

The role of environmental feedback in a brain state switch from passive to active sensing

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Coherent behaviour emerges from mutual interaction between the brain, body and environment across multiple timescales and not from within the brain alone [1, 2]. Perception and motor actions are inseparably bound [3]. Sensation is actively shaped by dynamical interaction of the brain and environment through motor actions such as sniffing, saccading, and touching. The onset of active sensing is often concomitant with qualitative changes in neural dynamics [4, 5] and responses to sensory input [6, 7]. Indeed, some neural responses are uniquely sensitive to the presence or absence of dynamical sensory feedback [8]. However, understanding how active sensing strategies impact on neural dynamics and sensory responses is an open challenge.

Whisking behaviour in rodents has been the model system for studying neural mechanisms of active sensing. During quiet wakefulness the membrane potential of neurons in the barrel cortex exhibit high power, low frequency fluctuations and nearby neurons become highly correlated [4]. As active whisking onsets, the brain state of the barrel cortex qualitatively changes: low frequency fluctuations are suppressed and nearby neurons decorrelate [4]. The brain state transition is also concomitant with changes in responses of barrel cortex neurons to whisker stimulation. The sensitivity of neurons to whisker perturbation drops with the onset of whisking [7]. However, robust and repeatable whisker response are recovered for more naturalistic stimuli, i.e., when the mouse palpate towards, and contacts with, an object [7,9].

The trigger for this brain state transition has been subject of recent study [4,10]. Activation of sensory thalamus is both necessary and sufficient for the observed changes in the cortical dynamics [10]. Interestingly, neural activity associated with the brain state transition persists even under a complete bilateral section of the sensory nerves [4]. Several mechanisms have been proposed as internal triggers for the brain state transition (see [11] for a review). Yet, in the natural condition re-afferent signals (sensory feedback related to self-action) are thought to be strongly represented in cortical activity and even modulate the responses of sensory cortex to input [12]. Furthermore interrupting whisking, by placing an object in the whisk field, increases both the power of low frequency fluctuations and intra-neural correlations, similarly to the brain state transition from the active sensing to quiet condition [9]. Consequently, despite the evidence for a centrally generated trigger for the brains state transition the exact role of sensory feedback in these changes, under a physiological condition, warrants further investigation. Furthermore, it is unknown how these qualitative changes in neural dynamics explain sensory responses to whisker stimulations under different conditions, i.e., large and small responses to brief whisker deflection during the quiet and actively sensing conditions, respectively, and robust responses to whisker contacts during whisking.

Here we propose a theory of active whisking that explains the core phenomenology of the brain state transition and the concomitant changes in neural response properties by the dynamical interaction between the brain and the environment. Below, we itemize three core assumptions underlying the theory:

1. Strong low frequency membrane fluctuations, intra-neural correlations between nearby neurons, and sensory responses to brief whisker deflection associative with quiet attentive state arise as result of network dynamics that are close to a dynamical instability.

2. Re-afferent input during whisking behaviour provides negative feedback to sensory neurons that stabilize cortical dynamics reducing low frequency fluctuations, intra neural correlations, sensory responses to brief whisker deflection, while increasing the correlation between cortical activity and whisker position.
3. Interrupting the refferent signal, via a whisker touch event, temporally destabilise the cortex and provides a strong internally driven response.

These three assumptions alone suffice to robustly reproduce all experimental findings about the brain state transition introduced above.

In order to demonstrate how our theory works in a real system, we construct a simple cortical circuit model of the barrel cortex that comprises a population of excitatory and inhibitory neurons (see Fig. 1 for model topology). Both populations receive sensory input from the whisker and only the excitatory population directly drives the whisker. In the absence of body/environmental feedback, a putative quiet attentive state, the barrel cortex is assumed to be close to dynamical instability (Assumption 1). This is similar to a previously proposed account of up/down dynamics in the auditory cortex [13]. In the presence of cortical noise, this instability produces strong low-frequency fluctuation, intra-neuronal correlation, and sensory responses to brief whisker deflection (Fig. 2), reproducing the experimentally observed quiet attentive state.

In the presence of body/environmental feedback, a putative whisking state, the re-afferent input is assumed to provide negative feedback signal to the cortical neurons (Assumption 2). This is implemented by the strong feedforward inhibition from the whisker variable to the excitatory population, consistent with the stronger thalamo-cortical drive to layer 4 inhibitory neurons than excitatory neurons in the barrel cortex [14]. This negative sensory feedback signal during whisking stabilizes the otherwise nearly unstable cortical dynamics and reduces low frequency fluctuations, intra-neural correlations, and sensory responses to brief whisker deflection (Fig. 2), reproducing the experimentally observed whisking state. Finally, despite small responses to brief whisker deflections during whisking, the model exhibits robust and repeatable response for more naturalistic whisker touch events. The negative environmental feedback via re-afferent is assumed to be interrupted during whisker contacts (Assumption 3). This cessation of re-afferent input temporally destabilised cortical activity resulting in strong excursions from the baseline activity (Fig 3). The model is also able to reproduce the partial destabilisation of cortical activity that is observed in the presence of successive contact events which results in an increase in low frequency fluctuations as well as intra-neural correlations [9].

