

# Is neocortex essentially multisensory?

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**Although sensory perception and neurobiology are traditionally investigated one modality at a time, real world behaviour and perception are driven by the integration of information from multiple sensory sources. Mounting evidence suggests that the neural underpinnings of multisensory integration extend into early sensory processing. This article examines the notion that neocortical operations are essentially multisensory. We first review what is known about multisensory processing in higher-order association cortices and then discuss recent anatomical and physiological findings in presumptive unimodal sensory areas. The pervasiveness of multisensory influences on all levels of cortical processing compels us to reconsider thinking about neural processing in unisensory terms. Indeed, the multisensory nature of most, possibly all, of the neocortex forces us to abandon the notion that the senses ever operate independently during real-world cognition.**

## Introduction

Early investigations of the cerebral cortex and its role in perception recognized that the convergence and integration of information from different sensory modalities is an essential component of cognition [1]. In traditional models of the sensory brain, however, multisensory integration is deferred until after extensive ‘unisensory’ processing has occurred [2]. This view arose from early neuroanatomical studies in cats and monkeys, which suggested few if any interconnections between somatosensory, auditory and visual cortices [3], and experimental lesions of discrete regions, which appeared to produce unimodal behavioural deficits [4].

Rapidly accumulating evidence on multisensory processing in primates and other mammals directly challenges this classical view. Strikingly, several anatomical studies suggest that the substrate for multisensory integration is already present at the primary cortical level [5–7]. In fact, the work published to date may reveal only the ‘tip of the iceberg’, as ongoing studies continue to reveal extensive interactions among low-level sensory areas and between those areas and association cortex. Here, we review multisensory processes involving vision, audition and somatosensation across the neocortical mantle. We advance the perspective that multisensory

influences are integral to primary as well as higher-order cortical operations. Although chemosensory processes are not considered here, it is noteworthy that pervasive multisensory interactions are also characteristic of these sensory systems [8].

Recasting the role of lower- and higher-order cortical processes in the light of multisensory interactions will compel us to reconsider the wisdom of reducing sensory perception and cognition into unimodal components. That is, the neurobiological data reviewed here suggest that focusing solely on unisensory processes will continue to provide us only with an impoverished view of both brain and behavior. The recent recognition of this fact by many scientists has led to different research strategies that are providing unique and fruitful perspectives in our understanding of perception and cognition [9].

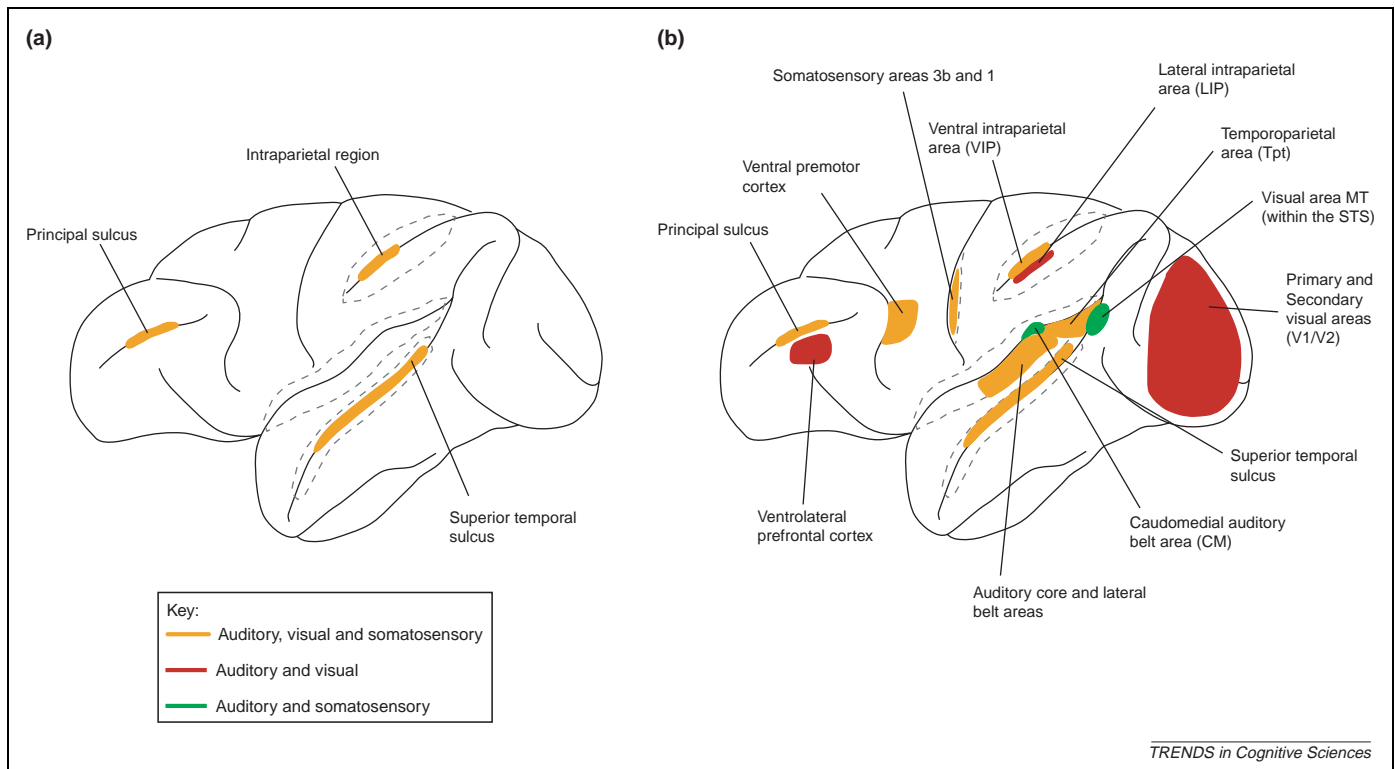
## Multisensory regions of higher-order association cortex

