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2012

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citation for published version (APA)

Stanisor, L. (2012). *Coding of object significance and reward in the visual and frontal cortex.*

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Chapter 6: Summary and Discussion

During our everyday lives, we possess the ability to ‘navigate’ through our visual environment by means of quickly selecting what is important and focusing our attention on relevant objects. More specifically, our attention is attracted by familiar patterns that are partly trained and perhaps partly innate and hardwired in our brains. This allows us to form meaningful concepts of our surroundings and act towards our goals.

All our actions are motivated by obtaining reward, be it on the short or longer term, in one form or the other. During this process, through repeated trials and errors, we refine our methods and become more effective in what we do. In the following paragraphs we will touch various aspects of the findings investigated in this thesis, going from attention to reward and arriving at learning. We will integrate all these results in a larger conceptual framework, in an effort to define the difference between attentive and non-attentive visual processing.

In a complex visual scene, attention is attracted according to Gestalt grouping cues (Wertheimer 1923). Following previous studies (Freeman et al 2001; Li et al 2006), **chapter 2** presents neuronal data that show that attentional enhancement of neuronal activity in V1 spreads from stimuli that are attended to stimuli that are irrelevant to the task, when they are grouped according to the Gestalt rules of good continuation, collinearity, color similarity and common fate. These cues promote the spread of selective attention to all parts of the same object, thus facilitating the reconstruction of coherent objects in the visual cortex. We

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propose that the propagation of enhanced responses in early visual cortex (including V1) can explain the spread of attention the psychological level of description.

In **chapter 3** we investigated the relation between the coding of attention and reward in area V1 with a curve-tracing task where we varied the amounts of reward associated with the curves. Similar to previous studies (Platt & Glimcher 1999; Leon & Shadlen 1999; Ikeda & Hikosaka 2003; Sugrue et al 2004), we found that highly rewarding stimuli evoked a stronger response than stimuli which were not rewarded. This effect was stronger in the presence of two curves compared to one curve, which suggests that the modulation of V1 activity by reward is similar to the modulation of V1 activity by attention. In addition, we found that the latency of the reward-induced effect was similar to the latency of the effect of selective attention in a simple curve-tracing task. Furthermore, these two effects were strongly correlated across the recorded neurons. Just as Maunsell (2004) suspected, we conclude that the effects of reward and selective attention manifest in a similar manner in V1, due to overlapping or even the same neuronal circuitry.

Researchers usually train monkeys to process 'attentional' cues by varying reward contingencies, for instance by only rewarding the monkey for responses to one (attended) stimulus and by not rewarding for responses to another (ignored) stimulus (Maunsell, 2004). Vice versa, it is likely that studies on reward processing influence the distribution of selective attention across the stimuli in a display. Rewarding stimuli attract attention so that the visual cortex highlights stimuli with a high relative value (Peck et al., 2009), and the same holds true for stimuli that need to be processed to gain access to rewards (see e.g. Treue and Maunsell, 1996). The computation of relative value requires a comparison between stimuli that can be far apart in the visual field and it is therefore likely that the V1

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modulation depends on feedback from higher visual and perhaps frontal areas (Matsumoto et al., 2003; Padoa-Schioppa and Assad, 2006), which explains why it is expressed during a delayed phase of the neuronal response.

The results presented in chapter 3, in combination with previous studies (Dorris and Glimcher, 2004; Peck et al., 2009; Platt and Glimcher, 1999; Sugrue et al., 2004) inspire a unification of theories of selective attention and relative value coding. We demonstrate that these attentional selection signals reflect the relative value of stimuli and suggest that there is a single, unified selection process at the level of the primary visual cortex. Future studies could determine the source of the V1 selection signals in brain regions that store the associations between visual stimuli and rewards.

The delivery of reward steers learning and this is the topic of the next two chapters. In **chapter 4** we investigated object-based learning in area FEF by using a reaction-time paradigm in which two unknown icons were presented each day and the monkey's task was to learn to make an eye movement to the end of a curve cued by one of the icons, because this eye movement was rewarded. Some trials included a positional cue which the monkeys could use due to their previous training in curve-tracing. We found that in the trials without positional cues there was an increased reaction time and the latency of modulation was later than in the other trials, while the level of pre-saccadic activity stayed the same. In addition, during the process of learning for the difficult condition (here the monkeys increased their accuracy), the reaction time as well as the latency of the modulation of the FEF response increased. We propose that during learning our monkeys change their behavior from a probing strategy in the beginning when they lack knowledge of the relevant icon to a later phase in which they integrate visual evidence and take slower but more

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adequate decisions. Our view shares common features with neurally inspired models of decision making (Stanford et al 2010; Carpenter & Anderson 2009; Beck et al 2008).

Chapter 5 investigates learning in area V1 using a similar paradigm to that in the previous chapter, but this time with a 500 ms delay before the go signal. Here we saw an even stronger increase in modulation latency in the difficult condition compared to the other two conditions. A remarkable and unexpected result was our finding of a consistent suppression of activity evoked by the target curve which was reversed later in time. We conclude that attentional processing differs between the difficulty levels. In the easy and intermediate condition we see the early attentional modulation specific to the positional cue (curve tracing) and in the difficult one there appears to be an extra process (elemental operation) that has to be performed (visual search). The early negative modulation suggests that visual input related to the target curve is suppressed in favor of input related to the relevant icon that must be detected first. As the attentional process switches to curve-tracing this is reflected in a positive late modulation. Our results suggest a push-pull mechanism of attention, with increased modulation in the center of an attentional focus and suppression in the surrounding visual area, sometimes described as a “Mexican hat” profile of modulation (Serences et al 2004; Hopf et al 2006).

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All these findings plead for a global interpretation of the interactions between neurons. We see how the various processes (incentive for reward, selective attention) modulate the activity in a similar fashion and that a cognitive endeavor such as learning induces almost similar changes in cortical areas far apart such as V1 and FEF. This suggests an integrative approach in which all neurons take part with cooperative interactions, much like the individual players who come together and make up the ensemble of an orchestra.



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