT not representing visual motion. This could be evidence of a multisensory motion mechanism in MT, or simply an example of visual dominance in spatial tasks. Further work with auditory and visual motion stimuli matched in perceptual salience, path length, and speed could help resolve this. For now, Rezk *et al.*'s study has shed light on a fascinating and previously unknown

fact: the area specialised for motion in the visual pathway — hMT+/V5 — also represents the direction of motion of auditory signals. While many interesting questions still need to be answered, their work offers a tantalising first step into understanding how motion in two sensory modalities is processed in the human brain.

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Evolution: Brainier Birds

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A groundbreaking study of brain evolution across birds and dinosaurs reveals potential drivers of increased brain size including biogeography and ecology. The most dramatic change occurred in the Neoaves after the Cretaceous-Paleogene extinction rather than earlier in bird evolution.

Despite the unflattering nature of the vernacular ‘bird-brain’, birds are in fact among the brainiest of living vertebrates, with some species exhibiting brain-to-body size ratios comparable to primates. Indeed, birds like parrots and crows (Figure 1), long known to have amazing cognitive abilities, have become model systems for studying learned behavior. Tool use by New Caledonian crows and the remarkable vocabulary of human words learned by some parrots are oft-cited cases of advanced learning parallel to our own evolutionary lineage. But the evolutionary history of how birds attained their large brain sizes and cognitive abilities, and what drove that evolution, has only been approached in piecemeal fashion in the past, hampered by a lack of both comprehensive phylogenies for the huge diversity of living birds and broad cross-species samples of brain sizes in living birds and their fossil relatives. This deficit has now been overcome in a landmark study [1] of avian brain evolution published in *Current Biology* by Dan Ksepka and a team of 40 of his fellow avian biologists, paleontologists and systematists.

Ksepka and colleagues [1] compiled a monumental dataset of over 2000 avian brains. To brain-size data obtained from the literature, they added nearly 300 brain volumes generated from computed tomography scans of living and fossil birds, and their closest relatives among non-avian theropod dinosaurs. As avian brains closely fit the confines of their surrounding skull bones, the internal volume of the braincase can be used as a reliable proxy for brain size in fossil species. The technology to reconstruct brain volumes, especially in fossils, is still relatively young but advances in scanning and modeling allow researchers to reconstruct internal 3D features from crushed or unprepared specimens with increasing fidelity [2]. Nevertheless, such reconstructions are laborious, and the compilation of this dataset represents an exemplary collaborative effort by a broad, international group of researchers.

At a macro-scale, brain evolution is classically studied by plotting log-transformed brain mass as a function of log-transformed body mass [3]. The slope of a line fitted to the coordinates is the allometric scaling factor, which estimates

the rate of evolutionary change, while the intercept represents the baseline or ‘grade’ to which the investigated taxa belong [4]. Differences between taxonomic groups have traditionally been investigated as differences in slope or grade in such plots. However, such plots treat species as statistically independent data points without acknowledging their shared evolutionary ancestry [5]. Raw values therefore have to be modified by estimating the inherited component in any species’ individual values prior to statistical analysis. Using recently developed statistical methods that account for evolutionary relatedness in conjunction with a recent comprehensive phylogeny of birds [6], Ksepka and colleagues’ [1] team examined their dataset for statistically significant shifts in either evolutionary rate or baseline grade changes. Amazingly — but perhaps not surprisingly — they find evidence for no less than eighteen such shifts across 150 million years of avian history, hinting at a complex picture of brain size evolution in response to a varying range of drivers from mass extinction to sensory and dietary specialization.