Several cortical areas were considered multisensory by virtue of their connections with multiple unimodal areas [10], their single neuron responses to multisensory input [11,12], and the behavioural deficits of patients with lesions in these areas [13]. Thus, included among the classical multisensory cortical areas of primates were the superior temporal sulcus (STS), the intraparietal (IP) complex, and the frontal cortex (Figure 1a). In this section, we will review the structural and functional evidence for each of these regions in turn.

### *The superior temporal sulcus*

A host of neuroimaging studies have demonstrated multisensory convergence in the human STS region (see [14] for review). Direct neuronal recordings from the corresponding superior temporal polysensory (STP) region in monkeys have revealed that neurons can respond to both visual and auditory stimuli in both the upper [11,12,15] and lower banks [16]. Roughly, 36–38% of STS neurons appear to be multimodal in the anterior part of the STS [11,16], and ~12% in the caudal portion of STS [12]. These early monkey studies, however, did not systematically investigate whether single STS neurons *integrate* auditory and visual information. Recently, however, Barraclough *et al.* [17] measured the integrative properties of single neurons using biologically relevant dynamic stimuli, including vocalizations, ripping paper and human walking. They showed that 23% of neurons responsive to the sight of biological motion could be significantly modulated by the corresponding auditory component. Importantly, multisensory modulation was

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**Figure 1.** (a) Traditional scheme of the cortical anatomy of multisensory areas in the primate brain. (b) Modern scheme of the cortical anatomy of multisensory areas. Colored areas represent regions where there have been anatomical and/or electrophysiological data demonstrating multisensory interactions. In V1 and V2, the multisensory interactions seem to be restricted to the representation of the peripheral visual field. Dashed gray outlines represent opened sulci.

dependent upon the auditory signal being congruent with the visual cue.

#### *The intraparietal sulcus and area Tpt*

The intraparietal region is part of a larger network for orchestrating multisensory-guided movements in space. One major node in that network is the lateral intraparietal (LIP) area of the posterior parietal cortex [18]. Although LIP was long considered a unimodal visual area, neurons in LIP are now known to be multisensory, receiving a convergence of eye position, visual and auditory signals [18]. During delayed-saccade tasks, where a monkey subject must plan eye movement to a remembered target in the periphery of extrapersonal space, LIP neurons are modulated by the onset of either visual or auditory cues (depending the modality of the remembered target) and responses to both types of sensory targets are spatially tuned [19]. Several subsequent studies suggested that the sensory responses in LIP driven by any input modality have a complex task dependence [20,21], although the strength of this dependence and its operational rules remain open questions.

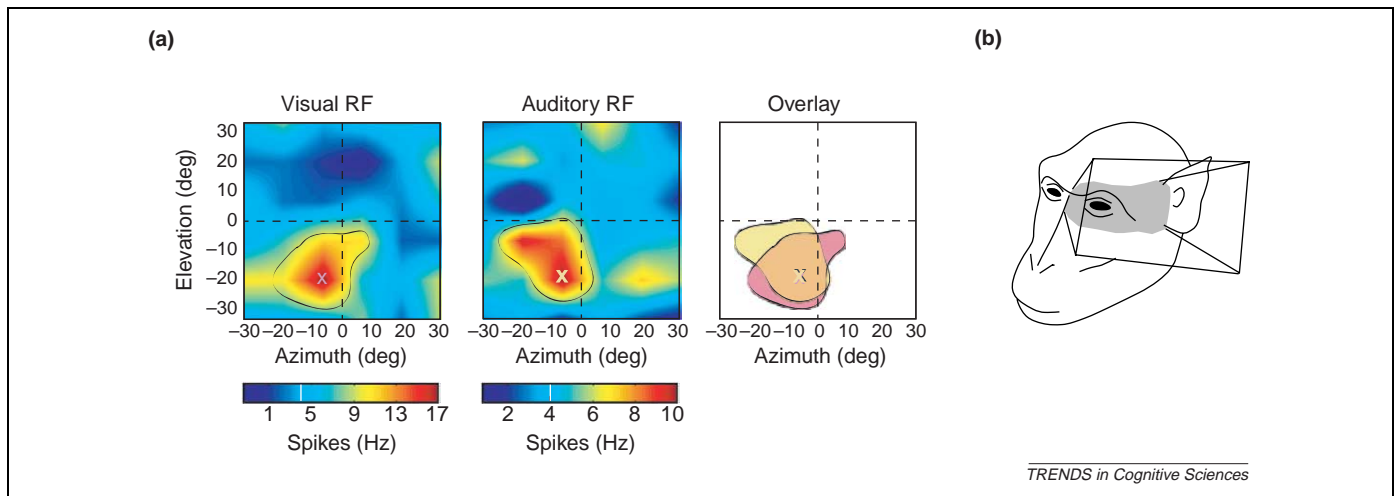
Another node in the network for sensory guided movements is the ventral intraparietal area (VIP), located adjacent to LIP in the fundus of the intraparietal sulcus of monkeys. VIP neurons respond to visual, auditory, somatosensory and vestibular stimuli, and for bi- or trimodal VIP neurons, receptive fields (RFs) driven through different modalities usually overlap in space [22–25]. Figure 2a shows an example of VIP neuron with overlapping visual and auditory RFs. Like LIP neurons, VIP neurons are likely to have task-dependent responses.

