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Review

On the functions, mechanisms, and malfunctions of intracortical contextual modulation

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ABSTRACT

A broad neuron-centric conception of contextual modulation is reviewed and re-assessed in the light of recent neurobiological studies of amplification, suppression, and synchronization. Behavioural and computational studies of perceptual and higher cognitive functions that depend on these processes are outlined, and evidence that those functions and their neuronal mechanisms are impaired in schizophrenia is summarized. Finally, we compare and assess the long-term biological functions of contextual modulation at the level of computational theory as formalized by the theories of coherent infomax and free energy reduction. We conclude that those theories, together with the many empirical findings reviewed, show how contextual modulation at the neuronal level enables the cortex to flexibly adapt the use of its knowledge to current circumstances by amplifying and grouping relevant activities and by suppressing irrelevant activities.

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1. Introduction

All life requires the coordination of many specialized activities so that their joint activities sustain the existence of the organism as a whole. The necessity of both specialization and coordination is particularly clear in the cerebral neocortex. A central achievement of the cognitive and neurosciences has been to map the extensive functional specializations that exist within as well as between cortical regions. All those specialized activities must be adequately coordinated, however, if they are to produce coherent percepts, thoughts, and actions that are well-adapted to current circumstances and long-term goals. How this is achieved has been, and still is, a major issue within the cognitive and neurosciences. The dynamic coordination required involves several different levels of organization. They range from the level of pyramidal cells and local cortical microcircuits up to the level of macroscopic subsystems, such as the executive functions of pre-frontal cortex. The focus of this review is on that lower level of organization, which we will argue is relevant to all cortical regions.

The central hypothesis reviewed here is that much of the coordination required is achieved by widely distributed processes of contextual modulation. They amplify the transmission of signals that are relevant to current circumstances, and suppress those that are irrelevant. They also synchronize selected signals into coherent sub-sets. The notion of 'contextual modulation' can be defined so as to refer only to a narrowly specified set of phenomena, such as surround suppression or figure-ground segregation in vision, for example. We define it in a broader way, however. In that broader form it refers to neuronal processes and mechanisms that underlie a wide range of phenomena such as predictive processing, Gestalt grouping, contextual disambiguation, selective attention, and cognitive control. Section 2 is devoted to presenting that broader conception in detail. Evidence for it from a wide variety of methodologies is then reviewed and assessed in the following sections.

Fig. 1 provides a simplified illustration of how contextual modulation operates in broad terms. It shows the driving feedforward inputs as coming from a narrowly specified set of sources. In primary sensory regions they come predominantly from the specific thalamic nucleus that relays the sensory information to which each microcircuit is selectively sensitive. In higher regions they come from a narrowly specified sub-set of microcircuits within other cortical regions. The modulatory contextual inputs to the local microcircuits come from a wide diversity of sources, such as distant locations within the same region, feedback from higher regions, non-specific thalamus, and various other sources. Evidence reviewed below suggests that in some psychopathological conditions, such as schizophrenia, contextual modulation is less effective, which leads to patterns of neural activity that are less coherent overall and behaviour that is less well adapted to current circumstances and more disorganized or impulsive.

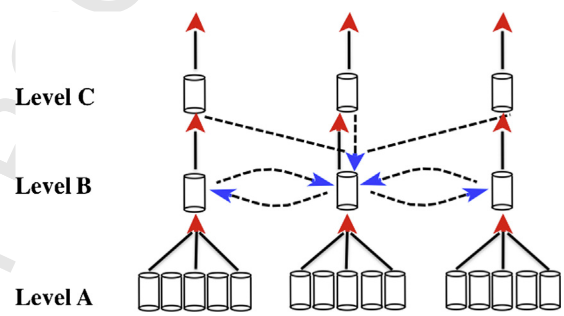

Fig. 1. Contextual interactions in a hierarchy of cortical regions composed of many local microcircuits. A few of the many microcircuits are shown here as small cylinders. Feedforward pathways are depicted by solid lines, and contextual interactions by dotted lines, which are shown here only for the central microcircuit at Level B, though all have similar connectivity. The contextual interactions include both feedback from higher regions and recurrent interactions with other microcircuits at the same level. The recurrent interactions include those between microcircuits that are in the same cortical region but which have non-overlapping feedforward inputs. They also include interactions between different regions that are at equivalent levels of the hierarchy. The contextual interactions modulate response to the feedforward drive so as to produce patterns of activity that are coherent across the network as a whole. The internal anatomy of the microcircuits and the convergence and divergence of feedforward pathways are not shown.

The minimal computational requirements for cortical microcircuits that use contextual inputs to modulate response are shown in Fig. 2. The modulatory inputs must be integrated separately before being used to modulate response to the integrated driving inputs (Kay and Phillips, 2011). The two separate sites of integration shown in Fig. 2A could be implemented by two distinct sets of neurons. Section 3 will cite evidence that local cortical circuits contain neurons that integrate inputs from various contextual sources before using their outputs to either amplify or suppress the responses of other cells in the local circuit. There is also evidence for modulatory interactions within pyramidal cells, however, and this is shown in Fig. 2B. That evidence will also be reviewed in Section 3. Until recently it has been widely assumed in the cognitive and neurosciences that, from a functional point of view, neurons can be adequately conceived of as simply adding up all of their excitatory and inhibitory inputs and transmitting an axonal spike if that integrated value exceeds a threshold. Though networks built from such 'integrate and fire' neurons can do a lot, there is now evidence that pyramidal cells have two distinct sites of integration with input to one site modulating response to the driving

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