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INVITED REVIEW

"The great mixing machine": multisensory integration and brain-breath coupling in the cerebral cortex

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Abstract

It is common to distinguish between "holist" and "reductionist" views of brain function, where the former envisions the brain as functioning as an indivisible unit and the latter as a collection of distinct units that serve different functions. Opposing reductionism, a number of researchers have pointed out that cortical network architecture does not respect functional boundaries, and the neuroanatomist V. Braitenberg proposed to understand the cerebral cortex as a "great mixing machine" of neuronal activity from sensory inputs, motor commands, and intrinsically generated processes. In this paper, we offer a contextualization of Braitenberg's point, and we review evidence for the interactions of neuronal activity from multiple sensory inputs and intrinsic neuronal processes in the cerebral cortex. We focus on new insights from studies on audiovisual interactions and on the influence of respiration on brain functions, which do not seem to align well with "reductionist" views of areal functional boundaries. Instead, they indicate that functional boundaries are fuzzy and context dependent. In addition, we discuss the relevance of the influence of sensory, proprioceptive, and interoceptive signals on cortical activity for understanding brain-body interactions, highlight some of the consequences of these new insights for debates on embodied cognition, and offer some suggestions for future studies.

Keywords Multisensory integration · Respiration-locked oscillations · Brain-breath coupling · Embodied cognition

> "Transcortical connections have been shown to exist even in the primary sensory regions of the cortex, indicating that sensory input is immediately mixed upon its arrival in the cortex with information about the state of the rest of the cortex." (V. Braitenberg 1974, [10])

Introduction

When electrophysiological approaches in brain research came of age in the 1950s and 1960s and allowed for stable recordings of action potentials in mammalian brains in vivo, it became immediately clear that the spike activity of neurons is quite variable and that the brain continually generates "ongoing background activity" [13]. A prevailing view was that the variability in neuronal activity or "neuronal noise" was an undesirable but inherent feature of biological nervous systems and that the brain had developed mechanisms to make precise neuronal computations possible, despite the presence of noise (e.g., [17]).

Early on, synaptic noise, i.e., random processes at synaptic junctions, was proposed as one possible source for the variability in neuronal activity [15]. The discovery of population coding provided a possible mechanism through which neuronal computations could reach precise outcomes in the presence of noise in individual neurons, by averaging the task-related activity of thousands of neurons (e.g., [23]). Consistent with the idea that neuronal noise was not task related, data analysis techniques were largely focused on averaging neuronal activity over multiple repetitions of stimuli or behavioral trials, in order to eliminate trial-by-trial variability and unmask the neuronal response specific to a stimulus or the neuronal activity controlling a cognitive or behavioral event (e.g., [4]). Current views on neuronal noise suggest that variability in neuronal activity can result from two sources: inputs from deterministic sources, such as sensory inputs or

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intrinsically generated activity, and from random processes at the cellular level, such as noisy biochemical processes or noise from voltage-gated ion channels (for a review see [19]).

In this review, we will focus on variability in cortical neuronal activity related to deterministic sources, which should not be considered noise but rather an element of cortical activity that interacts with experimentally targeted neuronal activity in a functionally meaningful way. We maintain that the new insights into how sensory inputs shape ongoing and event-related neuronal activity in the neocortex not only defy traditional views of areal functional boundaries in the neocortex but also help highlight a key neuronal mechanism for brain-body interaction. We take this to expand upon the proposed link between brain-breath coupling and embodied cognition, which we have described previously [51].

Functional boundaries and "mixing"

When it comes to the question of dividing the cerebral cortex into functionally distinct regions, a brief look at the history of the brain sciences reveals two opposing views. Finger [21] distinguishes between "holism"| and "reductionism" and maintains that while holism envisions the brain as functioning as an indivisible unit, reductionism holds that it is best understood as a collection of distinct functional units such that different cerebral cortical regions serve different functions. While reductionism found prominent supporters in the eighteenth century, it first rose to prominence in the nineteenth century [21].