At the temporo-parietal junction, area Tpt is reported to contain a multimodal representation of space as well [26]. Area Tpt occupies the posterior-most portion of the superior temporal plane and the superior temporal gyrus, at the border of auditory, somatosensory and visual cortices. It contains trimodal neurons with RFs over the head-neck-shoulder region, leading to the speculation that Tpt might be involved in orienting the head in space [26].

#### *Frontal and prefrontal cortices*

Relatively few studies have directly investigated multisensory processing in prefrontal cortex. Monkeys trained to make associations between high/low frequency tones and two different colors in a delayed match-to-sample task, however, have prefrontal neural responses that respond to both the auditory and visual stimuli [27]. More recently, Romanski and colleagues (Sugihara *et al.*, personal communication) adduced data from the ventrolateral prefrontal cortex which showed that neurons there integrate the auditory and visual components of vocal signals and that the integration was dependent on the congruence between the two signals.

Just posterior and ventral to the lateral prefrontal cortex, the premotor cortex contains neurons with responses to visual, auditory and somatosensory inputs [28–30]. The RFs of these cells tend to be located around the upper body, including the face, arm and upper torso (Figure 2b). Indeed, even auditory responses seem tuned to nearby sound sources independent of sound intensity [29]. For the most part, multisensory neurons are clustered in a ‘polysensory zone’ located just below the spur of the arcuate sulcus in the dorsal part of premotor



**Figure 2.** (a) Visual and auditory receptive fields of a ventral intraparietal area neuron. The receptive fields are spatially congruent. Horizontal and vertical axes indicate mapping range. The mean neural activity is color-coded. Spontaneous level of activity is indicated by the white line in the color bar. Crosses indicate locations of maximal spike discharge. The far right panel shows the superposition of the receptive fields from the two modalities. (Reproduced with permission from [25]). (b) The overlapping visual and tactile receptive fields of a multisensory neuron at a premotor cortical site. Electrical stimulation of this site elicits a complex defensive posture involving a facial squint, a head turn, and movement of the arm and hand into a guarding position. (Reproduced with permission from [34]).

area F4. The function of these neurons appear to be ‘defense’ related: monkeys (and humans) are exquisitely sensitive to visual, auditory and multisensory looming signals that indicate approaching danger [31–33] and microstimulation of the ‘polysensory zone’ elicits defensive-like movements [34]. Consistent with these findings, visual responses in the primary motor cortex are particularly sensitive to expanding ‘looming-like’ optic flow stimuli [35].

*The ectosylvian and lateral suprasylvian sulcus in cats*  
Inactivation of multisensory association cortical areas in the cat has a direct influence not only the integrative properties of superior collicular neurons [36], but can also influence orienting behavior. Cats typically show multisensory enhancement of orienting to congruent visual–auditory spatial targets when stimuli are near threshold. When the anterior ectosylvian sulcus or the rostral lateral suprasylvian sulcus is cryogenically inactivated, the multisensory behavioral enhancement is disrupted, but the inactivation does not impair orientation to unimodally presented targets [37]. Based on these data, it is clear that association cortical areas have an important role to play in multimodally driven behaviours. Nevertheless, for many behaviors (if not all) and contexts, synthesis of information from different modalities might be achieved, enhanced or processed in parallel through the interaction between ‘sensory specific’ cortical areas. These interactions might (i) enhance behavioral outcomes in conjunction with association cortex, (ii) be sufficient for certain behaviors, and/or (iii) be necessary for others.

