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Cortical Multisensory Processes: Neural Encoding Strategies

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Abstract

In our everyday environment, we are constantly bombarded with cues from different sensory modalities. Essential mechanisms within our brain have evolved that integrate signals from multiple sensory sources shaping perception and behavior. Much headway has been made characterizing subcortical multisensory processes, particularly in the cat superior colliculus (SC), which has also lead to the establishment of three working principles for multisensory integration. Although a good first step in understanding multisensory integration, studying subcortical processes has its limitations. In order to understand perception and behavior, we have to understand cortical processes. Most studies thus far have detailed the mechanics of cortical multisensory interactions in the primate brain, but direct links between these mechanics and perception and behavior have not been made. In the cat, there exists a unique multisensory structure – the anterior ectosylvian sulcus (AES) that is well-suited to study cortical multisensory processes. The AES is comprised of three unisensory zones and a region at their respective overlapping domains that has a high incidence of multisensory neurons. Studying how AES neurons integrate multiple modalities and establishing links to perceptual and behavioral processes will not only shed light on multisensory encoding strategies and their contributions to perception and behavior but may also further our understanding of how cortical processes lead to perception and behavior in general.

Keywords

Cortex
Multisensory
Cat
Primate
Electrophysiology

Introduction

In our daily environment we constantly experience sensory signals arising from various events. Sometimes, these cues take place alone but more often multiple signals occur in combination. In order to convey an accurate percept of our world, the brain must be equipped to manage and synthesize sensory information from a variety of sensory sources (Figure 1A). Research over the past four decades has focused on identifying structures within the brain that actively integrate multisensory signals and subsequent studies have also investigated the neural properties within these specific multisensory brain regions. Current data shows that there is something special about these multisensory neurons as their firing rates during multisensory trials most often significantly differ compared to the component unisensory responses alone[1, 2]. On a behavioral level, this is frequently indicated by speeded response times[3], higher response accuracies[2, 4], and increased detection rates[2, 5] during multisensory tasks. These neuronal as well as behavioral gains underscore that multisensory processes greatly contribute to the processes that shape perception and behavior. Nevertheless, these exact contributions have yet to be determined.

The superior colliculus in the cat and the principles of multisensory integration

Most studies to date have been carried out in the cat superior colliculus (SC) – a multisensory subcortical structure. The SC contains visual, auditory, and somatosensory neurons with around 50% of intermediate and deep layer neurons shown to be multisensory[6]. Research in the SC lead to the establishment of three widely-recognized working principles that clearly delineate a set of rules to which multisensory neurons adhere. These principles have subsequently been shown to be valid in various cortical regions within the cat and primate brain. The principle of spatial coincidence states that pairing spatially coincident unisensory stimuli will more likely elicit response enhancements (Figure 1B) as measured by firing rate changes than stimuli that are separated in space[7]. The principle of temporal coincidence applies the same idea to time. Two temporally coincident stimuli are more likely to lead to an enhanced neuronal response during multisensory trials than two temporally separated stimuli[8]. Temporal coincidence generally encompasses a range of stimulus onset asynchronies (SOAs; often also referred to as the temporal binding window[9]) brought about by the fact that different sensory signals propagate at differ-