Often noted as one of the first proponents of reductionism, eighteenth century Swedish scientist Emmanuel Swedenborg offered a detailed account of cortical localization of function. While highlighting the cortex as responsible for controlling the sensory organs, muscles and movement, cognition, imagination, judgment, and will, he rejected a unitary outlook on the structure of the cerebral cortex. Instead, he argued that different functions are realized in different areas in the cerebral cortex, which he took to explain why lesions to particular areas could selectively damage certain functions while leaving others intact [49]. In the nineteenth century, Paul Broca's groundbreaking reductionist attempts to localize the seat of function continued to draw evidence from clinical observations of lesions, and the study of lesions still plays an important role in attempts to delineate the functional boundaries of the cerebral cortex and their sub-specialization (e.g., [32]). In addition to studies of lesions, attempts to associate functions with particular areas draw on studies exploring brain responses to electrical stimulation (e.g., [38]), anatomical connectivity (e.g., [1]), and electrophysiological or—more recently—optophysiological characterizations (e.g., [55]).

Opposing at least strict versions of reductionism, a number of researchers have pointed out that cortical network architecture does not respect functional boundaries between cerebral cortical areas [10, 12]. Based solely on statistical considerations of the cerebral cortical network architecture, the neuroanatomist V. Braitenberg has suggested that an input to the neocortex is "[…] immediately mixed upon its arrival in the cortex with information about the state of the rest of the cortex," concluding that "the cortex is, to large extent, a thinking machine working on its own output" [10]. Further elaborating on this line of reasoning, in the second edition of Anatomy of the Cortex. Statistics and Geometry, Braitenberg and Schüz suggest that the neocortex serves as a "great mixing machine" of neuronal activity from sensory inputs, motor commands, and intrinsic processes [12]. The mixing of neuronal activity occurs in the form of electrical integration of thousands of synaptic inputs in postsynaptic neurons, resulting in membrane potential fluctuations at the soma. These fluctuations thus reflect the activity of each neuron's surrounding neuronal network, which, as we now understand it, extends beyond the traditionally assigned functional boundaries of cortical areas, supporting interactions between local and long-range inputs.

Braitenberg's notion of "mixing " is consistent with an anti-reductionist approach, stressing that neuronal activity involved in the processing of sensory input or the control of behavior is shaped by and contributes to ongoing activity in the cerebral cortex to such an extent that it casts doubt on the idea of neat functional boundaries between cerebral cortical areas. It is natural to comprehend such notion of "mixing" in a way that has implications for what counts as a suitable explanation. More precisely,"mixing" of two (or more) components X and Y refers to a close association of X and Y such that a full account of X requires taking into consideration the influence of Y on X (and/or vice versa) (for a discussion of the relevant epistemological and metaphysical issues, see [50]). We may note that this specific meaning of mixing can involve, but does not require that, the association of X and Y result in a novel product (entity or process) Z.

Figure 1 illustrates the anatomical substrates underlying the "mixing" of neuronal activity at the level of an individual neuron's axon collaterals (Fig. 1a) that form dense axonal networks with up to 4.1 km of axon per mm^3 of cortical grey matter [11, 12] (Fig. 1b) to long-range fiber tracks connecting distant cortical lobes (Fig. 1c). Together, these connections form brain-wide networks that are key to multisensory integration and the interaction between sensorimotor, association, and limbic brain areas (Fig. 1d).

Multisensory integration

Understanding the neurophysiological mechanisms of propagation and "mixing" of neuronal activity in the neocortex is key to understanding cerebral cortical function.