### Multisensory processes in unisensory areas

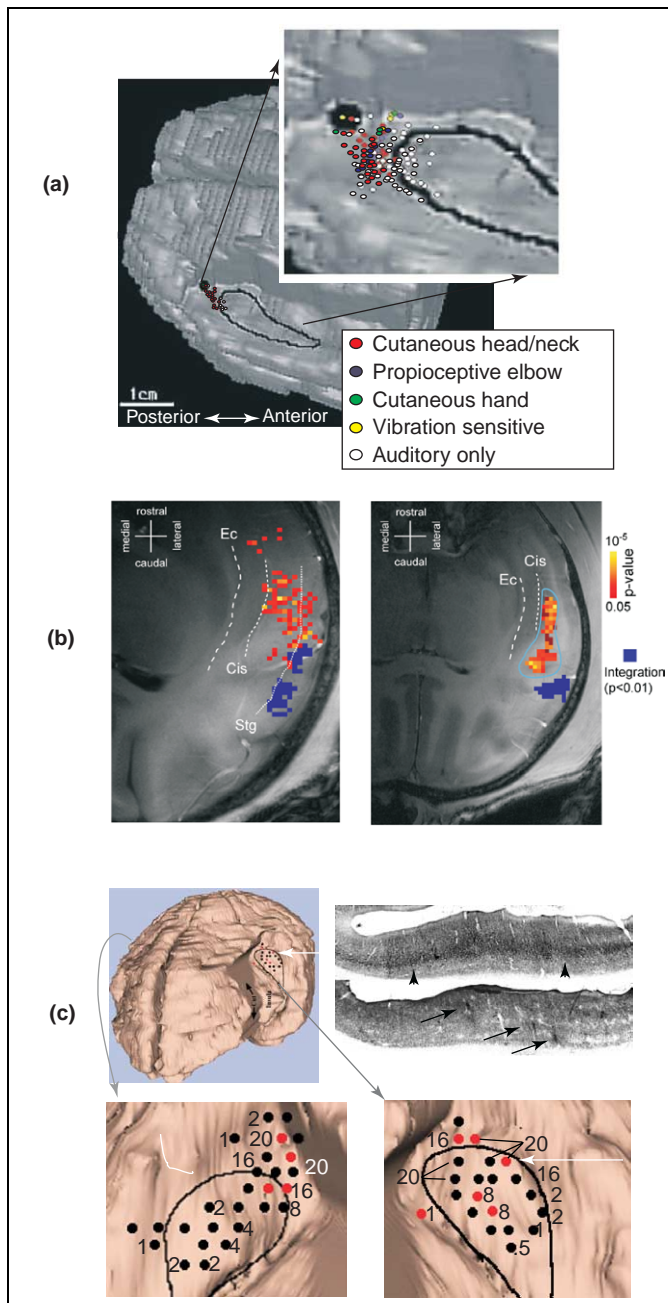
*Visual and somatosensory processing in auditory cortex*  
Functional imaging [38] and later, event related potential [39–43] studies, raised the possibility of audio-tactile and audio-visual interactions in human auditory cortex. Localization of these effects in the superior temporal plane was independently supported by techniques that

have better anatomical resolution, including magnetoencephalography [44,45] and fMRI [38,46,47].

In parallel to the human studies, intracranial recordings have directly confirmed multisensory convergence in auditory cortex in macaque monkeys [15,48–50]. Importantly, these studies have used a combination of single-unit, multi-unit and field potential measurements which might uncover instances of multisensory processes not discernable through an examination of either type of neuronal signal alone. The initial report of non-auditory inputs [49] used multi-contact electrode recordings in awake monkeys which allowed them to measure neural signals from multiple cortical layers concurrently. In this paradigm, the somatosensory responses triggered by electrical stimulation of the median nerve have approximately the same latency as co-localized auditory responses, and have a similar, although not identical, feedforward laminar profile (i.e. the initial response onset is in Layer 4). The laminar profile of the median nerve-evoked somatosensory response contrasts strongly with that of nearby visual inputs, which have a ‘feedback’ laminar profile (i.e. the initial response occurs above and below Layer 4) [15].

A subsequent study [51] used single microelectrode recordings in anesthetized monkeys to confirm that convergence occurs at the single neuron level. Fu *et al.* [51] further showed that, although proprioceptive and vibratory inputs are present, the dominant somatosensory input is a cutaneous representation of the head and neck. The anatomical reconstruction of these effects is depicted in Figure 3a; note that the localization of somatosensory responses appears to exclude A1. Recently, these findings were extended by an fMRI study in the anesthetized monkey which demonstrated that auditory and tactile stimuli presented simultaneously lead to enhanced activity (i.e. multisensory integration) in a region posterior and lateral to the primary auditory cortex (AI) in what is presumably the caudo-lateral belt area, CL [52] (Figure 3b). In addition to somatosensory and visual