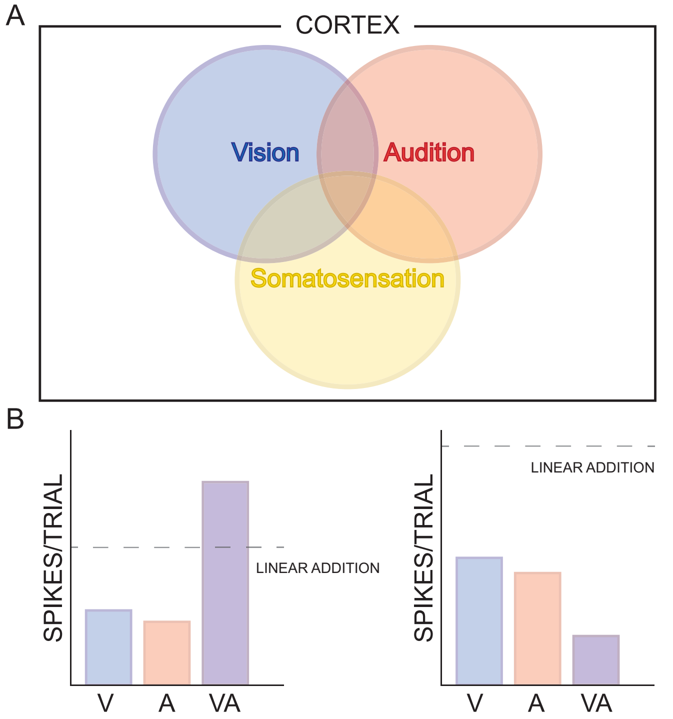

Figure 1. **A**. Schematic representation of multisensory interactions in cortex brought about by sensory overlap. **B**. Neuronal response profiles (visual - V, auditory - A, audiovisual - VA) demonstrating response enhancement (left) and depression (right) under multisensory (VA) conditions.

ent speeds. The principle of inverse effectiveness relates to stimulus efficacy. Combining two weakly effective unisensory stimuli will more often lead to response enhancements. Having spatially-offset stimuli, temporally-offset stimuli or strongly effective unisensory stimuli can either lead to a lack of integration or a response depression (Figure 1B). Thus far, these principles were studied in isolation but recent research indicates strong interactions within the principles[10, 11] leading to theories about one overarching principle - the principle of inverse effectiveness. Data analysis looking at these interactions implies that space and time just merely affect stimulus efficacy, meaning certain spatial locations within a receptive field (RF) or certain SOAs render the stimuli more or less effective, and consequently greatly influence neuronal responses and multisensory integration as defined by the principle of inverse effectiveness.

Cortical multisensory processes

Although, subcortical processing is undoubtedly important and has clearly established a set of principles that characterizes multisensory neurons, it cannot explain how multisensory processes shape and influence perception and behavior. Multisensory cortical processes have been mostly studied in the primate brain and so far, research has primarily focused on identifying regions within the primate brain that respond to multiple sensory signals and some headway has been made identifying whether or not these areas actively integrate multisensory cues. Studies involving the superior temporal sulcus (STS[12, 13]), the ventral intraparietal area (VIP[14]), and the ventrolateral prefrontal cortex (VLPFC[15]) demonstrated that they are involved in face-voice integration (STS, VLPFC) , speech perception (STS), and space representations (VIP), and that they display multisensory interactions but the exact contributions of multisensory processes to behavior and perception have not been established.

The superior temporal sulcus in the primate. STS is located within the temporal lobe in the primate brain. Studies identifying the roles of STS have identified a strong involvement in face[16, 17] and voice[18] processing, perception of biological motion[19, 20], and visual object recognition[21]. Moreover, very early on, STS was recognized as a region of sensory overlap with interactions between visual and auditory cues at the single neuron level[22-24]. Ghazanfar et al in 2005[13] demonstrated by pairing species-specific dynamic faces and vocalizations that auditory belt integrates multisensory signals as measured by local field potentials (LFPs) while multisensory responses were strongly face-voice specific. They also observed that response enhancements occurred significantly more often than response suppression. One interesting caveat is that STS neuron activity did not change with SOA since there was no correlation between SOA and magnitude of multisensory response. Prior to this study, Schroeder and Foxe in 2002[12] illustrated that visual, auditory, and somatosensory inputs to the STS are most likely feedforward projections as revealed by current source density (CSD) analysis. As of late, STS has also been shown to work in conjunction with auditory cortex to appropriately manage multisensory looming signals and bimodal speech[25, 26]. Further studies indicate that STS may be a locus for bimodal representations of observed actions[27] and studies in humans using fMRI also indicate a potential involvement in multisensory object recognition and object categorization[28].

