

Multisensory Integration: Vision Boosts Information through Suppression in Auditory Cortex

Signals from non-primary modalities can influence neural activity in ‘unimodal’ sensory areas of the neocortex, but whether this ‘extra-modal’ influence has any relevant consequences for neural coding has been unclear. Recent findings show that vision enhances the information content of neural signals in auditory cortex, but in a counter-intuitive fashion.

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The auditory sense has a bad rap. Along with taste and smell, it has long been considered inferior to vision in Western thought. Historians argue that, following the invention of moveable type in the 16th century, and the influence of the Renaissance and Enlightenment periods, vision came to dominate Western thinking, serving as the authenticator of truth, while the other senses were sidelined [1]. Indeed, at least one historian has argued that all of human history can be explained by shifts in the dominance of one sense over the others. In this scheme, ‘tribal societies’ are ear-dominated, relying on speech and oral traditions, whereas Western societies advanced to use eye-dominated traditions based on writing and typing and other electronic modes of communicating [2]. Sensory neuroscience has not been immune to these historical developments and biases, as evidenced by the hegemony of vision in our ideas about how the brain works and is organized. For instance, studies of vision far

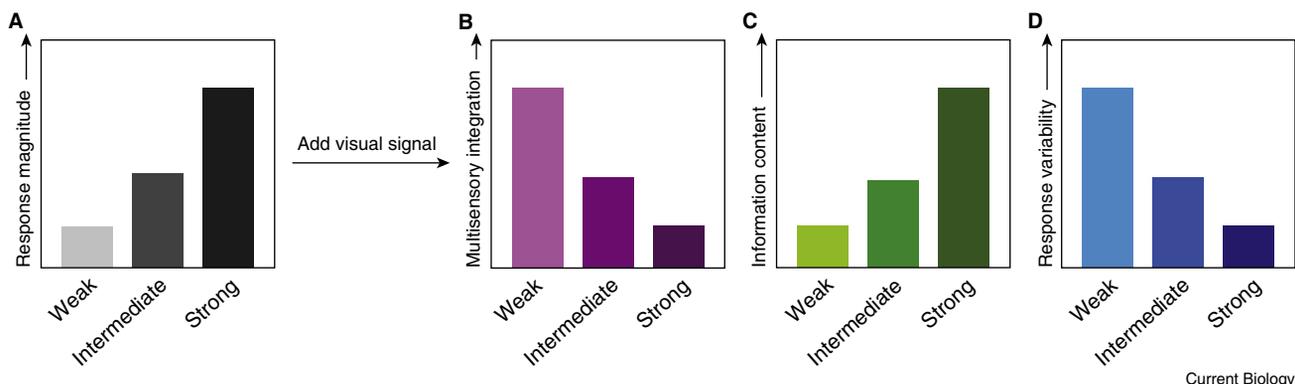
outnumber those of other sensory modalities, and the neocortex of primates is generally thought to be over-run with visual areas [3,4].

In recent years, however, the sovereignty of vision — or any other sensory modality, for that matter — over our thinking about brain organization and function is slowly crumbling, with a more pluralistic view emerging from the rubble. While an ear is an ear, and an eye an eye — each taking in their specific energies — we now know that separating one modality from another is difficult, if not impossible, in the neocortex [5]. The available neurophysiological evidence overwhelmingly reveals that sensory neocortical areas, while perhaps chiefly driven by one modality, can be modulated, and occasionally driven, by others. In nonhuman primates, somatosensory cortical neurons respond to both auditory and visual signals [6,7], and auditory cortical neurons are influenced, either suppressed or enhanced, by both somatosensory [8,9] and visual [10,11] signals. This ‘multisensory’

organization of the neocortex seems to more accurately reflect the nature of real world events — they rarely, if ever, consist of a unimodal sensory signal. Nevertheless, a key question remains unanswered: while vision, for example, can suppress or enhance auditory cortical responses, does this modulation of neural signal strength have any information content or is it just adding noise? In this issue of *Current Biology*, Kayser *et al.* [12] provide an unexpected answer.