**Figure 3.** Distributions of non-auditory inputs into auditory cortex derived from three separate studies in macaque monkeys. **(a)** Locations and relative proportions of cutaneous head/neck, cutaneous hand, proprioceptive, vibratory somatosensory inputs (colors as in key) to caudo-medial area, based on microelectrode mapping during acute recording experiments in two anesthetized monkeys. White symbols denote locations that were tested for somatosensory and auditory inputs but had only the latter. The inset depicts the composite reconstruction of the four hemispheres tested (Reproduced with permission from [51]). **(b)** Integration of touch and sound in the anesthetized monkey auditory cortex. Activation map is overlaid on anatomical image for tone stimulation (encoded in red voxels) and multisensory integration (encoded in blue voxels). The location of integration is posterior and lateral to the primary auditory cortex, presumably in the caudo-lateral belt region. (Reproduced with permission from [52]). **(c)** 3-D reconstruction of an individual macaque brain showing the location of eye-position-sensitive regions in auditory cortex. The superimposed dots indicate the positions of the electrode penetrations and the line indicates the boundary of the core areas (A1/R). An example of adjacent sections, taken at the level of the white arrow, and stained to show glial scars left by electrode penetrations (arrows, lower section). Bottom panels: surface view of each superior temporal plane is expanded (left hemisphere on the left, right hemisphere on the right). Individual penetration locations are indicated by dots. Numbers indicate the local best frequencies (in kHz). The white arrow in the right panel corresponds to the white arrow in the 3-D reconstruction at the upper left. The red dots signify penetration sites that were tested for eye position effects; nearly all of the sites tested had eye position effects. The black dots signify penetrations made

inputs, eye position inputs into auditory cortex have been observed [53,54], and these clearly invade A1 as well as surrounding belt regions (Figure 3c).

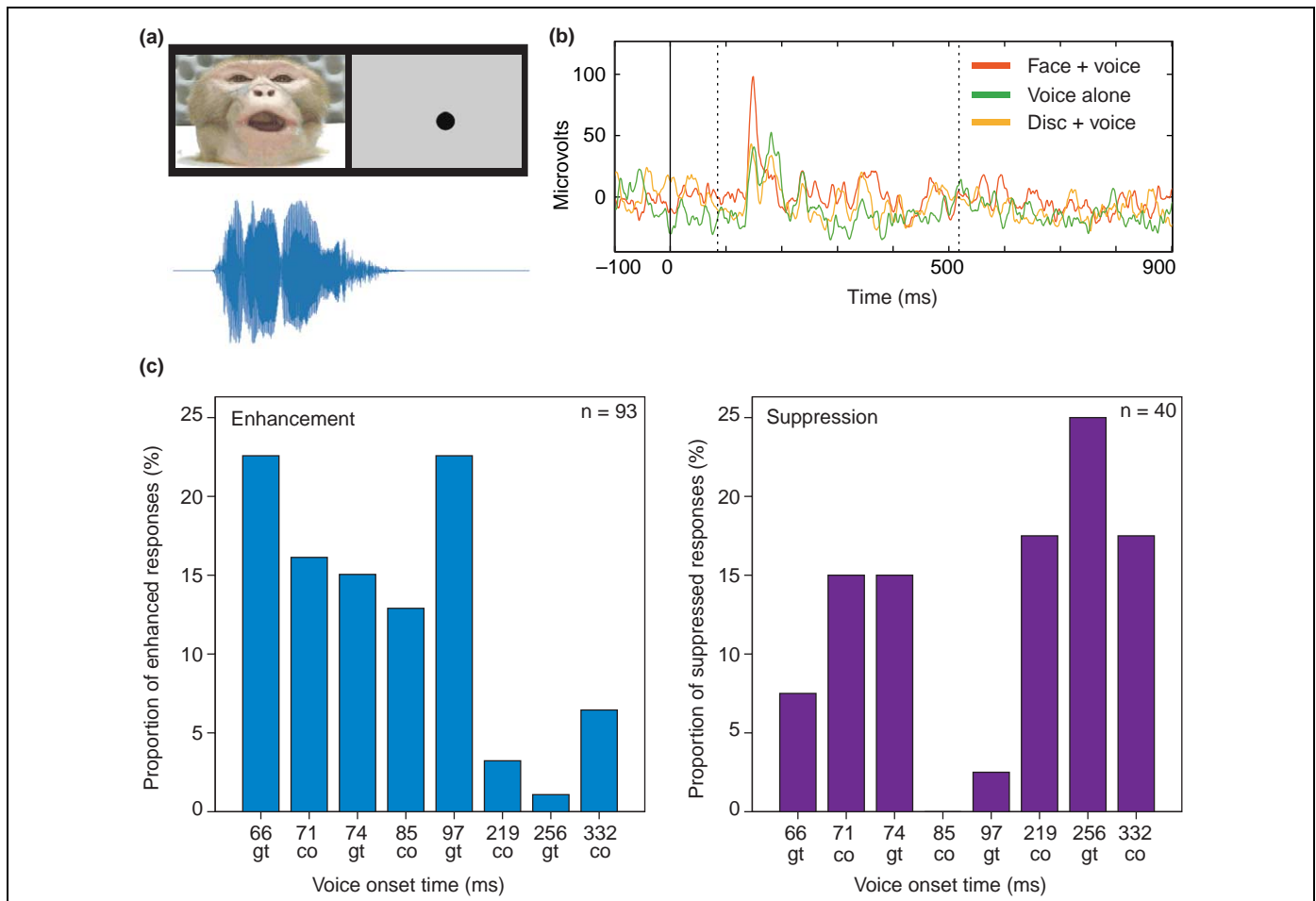
Non-auditory modulation of primary auditory cortex (A1) has also been observed under conditions in which visual cues and bar press responses were relevant to an auditory sensory task; interestingly, the ability of the same cues and behavior to modulate auditory cortical activity disappears when the monkey performs a similar visual task [50]. Finally, non-auditory modulation of A1 has been observed during studies of audiovisual communication both in humans [46,47] and monkeys [48]. In monkeys, nearly all multisensory integrative responses in the lateral belt and A1 were specific to face-voice integration: if the face was replaced by a high contrast dynamic disc mimicking mouth movements [55,56], integration was not as frequently observed (Figure 4a,b). Thus, as in the STS [17] multisensory interactions are optimized for *congruent* multisensory stimuli.