The ventral intraparietal area in the primate. VIP, is buried within the fundus of the intraparietal sulcus of the posterior parietal cortex[29], a processing core for spatial coordinate transformations[30]. VIP is thought to play a role during visual motion processing with neurons being strongly driven by direction of movement[29] and may contribute to movements associated with defense or avoidance behaviors[31]. Anatomical tracer studies have shown VIP's strong connectivity patterns with visual, somatosensory, and motor areas[32] and thus recent research has focused on identifying multisensory interactions within VIP. Initial studies demonstrated vestibular-visual[33] and somatosensory-visual[34] interactions whereas neurons were responsive to bimodal stimuli that had RFs in close spatial registry. Schlack et al in 2005[14] showed for the first time that VIP neurons are responsive to auditory in addition to visual stimulation. Although auditory and visual RFs were generally well aligned, most bimodal neurons encoded space in their native reference frames (auditory – head-centered and visual – eye-centered) and yet significant multisensory interactions could be observed. Whether or not these neurons actively integrate these sensory modalities remains unclear. Altogether, these findings demonstrate that VIP may play an integral role in multisensory coordinate transformations as seen during peripersonal space and movement processing, in particular during tasks requiring shifts within modality specific reference frames. The lateral and the medial intraparietal areas (LIP and MIP) are also found within the posterior parietal cortex and both have been implicated in coordinate transformation[35]. Multisensory integration has not been overtly studied but LIP has been shown to be responsive to auditory cues[36], particularly in context of a saccade task[37, 38].

The ventrolateral prefrontal cortex in the primate. VLPFC, has extensive connections from sensory cortices and strong projections to the motor cortex and areas involved in cognitive processes[39-41]. VLPFC has been associated with memory retrieval[42], processes involving behavior inhibition[43], and visual object recognition[44, 45]. Research also shows that VLPFC neurons are responsive to visuo-spatial cues[46] and to conspecific vocalizations[47-49]. Sugihara et al in 2006[15] were the first to demonstrate that VLPFC neurons actively integrate audiovisual stimuli with strong preferences for interactions of face and vocalization stimuli. Moreover, neurons abode by the principles of multisensory integration exhibiting enhancement as well as suppression as seen in spike firing changes depending upon stimulus efficacy.

The anterior ectosylvian sulcus in the cat. To date, the AES is the most studied multisensory cortical region in the cat. AES is located within the parietotemporal lobe and is comprised of three distinct unisensory zones: the auditory field AES[50-52] (FAES), the anterior ectosylvian visual area[53-55] (AEV), and the fourth somatosensory area[56, 57] (SIV), as well as multisensory domains at the respective overlapping unisensory representations[58]. Auditory neurons within FAES exhibit short latencies, broad tuning curves, and are mostly monaural[50]. FAES has been associated with sound localization as shown by considerable behavioral detection deficits caused by cooling FAES[59], particularly the deeper layers[60]. Visual neurons within AEV are characterized by a robust preference for small and quickly moving stimuli – frequently being strongly directionally sensitive, usually have large RFs often spanning the entire contralateral hemifield and respond most vigorously to binocular stimulation. Moreover, no obvious retinotopic organization could be detected[53]. Although AEV has substantial connections to the frontal eye field[61] (FEF), an area highly important for saccade production, microstimulation studies have shown that eye movements can be evoked with intracortical stimulation of AEV[61] even after removal of FEF. Furthermore, within this eye-movement area in the ventral bank of AES, a large percentage of neurons respond to multisensory stimuli[62] suggesting that AES may have a potential role in multisensory coordinate transformation (or sensory transformation in general), a process often used during orientation behavior. Additionally, AEV neurons seem to be selective for pattern over component motion, which has been hypothesized to signal the salience of local motion information[63]. Area SIV contains a somatotopic map that represents the head rostrally and the hind legs caudally. SIV neurons can be stimulated by hair displacement, low threshold cutaneous stimulation, or distortion of subcutaneous tissue[56]. Further studies have shown that deactivating AES impedes successful integration of multisensory stimuli within the SC[64] and alters approach and orientation behaviors thought to be mediated by the SC so that accuracy gains with spatially coincident stimuli as well as response inhibitions associated with spatially disparate stimuli are significantly reduced[65]. A first attempt to better characterize multisensory AES neurons has utilized spatial receptive field (SRF) analysis – an approach that looks at the spatial influences on multisensory integration across the RF of a neuron. SRF analysis has demonstrated that RFs are heterogeneous in nature and that often multisensory SRFs differ markedly from the prediction plots (linear addition of the unisensory SRFs) frequently including one very defined hot spot surrounded by regions of subadditivity[10]. SRF analysis, as a first step to see how spatial location can influence stimulus effectiveness, suggests that there are strong interactions between stimulus location and efficacy in that location with low neuronal firing rates during unisensory conditions show strong response profiles during multisensory trials. A first effort to characterize temporal coding strategies within the AES revealed higher peak firing rates, shorter response latencies, and longer discharge durations during multisensory stimulation[11]. Altogether, due to its unique anatomical layout including a high incidence of multisensory neurons, the AES is an ideal candidate to study multisensory processes in the cortex. Furthermore, establishing the role of AES in perception and behavior may allow for direct links between multisensory processes and perception and behavior.

