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Influence of Attention on Perception, Learning, Memory and Awareness

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Chapter VII

Summary

In the introduction, I described our current understanding of the neural mechanisms underlying our visual perception. To reiterate, the visual system comprises specialized processors that, in a stepwise manner, process signals representing different aspects of the stimuli detected by our sensory neurons. They effectively combine and transform these signals to construct our perceived reality. As remarkable as our brain might be, it has limitations of how much information it can process at any given time.

Visual stimuli undergo two processing sequences namely, feedforward and feedback processing; in the feedforward sequence, input signals from the eye travel along anatomical connections from lower areas to higher areas. Psychologically, this is called pre-attentive processing (i.e. processing that occurs in the absence of attention). In the feedback sequence, information flows back from higher areas to lower areas. This process is often context driven, based on task or internal goals, and can be influenced by previous knowledge or experience. Psychologically, this process is akin to attention. It is theorised that attention invariably helps select inputs arising from the feedforward process that are relevant for further processing. Consequently, many other cognitive processes occurring in the brain such as learning, working memory or even conscious awareness may be influenced by attentional-feedback signals, but much about this is unknown.

In Chapter II, we addressed a fundamental question of how the release of acetylcholine (ACh), a neuromodulator released by the cholinergic system, could be measured. In the past, several studies have tried to measure the amount of ACh secreted, but the techniques used were not useful for the fast changes in shifts of attention that occur during a task or in our everyday circumstances. Here, we measured choline levels (*a by-product formed when acetylcholine is broken down in the synapses*) during a curve-tracing task in the dorsolateral prefrontal cortex using an enzyme based electrochemical probe. The experiment

consisted of an in-vitro and in-vivo setup. We successfully calibrated the probe and measured choline in the in-vitro setup. In the in-vitro setup, the probe showed a high sensitivity for choline and small limit of detection (LOD) i.e. the minimum amount of substance required for detection and exclusivity for choline as well. However, the experiments performed in the in-vivo setup were not as successful. In most recordings, the signals at the enzyme-coated channels and the sentinel (non-enzyme coated) channels were identical. We inspected the slow changes across the 'TASK ON' and 'REST' conditions and observed that the fluctuations and differences between them became very similar after an hour. We also looked at fast changes across tens of milliseconds; here too, we did not observe reliable modulation.

We postulate that the lack of difference in signals between the enzyme and sentinel signals was due to the degradation of the coating of the electrode with enzymes. Furthermore, we observed an overall degradation of signal over time during the in-vivo experiment. A post-experiment calibration revealed that the probe had reduced sensitivity, LOD, and reduced exclusivity for choline. We postulate that this was due to either tissue reaction to the probe or mechanical damage during probe insertion. We have proposed that the technique requires several improvements before it can be successfully applied in non-human primates. In the discussion, we have described potential improvements such as a new design for the probe, the use of artificial dura to make penetration easier and the use of new materials for sensors with the hope that it will aid future research.

In Chapter III, we addressed the conjoint effects of attentional-feedback and reward modulation during learning. Learning induces connectivity changes in the brain. Two mechanisms have been known to influence learning. Firstly, 'reward', which has garnered support from reinforcement learning theories, postulating that connectivity changes should depend on reward prediction errors (i.e. the difference between expected versus attained rewards for a given action in a task). Secondly, selective attention that is known to enhance

learning. Previous studies have independently shown the effect of reward and attention on learning. However, their conjoint influence on learning remained to be explored. We devised a unique paradigm allowing us to manipulate attention and reward in a single task. We measured behavioural parameters such as the rate of learning, accuracy of the responses, the latency of the response, the sensitivity, and the bias towards the learnt stimuli. Our results suggest that only objects that were attended were learnt and unattended objects were not, indicating that selective attention gates learning. Additionally, we found that reward had an overall general effect on the learning of both attended and unattended objects, but that the influence of reward was the strongest for the attended objects. Our experiment demonstrated that attention and reward jointly determine learning.