#### *Auditory and somatosensory processing in visual cortex*

Auditory sensitivity was reported by early studies in the cat visual cortex [57]. Morrell reported that up to 41% of visual neurons could be driven by auditory stimuli *and* that these neurons showed a remarkable degree of auditory spatial tuning [57]. In monkeys, the strongest case for audiovisual convergence in visual cortex comes from anatomical tracing studies. The primary visual (V1) area receives inputs from the core and belt regions of auditory cortex and the upper bank of the STS [6,7]. The pattern of inputs into V1 is not uniform – connections with auditory cortex occur primarily in the representation of the peripheral visual field [6]. The auditory cortical projections to both V1 and V2 terminate primarily in cortical layers 1 and 6 (a ‘feedback’-style projection) [7].

Beyond the low level visual cortices, large-scale mapping techniques have revealed that auditory and somatosensory stimuli can even activate parts of the inferotemporal (IT) cortex. For example, Poremba *et al.* [58] used 2-deoxyglucose utilization to delineate the extent of awake rhesus monkey neocortex activated by complex auditory stimuli. They found that large expanses of the neocortex were activated by sounds, including unimodal visual areas in the temporal and parietal lobes. This extensive activation of visual areas by auditory stimuli is reminiscent of an earlier finding by Pribram *et al.* [59]: using auditory clicks as stimuli and field potential recordings in anesthetized monkeys, they found that, beyond traditional auditory areas, much of the superior temporal gyrus, insula and parts of the parietal lobe were responsive. Single unit recordings in monkeys performing a crossmodal delayed-match-to-sample task also revealed sample- [60] and delay-period [60] auditory activity in IT cortex. These data suggest that ventral temporal lobe may represent objects and events independent of modality. In support of this, a recent fMRI study demonstrated that an area overlapping the fusiform face area is activated not only by familiar faces, but by familiar voices as well [61].

earlier, unrelated experiments in this subject; these help to functionally establish core/belt boundaries. (Adapted from [53].)



**Figure 4.** Multisensory integration of faces and voices in monkey auditory cortex. **(a)** One frame of a 'coo' face at maximal mouth opening for one stimulus monkey and the corresponding frames from the 'disc' control videos. Time waveform below represents the coo vocalization paired with both videos. **(b)** Auditory cortical responses to multimodal vocalization shown in (a). Rectified local field potential responses to Face+Voice (F+V), Disc+Voice (D+V) and Voice alone (V) components were compared. Discs were dynamic and mimicked the aperture and displacement of the mouth in the original video. The solid vertical line indicates the onset of the Face or Disc signal. Dotted vertical lines indicate the onset and offset of the Voice signal. Graphs represent the mean of 10 repetitions. Histograms show enhanced response that was specific to the combination of face + voice, but not disc + voice. **(c)** Relationship between voice onset time and multisensory integration. Proportion of enhanced ( $n=93$ ) and suppressed ( $n=40$ ) responses across the different voice onset time categories. Note that enhancement was more frequently observed for short voice onset times, whereas suppression was more common at longer voice onset times. 'gt' represents grunts, 'co' represents coos. (All figures reproduced with permission from [48]).

Extrastriate visual cortical areas also appear to be activated during tactile perception (see [62] for review). Haptic object discrimination and identification activates the lateral occipital complex (LOC) [63–65], a human visual cortical area homologous to macaque IT cortex.

Perception of tactile motion activates the human MT complex [66,67]. These studies reinforce the earlier suggestion [60] that extrastriate visual cortical regions are recruited in a task-specific manner, such that the specific areas of extrastriate visual cortex that mediate

### Box 1. Multisensory integration beyond the neocortex

The abundance of multisensory interactions in the neocortex begs the question: Do subcortical structures integrate the senses as well? Given the extensive connections between the neocortex and the superior colliculus, the thalamus and the amygdala, it is reasonable to assume that regions beyond the neocortex are multisensory.

The pioneering studies by Stein and colleagues of multisensory integration in the cat superior colliculus [71] outlined key principles of multisensory integration that have served to guide investigations in other species and brain structures. Their subsequent studies show that multisensory integration in superior colliculus depends on input from neocortex [72], and thus appears to contribute more directly to motoric orienting than to perceptual processing. Studies of the superior colliculus in behaving monkeys have extended our knowledge of the subtleties of integration in this structure [73,74].

