Chapter 1

General Discussion

1.1 Summary of principal results

The work described throughout this thesis has centered around how prediction is used in sensory processes such as object recognition and prolonged learning. The work is heavily motivated by the LeabraTI (TI: Temporal Integration) framework (Chapter **??**) which leverages the laminocolumnar structure of the neocortex (Mountcastle, 1997; Buxhoeveden & Casanova, 2002; Horton & Adams, 2005) to learn to predict temporally structured sensory inputs. Predictive learning in the LeabraTI framework is made possible by temporally interleaving predictions and sensory processing across the same populations of neurons so that powerful error-driven learning mechanisms (O'Reilly & Munakata, 2000; O'Reilly, Munakata, Frank, Hazy, & Contributors, 2012) can be used to compute a prediction error that can be learned against to minimize the difference between predictions and sensory events over time.

LeabraTI relies on a 10 Hz prediction-sensation period as its core "clock cycle", suggested to correspond to the widely studied alpha rhythm observable across posterior cortex using scalp EEG (Palva & Palva, 2007; Hanslmayr, Gross, Klimesch, & Shapiro, 2011; VanRullen, Busch, Drewes, & Dubois, 2011). Chapter **??** investigated the role of the alpha rhythm in prediction by using an entrainment paradigm (Schroeder, Lakatos, Kajikawa, Partan, & Puce, 2008; Calderone, Lakatos, Butler, & Castellanos, in press) in which stimuli were presented rhythmically at 10 Hz so that predictions and sensory information could be interleaved regularly at the optimal rate proposed by LeabraTI. The experiment made use of three-dimensional objects that required integration over multiple sequential views to extract their three-dimensional structure. Thus, relatively rapid predictive learning mechanisms that operate over subsequent 100 ms periods could be leveraged to optimally encode the the objects. The spatial coherence between views and temporal onset of each view were independently manipulated to determine their effect on stimulus encoding quality and the putative role of the alpha rhythm in predictive processing.

The results of the Chapter **??** experiment indicated that spatial coherence and predictable temporal onset of each stimulus in an entraining sequence enhanced discriminability of a subsequently presented probe stimulus. Oscillatory analyses indicated strong bilateral alpha power and phase coherence modulation as a function of stimulus predictability. Specifically, spatial predictability of entraining stimuli suppressed alpha power with a lower degree of phase alignment relative to unpredictable stimuli. Temporally predictable entraining stimuli had the opposite effect, with increased alpha power and phase alignment, indicating successful entrainment. Importantly, phase alignment due to temporal predictability remained elevated compared to temporally unpredictable stimuli during a 200 ms blank period between the entraining sequence and probe, indicating that the effects of temporal predictability could persist without exogenous entrainment. In addition to these bilateral main effects, right hemisphere sites exhibited synergistic effects of combined spatial and temporal probe predictability on EEG amplitude and 10 Hz phase coherence approximately 200 ms after probe onset.

Overall, the results of the Chapter **??** experiment support the basic claims put forth by the LeabraTI framework. The predictable 10 Hz presentation rate of the entraining sequence improved encoding of the target object, enhancing discriminability for the subsequent probe stimulus. This finding was accompanied by increased alpha phase alignment that remained elevated until the onset of the probe, which was necessary for ensuring that the probe event was processed precisely when the brain was expecting sensory information and not when it was generating a prediction.

Given this basic support for the LeabraTI framework, the Chapter **??** experiment was designed to investigate the role of prolonged predictive learning of dynamic stimuli. Previous work has indicated that a temporal association rule similar to the one central to LeabraTI might be leveraged for constructing stable representations of spatially coherent visual inputs (Stringer, Perry, Rolls, & Proske, 2006; Wallis & Baddeley, 1997; Isik, Leibo, & Poggio, 2012) and indeed, a line of experiments by Di Carlo and colleagues has indicated that predictable object transformation sequences build object invariance (Cox, Meier, Oertelt, & DiCarlo, 2005; Li & DiCarlo, 2008, 2010; Li & Dicarlo, 2012). Given these results, one might hypothesize that combined spatiotemporal predictability would be optimal for prolonged learning of three-dimensional objects.

The Chapter **??** experiment used a subset of the object stimuli from the previous chapter's experiment along with an explicit training period during which observers studied the objects while they were rotated were rotated through their views while spatial and temporal predictability were independently manipulated. The study period was followed by a series of test trials that required same-different judgements about static probe stimuli. Somewhat surprisingly, the results of the experiment were an almost complete reversal of the previous chapter's experiment. Discriminability was lowest when stimuli were learned in a combined spatiotemporally predictable context and highest when learned in a completely unpredictable context. Furthermore, there was some indication that the principal differences between predictability conditions during training were driven primarily by degenerate viewing angles caused by three-dimensional foreshortening in the objects used (Balas & Sinha, 2009; Farah, Rochlin, & Klein, 1994; Pizlo & Stevenson, 1999). In three out of four of the objects used in the experiment, accuracy was lower for degenerate views learned in a spatiotemporally predictable context compared to a completely unpredictable one.

Chapter **??** revisited the LeabraTI framework and described a neural network model that implemented the columnar substructure necessary for predictive learning. The model was trained to recognize the same three-dimensional objects used in the Chapter **??** and **??** experiments with the goal of being able to reproduce the conflicting behavioral results of the experiments. LeabraTI predicts that spatially predictable sequences presented at a regular temporal interval should elicit a synergistic effect on behavioral measures due to the multiple prediction-sensation cycles that successfully integrate visuospatial information at optimal temporal intervals (see also Doherty, Rao, Mesulam, & Nobre, 2005; Rohenkohl, Gould, Pessoa, & Nobre, 2014). Such a synergistic effect was demonstrated in the Chapter **??** EEG results, but was simply additive for behavioral measures. Still, the model provided a reasonable fit to these data. Furthermore, the model was able to account for the reversal effect observed in Chapter **??** by increasing the scale of a single rejection of synaptic weights as a simple proxy for prolonged learning.

The model further indicated that the synaptic weight scaling assumed to occur with prolonged learning caused object invariance to "trickle down" to lower-level feature representations. This was problematic for the objects used, since some of them suffered from extreme foreshortening, causing severely degenerate views. This caused confusion between objects, potentially accounting for the overall reversal observed between the Chapter **??** and **??** experiments.

1.2 Open questions

1.3 Conclusions

References

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