Our behavior depends on how well the brain is able to represent sensory information; it is crucial for this sensory representation to be as clear as possible. We know from numerous behavioral studies that concurrent signals from different modalities enhance the detection and discrimination of events and objects [13]. It has long been assumed that the enhanced multisensory responses of neurons mediate this behavioral enhancement. Kayser *et al.* [12] tested the veracity of this idea by recording neurons from several auditory cortical areas of macaque monkeys while they viewed and/or heard natural scenes or primate vocalizations. They then compared the auditory-only versus audiovisual responses of these neurons by first dividing the auditory-only response magnitudes into three different levels: weak, intermediate and strong (Figure 1A).

Kayser *et al.* [12] found that the visual influence on these different types of response was as predicted from the ‘principle of inverse effectiveness’ [14]: weaker auditory responses yielded the



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Figure 1. Suppressed multisensory responses are more informative than enhanced responses.

(A) Auditory-only responses were arbitrarily divided into three levels of response magnitude: weak, intermediate and strong. (B) Adding a congruent visual signal enhances the weak auditory responses, has no effect on intermediate responses, and suppresses strong responses. (C) Suppressed responses are more informative than enhanced responses. (D) The greater information in suppressed responses is due to a decrease in variability when a visual signal is added. In contrast, variability increases for enhanced responses.

largest enhancement effects when accompanied by the visual component of the same event, while strong auditory responses did not yield large enhancement effects when the visual signal was present. Indeed, the congruent visual signals *suppressed* those responses that were strong in the auditory-only condition (Figure 1B). Here is the real twist: when the authors measured the amount of information contained in bimodal versus unimodal responses — in essence, a measure of how well the responses of a neuron can predict which stimulus was presented — they found that not only did bimodal events yield more information than unimodal ones, but that the suppressed responses yielded more information than the enhanced responses (Figure 1C). The suppressed responses were more informative because their variability was reduced by the addition of a visual signal, while the enhanced responses were less informative because their variability was increased (Figure 1D).

This is a remarkable finding primarily because it runs counter to the general assumption that enhanced neural responses underlie enhanced behavioral responses. The data from Kayser *et al.* [12] suggest the opposite: it is the suppressed responses that carry more information about what stimulus was just presented. This suggests that the ubiquitous ‘principle of inverse effectiveness’, reported in multiple brain areas and in multiple model systems, is not relevant for multisensory identification or discrimination. The principle’s predictive value may be limited solely to the detection of multisensory events, a fact consistent with some behavioral results [14]. Along these lines, the authors put forth the idea that there may be two different modes of integration, one in which enhanced, but less reliable, responses are involved in detecting rare or faint events in the world, and another mode in which suppressed, reliable responses are used to represent the detailed characteristics of those events.

The Kayser *et al.* [12] study raises other deep questions. Here are a few. Because behavior emerges from an interaction between stimulus structure, context and neural processes, how much does redundancy between the auditory and visual signals influence the amount of information that gets

added to the neural signal? One might predict that if the visual signal carried information that was redundant with the auditory signals (such as signal duration or rhythm), then the added information at the neural level would be minimal. To address such a question, a carefully constructed and exhaustively characterized stimulus space would be needed. Another puzzle: How does the information content change according to multisensory experience [15]? It’s possible that the added information that vision provides the auditory cortex requires prior learning or experience. We don’t have any inkling of answers to such questions, but without a doubt, the results of, and analytical approach taken by, Kayser *et al.* [12] illuminate exciting new directions to consider when interpreting multisensory responses.

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Experimental Evolution: The Rate of Adaptive Evolution

Next-generation sequencing technology allows the identification of molecular changes that have arisen in the genomes of microorganisms undergoing experimental evolution. This permits the elucidation of the molecular evolutionary dynamics in these populations.

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An influential idea in molecular evolution is the ‘molecular clock’ [1], which postulates a constant rate of molecular evolution with time; among other advantages, the molecular clock allows bifurcations in phylogenetic trees to be dated. The clock does not ‘tick’ regularly, but describes a Poisson process of change with a constant rate. This idea has a strong theoretical background — if molecular evolution is

selectively neutral, the evolutionary rate should simply be equal to the neutral mutation rate, and unaffected by the inevitable fluctuations in population size [2]. Conversely, there are at least two reasons why adaptive evolution should not be clock-like. The first is that environments may be constant or may change, and an evolving species might show a suite of adaptive changes following a new environmental challenge. The second is that the rate of adaptive evolution