In the primate amygdala, many neurons respond to visual, auditory and somatosensory stimuli [75]. These neurons are not distributed randomly throughout this structure: rather, visually responsive

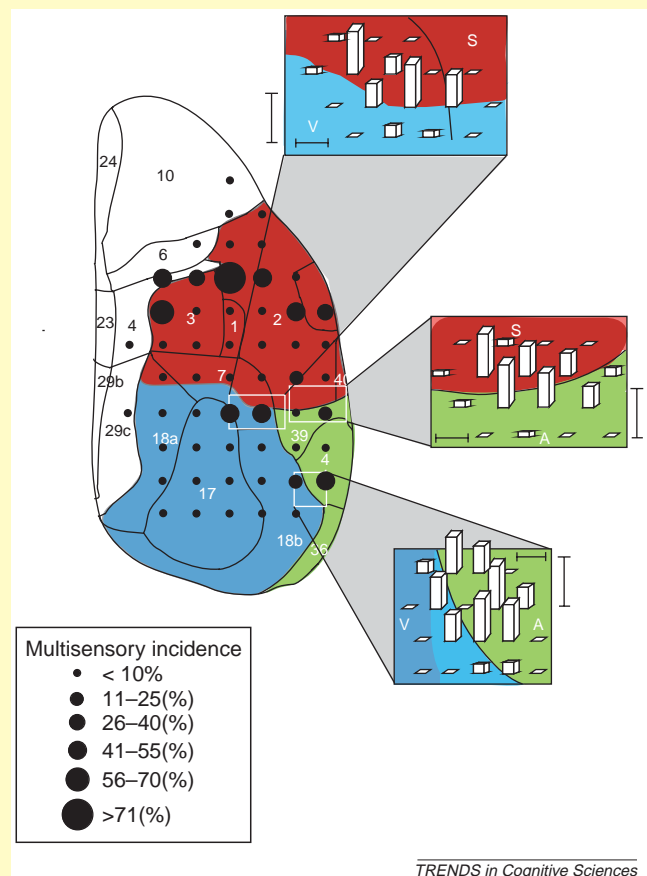
neurons are clustered in the anterior portion of the basolateral nucleus, and neurons responsive to auditory stimuli are clustered in the posterior portion [75]. A smaller percentage of neurons respond to multiple modalities. In contrast to the many multisensory studies suggesting that behaviorally relevant, familiar stimuli are needed to drive responses, in the amygdala neurons respond most vigorously to novel, unfamiliar stimuli.

Thalamic structures also appear to be multisensory in nature. A recent physiological study demonstrated multisensory integration in the rat thalamus. Komura *et al.* [76] trained rats to perform an auditory spatial discrimination task in which either auditory cues or auditory–visual cues were presented. Importantly, only the auditory cues were 100% predictive; the visual cues could either be in agreement with the auditory cue or conflicting. In this context, almost 15% of auditory thalamic neurons were modulated by the visual cues. When the visual cue was congruent with the auditory cue, responses were enhanced. By contrast, when the visual cue was in conflict, auditory responses were suppressed.

## Box 2. The border regions between sensory areas

How discrete are the borders between sensory cortical areas? Using the rat as a model system, Wallace *et al.* [77] mapped single-neuron responses across a large expanse of the postero-lateral neocortex encompassing the primary auditory, somatosensory and visual areas. They found that, as expected, within each of these unimodal areas there were few neurons that responded to an 'inappropriate' modality. However, *between sensory-specific areas*, there were clusters of neurons that not only responded to inputs from more than one modality, but were capable of *integrating* these multisensory inputs (see Figure 1). For example, the border between visual and auditory cortex had neurons that were enhanced or suppressed when stimuli from these modalities were presented simultaneously. The same was true for the other borders. These data are generally supported by similar studies using different methods. Field potential recordings by Barth and colleagues found that the border of rat secondary somatosensory cortex (SII) is multisensory and able to integrate auditory with somatosensory signals [78]. Indeed, they found a rather large zone of cortex between SII and auditory cortex that is multisensory [79]. Even within the human STS, there appear to be patches of unimodal regions that overlap to produce a border zone that is multisensory in nature [80].

Although it is clear that the border zones between sensory-specific cortical areas are biased towards multisensory representation in primates as well as rodents, it does not appear that 'proximity' is the sole determinant of multisensory convergence across the neocortex. For example, in addition to the multisensory visual-auditory convergence predicted by its location at the border between visual and auditory cortices, STS receives somatosensory input [12,15], which is not predicted by a proximity rule. A similar example is found in the lateral intraparietal area (LIP), which exhibits visual-somatosensory convergence, as predicted by its location between visual and somatosensory cortices, but also receives auditory input, again not predicted by a proximity rule.