In Chapter IV, recognizing that both attentional-feedback modulation and luminance contrast enhance activity in the visual cortex and affect grouping of objects, we asked if and how both processes interact with each other. In the literature, there has been a debate about which models best predicted the interaction of attention and luminance contrast. The ‘contrast gain’ model states that attention increases the neuronal response to the stimuli by increasing its apparent contrast, an effect that is strongest at intermediate contrast levels and weaker at high contrast levels. Another model called the ‘response gain’ model posits that attention and contrast interact multiplicatively. Consequently, attention has a stronger effect at higher-contrast levels. A third model, called the ‘additive’ model, suggests that attention and luminance contrast influence the neuronal response to the stimuli in a fairly additive manner. We used a curve-tracing task with varying contrast levels to determine which model best described the interaction between attentional feedback and luminance contrast. We performed three different experiments wherein subjects had to trace a target curve among other distractor curves with varying contrast conditions while we measured the latency and accuracy of the subjects’ responses. Our results are in support of the additive model indicating that the object-based attention and luminance contrast have

largely additive and hence separable effects on visual processing.

In Chapter V, we investigated the contribution of ionotropic glutamate receptors in working memory. Working memory is a process that allows for storing and manipulating information for a small period of time. The neural mechanisms of working memory are not clearly understood. Previous studies have suggested that ionotropic glutamate receptors such as NMDA and AMPA might play an important role by facilitating feedback processing and maintaining activity in recurrent loops during working memory. We trained monkeys to perform an oculomotor delayed response task where they had to remember the spatial location of a stimulus for a short period of time while we ejected small amounts of selective antagonists for NMDA and AMPA receptors in the dorsolateral prefrontal cortex. The selective antagonists allowed us to differentiate between contributions of the receptors during the different stages of the task. Moreover, the iontophoretic technique allowed us to inject very small quantities of the antagonists so as to only attenuate the individual cell responses and not completely abolish them.

We analysed the contribution of NMDA and AMPA in (1) the early phase representing the feedforward response and (2) the sustained or delay phase. We found that both NMDA and AMPA contributed to neuronal activity for the entire task period. Furthermore, our results indicated that the effects of AMPA were additive whereas the effects of NMDA were largely multiplicative. Our results show a general contribution of NMDA and AMPA to working memory processing, but both NMDA and AMPA do not seem to have a specific role in persistent firing. Our results suggest that persistent firing observed in higher areas such as dorsolateral prefrontal cortex involves recurrent processing within or across cortical areas.

In Chapter VI, we have explored the role of recurrent (feedforward-feedback) processing in how information reaches conscious awareness. An influential theory called the 'Global Neuronal Workspace (GNW)' model aims to link psychophysical and neurophysiological findings on conscious awareness. The

GNW posits that if activity representing the stimulus is strong enough it will lead to 'global ignition' throughout the cortex, and that this corresponds to entry of the stimulus into awareness. However, if the propagation is not strong enough, the global ignition will not occur and the information will remain subliminal. In this study, we explored the factors that determine whether activity propagation leads to conscious awareness of sensory information.

We investigated neuronal activity along the cortical hierarchy, specifically in area V1, area V4, and the dorsolateral prefrontal cortex. We used low contrast stimuli at the threshold of perception and created illusory percepts of light (*phosphenes*) with cortical microstimulation. The monkeys were trained to report to these low contrast (or electrical) stimuli. We observed that 'perceived' stimuli elicit a stronger initial feedforward response in all areas compared to 'non-perceived' stimuli. The difference in activity for stimuli representations between 'perceived' and 'non-perceived' stimuli increased along the cortical pathway, from area V1 to the dorsolateral prefrontal cortex. If the activity level in higher levels is strong enough, it can cause sustained activity through recurrent (*feedforward-feedback*) processing, as suggested in the GNW theory. Hence, our results show that the stimuli first need to reach higher cortical areas to initiate recurrent interactions between higher and lower areas for the 'ignition' state, which enables conscious perception, whereas weak stimuli are lost if ignition does not occur.