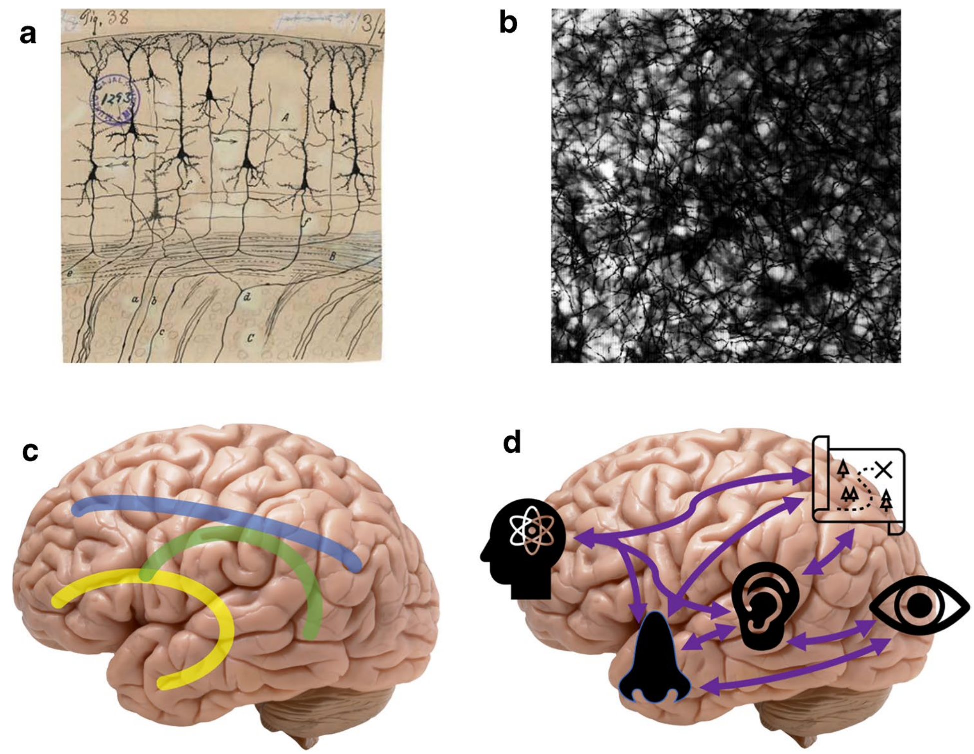

Fig. 1 Anatomical substrates for the mixing of information in the cerebral cortex. **a** Drawing of cortical pyramidal neurons by Ramon y Cajal showing horizontal axon collaterals forming connections to neighboring neurons and long-range projections of the same axons leaving the local network to connect to other cortical areas or subcortical structures [40]. **b** Silver stain of axons in the cerebral cortex forming a dense network with projections running equally in all directions [11, 12]. **c** Schematic illustration of some of the long-range axonal pathways forming connections between distant brain areas (yellow: uncinate fasciculus; green: arcuate fasciculus: blue: superior longitudinal fasciculus). **d** Schematic illustration of how neuronal activity propagates between cortical areas, resulting in the convergence, divergence, and integration of information via brain-wide networks

The investigation of multisensory integration in the cerebral cortex and its relevance for an organism's survival in an evolutionary sense is a rapidly growing and promising field. Important new insights have been gained from the investigations of audiovisual interactions and from the influence of breathing on brain functions. We review some of these findings in the following two sections. In addition, we discuss how the influence of sensory, proprioceptive, and interoceptive signals on cortical activity is highly relevant to understanding brain-body interactions.

Propagation of sensory activity and ongoing cortical activity

The view of the cerebral cortex as a great mixing machine predicts an incessant, dynamic interaction between intrinsically generated and sensory activity. Intrinsically generated activity here refers to neuronal activity resulting from cognitive processes, such as creativity or memory that do not require and are not directly driven by sensory inputs. Some early experiments using voltage-sensitive dyes [43] to monitor neuronal activity in the visual cortex of primates revealed how surprisingly similar the magnitude of fluctuations in the "ongoing" cortical activity is to the magnitude of stimulus-induced neuronal responses [2]. Findings by Arieli and colleagues demonstrated how fluctuations in ongoing cortical activity contribute significantly to the trial-by-trial variability of sensory-evoked responses [2]. It is currently not possible to design an experiment to monitor all sources of activity in the cerebral cortex and to evaluate and ultimately predict their interactions. Correspondingly, it is not possible to predict the influence of this interaction on the neuronal representation of any specific sensory input. Given the plethora of sensory and intrinsic sources driving neuronal activity in the cerebral cortex, it is unlikely that we will be able to address this question even partially any time soon. However, it is possible to study the propagation of neuronal activity elicited by an isolated sensory input. Using voltage-sensitive dyes in awake mice, Ferezou and colleagues investigated the neuronal processing of sensory inputs from a single mystacial vibrissae while monitoring neuronal activity in the entire contralateral cerebral cortex of awake, head-fixed mice [20]. Their results show that tactile sensory input from a single isolated whisker initially elicited an expected increase of neuronal activity in a small patch of the sensory whisker barrel cortex. Next, the neuronal activity rapidly expanded from the barrel cortex, igniting the entire cortical hemisphere within only 40 ms [20]. For an illustration of the rapid and seemingly unhindered propagation of sensory activity across the cerebral cortex see Fig. 7 in the publication by Ferezou et al. [20]. This finding gives some indication of how fast and far even small sensory inputs spread through the cortical, and likely thalamocortical, networks, resulting in a constant and complex interaction that drives “ongoing” activity across large areas of the cerebral cortex and likely modulates cortical function.