**Figure 1.** The distribution of multisensory neurons in the rat sensory neocortex. Numbers and lines depict the subdivisions on the dorsal surface of cortex. Red is parietal cortex, green is temporal cortex, and blue is occipital cortex. Filled circles show electrode penetrations and the size of the circles indicate the relative incidence of multisensory neurons at each site. Insets show the results of higher resolution sampling in the transitional regions between sensory areas. V, visual cortex; A, auditory cortex; S, somatosensory cortex. Horizontal scale bars = 250  $\mu$ m. (Reproduced with permission from [77].)

particular visual tasks, such as object recognition or directional discrimination are recruited in the corresponding tactile tasks.

### Visual and auditory activation of somatosensory cortex

Very few physiological studies have searched somatosensory cortex for visual and/or auditory responses. Studies by Fuster and colleagues show that in monkeys trained to make visual-haptic or auditory-haptic associations, a subset of somatosensory cortical neurons would, like the prefrontal neurons described above, respond both to the visual/auditory cue and the tactile stimulus [68,69]. In somatosensory, as in visual cortex, the best case for multisensory convergence may be based on anatomy. Anatomical tracer studies in marmosets reveal projections from visual areas FST and MT to somatosensory Areas 1 and 3b, as well as connections between auditory cortex and several somatosensory areas, including S2 [5].

We should note here that multisensory processes are not the exclusive domain of the cortical mantle (Box 1). Indeed, the pioneering neurophysiological work

investigated multisensory integration in the superior colliculus. Furthermore, across cortical regions, it may be the case that the border zones between sensory specific areas may be patches of multisensory neurons (Box 2).

### Higher-order versus lower-order cortical areas

The findings reviewed here demonstrate that *both* higher-order association areas and presumptive unisensory areas of the cerebral cortex are in fact multisensory in nature (Figure 1b). The research defining the specific role each type of cortical area plays in real-world sensory/cognitive processing suggests the emergence of two broad themes. First, the multisensory processes in association cortex reinforce the widely held view that a primary role of these regions is to compute a veridical representation of the outside world. For example, in parietal areas such as LIP, VIP and area Tpt, there is a high degree of spatial correspondence between the RFs from different modalities (Figure 2). Along the same lines, activity in the temporal lobe (e.g. STS and extrastriate areas) seems to represent more concept-related events – the modality-independent



### Box 3. Questions for future research

- What are the functional similarities and differences between multisensory processes in the higher-order versus low level sensory cortices?
- What are the cellular mechanisms that give rise to multisensory enhancement/suppression, and how does this contribute to perception and behavior?
- What is the role of attention in multisensory processing and does the impact of attention vary across processing stages?
- What are the stimulus-related factors controlling multisensory modulation of unisensory processing?
- Are any multisensory mechanisms species- or brain area-specific?
- What are the criteria needed to designate a brain region as multisensory?

representations of objects, individuals or motion. The role of temporal cues has not been systematically investigated in these areas and will probably be important, although its precision might be entirely context- or task-dependent.

Second, a characteristic of low-level multisensory interactions appears to be a *lack* of spatial precision. For example, somatosensory input to auditory cortex appears widespread, and although it might be biased towards the upper body surfaces, it lacks a precise somatotopic representation [51]. Similarly, anatomical cross connections between low-level visual and auditory areas appear to target the peripheral visual field representations, pointedly avoiding the more precise central visual field representations [6,7]. Thus, the degree to which low level multisensory processes contribute to spatially precise higher-order multisensory representations is an open question (see also Box 3). On the other hand, low-level multisensory interactions are characterized by a high degree of temporal precision. For example, during audiovisual vocalization processing in auditory cortex [48], the sign of the integration appeared to be dependent on the timing between the initial mouth movement and the onset of the auditory component of the vocal signal (Figure 4c). The longer the time interval between the initial mouth movement and the onset of the voice, the greater the likelihood of observing response suppression. By contrast, a short time interval leads to enhanced responses. One hypothesis is that the primary function of non-auditory inputs is to reinforce unisensory auditory processing. For example, Schroeder and colleagues posit that non-auditory inputs reset the phase of ongoing oscillations in auditory cortex so that arrival of crucial auditory input coincides with peaks in the oscillatory cycle (Lakatos *et al.*, personal communication).

### Conclusions

The integration of information from different sensory systems is a fundamental characteristic of perception and cognition – qualitatively different kinds of information from the various sense organs are put together in the brain to produce a unified, coherent representation of the outside world. Traditionally, it has been assumed that the integration of such disparate information at the cortical level was the task of specialized, higher-order association areas of the neocortex. In stark contrast to this assumption, the neurobiological data reviewed here

suggest that much, if not all, of neocortex is multisensory (Figure 1b). This necessarily forces us to reconsider the validity of probing the brain unimodally and suggests a different perspective when considering other aspects of cognition – from cognitive development to social cognition. For example, it is likely that neither the brain nor cognition develops one sensory modality at a time [70], nor do we represent individuals in one modality at a time [61]. The world is barrage of sensory inputs, our perception is a unified representation of it, and the neocortex is organized in a manner to make the underlying processes as efficient as possible.

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