Spatiotemporal receptive field (STRF) analysis. STRF analysis is a method to better characterize the interactions of the three principles of multisensory integration and to aid in determining the role of the AES. It examines how space and time within the RF of a multisensory neuron affect stimulus efficacies and the neuron's response to these multisensory stimuli. This becomes increasingly important when examining biologically relevant stimuli as they often have complex spatial and temporal features. STRFs are constructed using neuronal firing data at the tested stimuli locations and SOAs (in spikes/trial) across the RF of a neuron. Figure 2 illustrates a hypothetical audiovisual STRF at four locations with 6 different SOAs. Within the classical RF presentation (azimuth versus elevation), neuronal discharge profiles at the tested locations depict the different SOAs (x-axis) and the resulting response spike rates in spikes/trial (y-axis). Multisensory responses at each SOA are subsequently compared to the maximum unisensory response (referred to as multisensory index) and to the linear addition of both unisensory response profiles (referred to as multisensory contrast). Both measures will give a detailed look at response enhancements (superadditivity) as well as response suppressions (subadditivity) across space and time within the RF of the tested neuron. STRF analysis does not just give insight into encoding strategies but may also indicate AES function. For example, having heterogeneous STRFs, similarly to SRFs[10], could be a means to code for moving stimuli (i.e. firing rate differences within and outside of a hot spot) in relation to head/eye orientation and thus may give further evidence for a role in motion perception and sensory transformation.

Concluding remarks

In our everyday environment, the brain is constantly tasked to integrate signals from several sensory modalities. Understanding cortical multisensory processing is essential in understanding perception and behavior. The cat AES is a well suited model structure to identify multisensory encoding strategies and their effects on perception and behavior. STRF analysis is a great tool to investigate multisensory neuronal responses as determined by time, space and stimulus effectiveness and will aid in establishing AES function. Furthermore, comparing findings across species may allow for generalizations about multisensory processes in the healthy brain, which may contribute to research targeting disorders of the central nervous system.

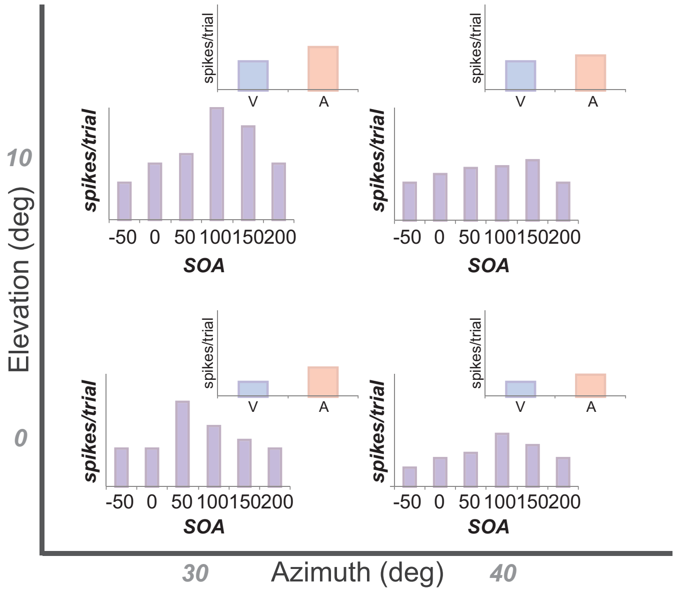

Figure 2. Hypothetical multisensory spatiotemporal receptive field at four locations. Bar graphs represent the neuronal firing rates at the different locations for the unisensory visual (V, blue) and auditory (A, red) trials as well as the audiovisual trials (VA, purple) over all tested SOAs. Note the different firing rates depending upon SOA, giving a temporal window over which multisensory integration occurs. Furthermore, the temporal window varies with spatial location.

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