Audiovisual interaction

Efficient perception of the environment in real-life situations requires the integration of information from different sensory channels. The most closely studied integration of multisensory neuronal activity in the cerebral cortex is the interaction between visual and auditory information. Kayser and colleagues used high-resolution fMRI imaging to investigate the influence of visual stimuli on neuronal processing of auditory information in the auditory cortex in non-human primates. Their results showed that the auditory cortex could be activated by the presentation of visual stimuli alone, and that the representation of auditory stimuli was enhanced by concurrent presentation of visual stimuli [34, 35]. The analysis of trial-to-trial variability and information carried by the spike activity of auditory cortical neurons responding to repeated presentation of audiovisual stimuli showed that response variability was reduced and information encoding was enhanced over time [33]. Importantly, these changes were considerably reduced when the visual stimuli did not match the auditory stimuli [33], suggesting that this mechanism is fine-tuned to detect physically plausible events. Audiovisual interaction goes both ways, with the presentation of auditory stimuli also enhancing the detection of visual stimuli [44, 45]. Importantly, Stein and colleagues showed that neurons responding to multisensory audiovisual inputs showed proportionally greater response enhancements when the unimodal stimuli were less effective [44]. Together, these findings suggest that multisensory integration enhances information processing and increases the reliability of perception, improving an organism’s chances of survival.

The influence of breathing on brain activity and function

The modulation of rhythmic brain activity by respiration outside the olfactory system was first described in the primary sensory barrel cortex of mice [30], and is not fundamentally different from the cross-modal audiovisual interactions between primary sensory areas discussed above. However, compared to audiovisual interactions, which seems to be limited to the mutual modulation of neuronal processing in visual and auditory cortical areas, respiratory rhythm modulates neuronal activity across a broad range of cerebral cortical areas, including sensory, motor, limbic, and association areas [9, 29, 30, 36, 56]. The influence of respiration on neuronal rhythms in brain areas involved in cognitive and affective functions suggest that the act of breathing could influence cognition and emotion at a behavioral level. This has now been confirmed in several studies showing that cognitive and affective functions are significantly modulated by respiration [3, 26, 31, 37, 39, 56] (for recent reviews see: [27, 28, 48]). How respiration drives this seemingly brain-wide rhythm is not fully understood. A plausible assumption is that it propagates unhindered through the highly interconnected corticocortical and cortico-thalamic networks because of its slow frequency. Slow oscillations such as the alpha rhythm (~ 10 Hz) tend to propagate over large distances in the brain, whereas fast rhythms, such as gamma, remain more locally confined [14, 52].

The great mixing machine supports widening the scope of embodied cognition

The idea of “a great mixing machine” has interesting links with current debates on theoretical frameworks in cognitive science and sits well with recent efforts to widen the scope of various research endeavors often subsumed under the umbrella Embodied Cognition (EC) (also 4E Cognition or Grounded Cognition). EC is not a homogenous and unified area of research and some of its most important findings come from a variety of disciplines, including psychology, robotics, and neuroscience [6, 53]. However, while cognitive science has undergone major changes in its theoretical commitments, such as the shift from abstract formal descriptions to connectionist approaches [8, 47], it has remained committed to the ideas that (a) cognition is realized in the brain and (b) it can be explained in abstraction from the body [16, 22]. Opposing both (a) and (b), some of the various EC research endeavors maintain that at least some cognitive processes are best comprehended in terms of a dynamic interaction of bodily (non-neural) and neural processes. Opposing only (b), some EC endeavors are committed to a less radical idea according to which the body exerts a significant and often unexpected influence on cognitive processing, to the extent that failing to include bodily aspects leads to accounts of cognition that are at best incomplete.

