The role of sensorimotor feedback in a brain state transition from passive to active processing

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Abstract. Both the sensorimotor and enactivist accounts have successfully emphasised the centrality of sensorimotor feedback for accounts of cognition. Despite this success the migration of this focus to mainstream systems neuroscience has been slow. Recent experimental innovations mean that this state of affairs is beginning to radically change. Closed-loop experimental paradigms that utilise virtual reality in mice and fish and well circumscribed sensory-motor systems are becoming more widespread. Consequently, in vivo electrophysiology and optogenetics of behaving animals is quickly becoming an achievable gold standard. This work places the sensorimotor loop at the heart of neural processing and promises to give sensorimotor accounts renewed relevance for mainstream neuroscience. Here we utilise these technologies to examine the role of sensorimotor feedback for accounts of neural dynamics and brain function.

Sensory perception and motor action are inseparably bound by reafferent sensorimotor feedback (sensory input resulting from an animal's own actions) mediated by the body and environment [1]. Both the sensorimotor and enactivist accounts have successfully emphasized this aspect of cognition to mount a systematic challenge to some of the dominating concepts in the cognitive sciences [2, 3]. Despite this success the migration of these ideas to mainstream systems neuroscience has been slow. However I would argue this does not amount to conceptual resistance to the role sensorimotor feedback but, at least in part, reflects experimental practices which are dominated by heavily restrained, or anaesthetised animals, where body/environment feedback is minimised. Recent experimental innovations mean that this state of affairs is beginning to radically change. Closedloop experimental paradigms that utilise virtual reality in mice and fish [4,5] and well circumscribed sensorimotor systems are becoming more widespread [6]. Consequently, in vivo electrophysiology and optogenetics of behaving animals is quickly becoming an achievable gold standard. This work places the sensorimotor loop at the heart of neural processing and promises to give enactivist and sensorimotor accounts renewed relevance for mainstream neuroscience. Here we utilise these technologies to examine the role of sensorimotor feedback for accounts of neural dynamics and brain function.

It has been understood for a long time in the neurosciences that engaging world, and thus engaging sensorimotor (or reafferent) feedback, can have a profound effect on brain state (a pattern of brain activity and responses)[7]. Transitioning from a passive to an actively engaged state suppresses both neural fluctuations and intraneural correlations, e.g. opening one's eyes [7] or the onset of whisking in rodents [8]. Furthermore, the onset of active behaviour strongly modulates sensory processing [9,10,11]. Typically the sensitivity of neurons to perturbation is larger in passive rather than active states [10] however robust response in the active state are recovered for biologically relevant sensory events [10,12]. The trigger for this brain state transition has been subject of several recent studies [10,8,13].

Most investigations have focussed on describing centrally generated mechanisms. It is likely that multiple internal factors are involved in brains state transitions [13,14,15]. However here we describe a simple theory that can account for all brain state phenomenology by appealing to the role of sensorimotor feedback. Specifically we hypothesise that when an animal engages the world its body and environment mediate negative feedback to the brain. We show that this negative sensorimotor feedback can suppress brain dynamics and thus account for the reduction of intraneural correlations, fluctuations and response to perturbation associated with the onset of a brain state transition. In effect we suggest the body and environment stabilises the brain. We ground this idea in the rodent whisker system and provide experimental evidence by describing work on zebrafish larvae behaving in a virtual reality environment.

We show how this hypothesis suggests a new sensory mechanism that can explain active sensing in the rodent whisker system. Specifically in the rodent barrel cortex response are large in a passive nonwhisking condition but are suppressed during active whisking [10]. However large responses are recovered during active whisking for more natural touch events, i.e., when the whisker collides, and temporarily remains in contact with, an external object [10]. Our theory can account for this phenomenon by idealising these touch events as brief interruptions of negative sensorimotor feedback which temporarily destabilise the cortex and thus evoke large responses in the active condition . The implication of this mechanism is that animals are particularly sensitive to the interruption of their own sensorimotor feedback rather than just external (exafferent) input. This mechanism has strong similarities to, and indeed we regard it as a special implementation of, the principle of reafference [1] (or more broadly predictive coding). However there are strong functional differences thus we compare and contrast both mechanisms.

Lastly, there is a strong current trend in neuroscience to stress the importance of using naturalistic, e.g natural movies, rather than artificial stimuli in order to faithfully characterise the response properties of different sensory modalities. However our theory predicts that even if the input from a closed-loop active behaviour is recorded and exactly replayed, at a later time, to an identical but passive brain, the brain dynamics between the two conditions will still be qualitatively different. In effect our theory suggest that neural function is strongly contingent on presence or absence of sensorimotor feedback. We confirm this prediction by studying neural activity in larval zebrafish behaving in a virtual

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reality environment [5] and comparing brain dynamics between a closed virtual reality and passive replay condition.

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