The above hypothesis suggest that sensory feedback via refference signals can account for the changes in cortical dynamics that appear with the onset of active whisking, providing a novel mechanistic account for sensory processing during active whisking. We conclude by comparing the feedback stabilization theory to the predictive coding theory and also describe the prospects of extending this hypothesis to other active sensing modalities. We discuss how this feedback stabilization mechanism coexists and interacts with other internal mechanisms that modulate cortical dynamics within the brain [10]. More generally we discuss the wider implications of these results for experimental work attempting to characterise neural activity and responses in an open-loop (in the absence of sensory/motor feedback) condition.

References

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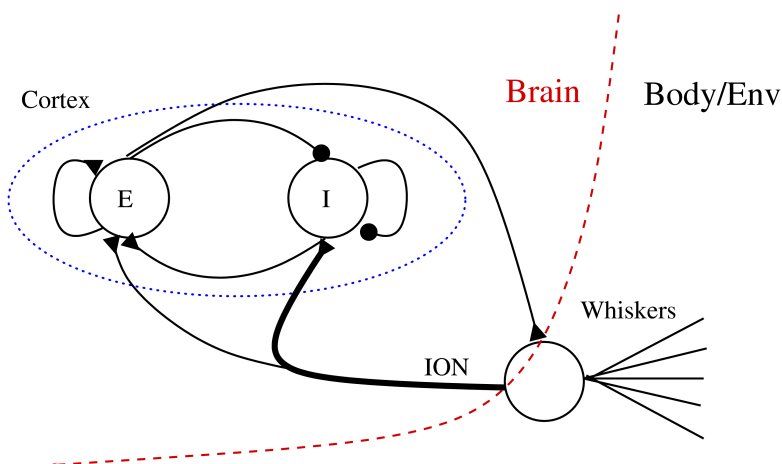


Fig 1. A simple cortical circuit comprising of population of excitatory and inhibitory cells receive sensory feedback via whisking. Triangle and circles represent excitatory and inhibitory synapses respectively. Sensory feedback is overall negative in sign because inhibitory projections from the thalamus to cortex dominate excitatory projections, thick and thin projections respectively.

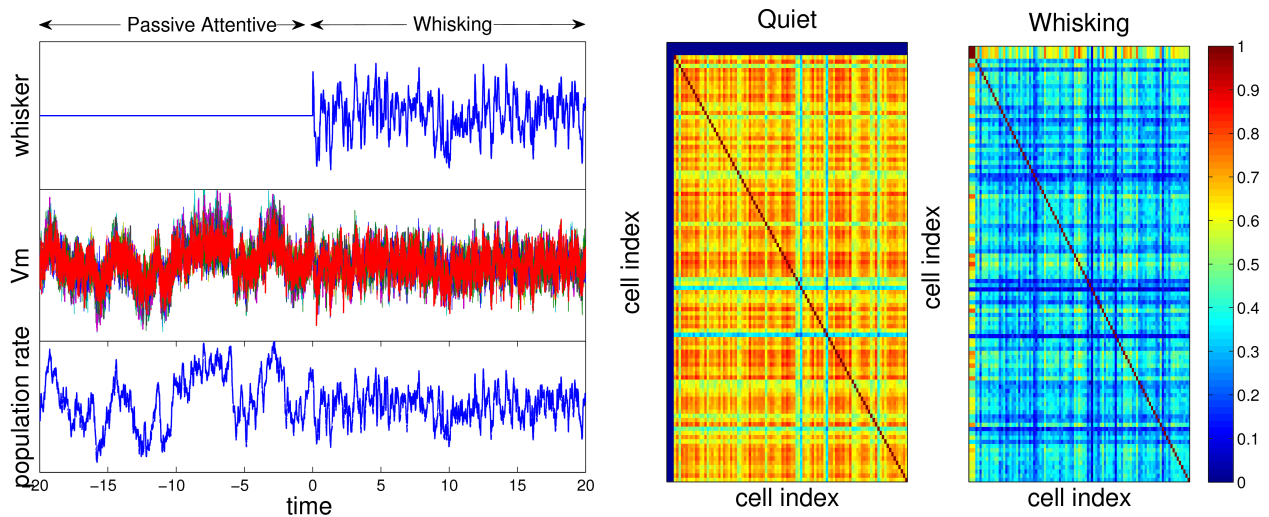


Fig 2. Left: Traces for the whisker variable, membrane potential (V_m) and population rate, top, middle and bottom traces respectively. Whisking onsets at $t=0$ ms. The membrane potential and population rate are stabilised by whisking. Right: Correlations between the membrane potential of excitatory/inhibitory cells in the passive attentive (no whisking) and actively whisking condition. Correlations between cells drop significantly with the onset of whisking. The top/left outer row/columns give the correlation between the whisk variable and the membrane potential. Correlation between environment and membrane potential is much higher than intra-neural correlations during whisking.

Fig 3. Response of the whisker variable, membrane potential (V_m) and mean population rate to perturbations (red lines) and an active touch event (turquoise line), top, middle and bottom respectively. Response to perturbation in the stable whisking state is smaller and less robust than response in the unstable passive attentive state. However, robust responses are recovered for the active touch event i.e., a temporary interruption of the whisker variable (top panel, turquoise line) results in a robust and large deflection of the membrane potential and population rate (middle and bottom panels, turquoise line).