While this is not the place for a comprehensive exploration of this issue, we may briefly note that the idea of the cerebral cortex as “a great mixing machine” is well suited to support recent efforts to widen the scope of EC research. Traditionally, much research under the EC umbrella has focused on action (e.g., gestures, facial expressions, eye movements), highlighting for instance the role of sensorimotor variables [54, 57] and gesturing [24, 25] in cognition. But while action is undoubtedly an important aspect, more recent research endeavors have widened the perspective of EC and include other bodily systems that seem important for cognition, such as the autonomic system, the endocrine system, the immune system, the cardiovascular system, the digestive system, and the integumentary system (for a recent reviews, see [7, 46]). Consistent with this widened the perspective, we have in an earlier publication provided some evidence supporting the less radical EC view, showing that a comprehensive account of cognitive activity requires taking into consideration the various ways in which respiratory activity influences cognition [51]. The great mixing machine concept supports this movement towards widening the scope of EC while it simultaneously offers a framework that helps make sense of seemingly disparate findings. The emphasis on the mixing of activity and the modulation of cerebral cortical ongoing and event-related activity by signals from the body helps make sense of how not merely action, but also sensory inputs from bodily systems can be vital for cognition.

Summary and conclusions

As neurophysiological findings document the cross-boundary interaction of different sensory inputs and the large-scale spread of sensory activity linked to breathing across the cerebral cortex, the view of the cerebral cortex as a collection of functionally distinct computational units is being revised. New findings indicate that functional boundaries are rather fuzzy and context dependent. Information arriving in one cerebral cortical area can propagate through intra-cortical, cortico-thalamic, or other subcortical networks and influence neuronal computation in distant areas that were previously considered functionally unrelated. In this brief review, we highlighted experimental findings linked to audiovisual interaction and brain-breath coupling, two areas that have received much attention in the recent years.

It is worthwhile to briefly mention two other lines of research that are relevant in this context. First, studies of visceral sensory signals have produced a rich set of evidence showing that visceral sensory signals affect rhythmic neuronal activity in the cerebral cortex and cognitive function (see the recent review by Azzalini and colleagues [5], underlining the importance of even the unconscious sensory representation of the body for brain function and embodied cognition). Second, studies of creativity suggest that a reduction of sensory inputs can be functionally meaningful. For example, creativity appears to be linked to visual sensory inputs in the sense that directing the gaze at an empty portion of the visual field ("looking at nothing") seems to benefit creativity [42]. The hypothesis is that the reduction of the cognitive load associated with processing visual sensory input frees up cognitive capacity that can be directed towards creative pursuits.

Many questions remain about how the cerebral cortex mixes intrinsic and external sources of neuronal activity, how this process affects normal brain function, and the consequences of pathological changes to the mixing process. To address these questions, it will be crucial to understand the mechanisms that determine the strength of influence that a specific source of activity exerts on other sensory, motor, or association cortical areas and how much this influence is shaped by context. Synesthesia might be an illustrative example of a case in which the functioning of the mechanisms controlling the strengths of sensory influences on other brain areas are altered, leading to patterns of perception that are not directly linked to physical reality (e.g., the very common association of days of the week or letters with colors) [41]. It is possible that the magnitude of cross-modal influence reflects the environmental relevance of a particular combination of sensory modalities in a particular behavioral or environmental/sensory context and may thus differ greatly between individuals living in different social and environmental contexts.

Future evaluations of brain function should consider that primary and proprioceptive sensory information shape the context in which the neocortex processes information. The long-overlooked influence of breathing on brain activity and function is a good example of an easy-to-track sensory input that introduces variability into neuronal and behavioral responses. Experimental designs should aim at capturing as many sources of sensory input as possible. Multisensory shaping of brain activity is likely to be especially relevant in contexts where sensory information changes rapidly, for example, due to active body movements during flight, fight, or exploration. Such conditions are notoriously difficult to tackle experimentally as current techniques for monitoring brain activity are sensitive to artifacts created by body movements. But technological progress may bring monitoring of multisensory inputs during movement within reach. For example, EEG recordings, which are notoriously sensitive to even small movements, are improving and can provide some usable recordings during body movements [18]. While there are still considerable challenges to tackle, the awareness of the complex dynamic interactions of neuronal activity from intrinsic and external sources within the cerebral cortex is a crucial first step towards improving evaluation and understanding of brain activity and function.

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