

**What happens next versus when “next” happens:
Dissociating spatial and temporal prediction mechanisms**

by

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The final copy of this thesis has been examined by the signatories, and we find that both the content and the form meet acceptable presentation standards of scholarly work in the above mentioned discipline.

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Chapter 1

Introduction

How does the brain predict what happens from one moment to the next? This is an important question in research on perception across all modalities that is surprisingly often overlooked in the fields of psychology and neuroscience. For example, most experiments are designed to measure evoked responses to a randomly chosen, isolated stimulus under the tacit assumption that response variability is irrelevant noise that should be averaged out across many presentations. Computational models of perceptual processing often operate under similar assumptions in which stimuli are presented as random “snapshots” from which some common set of features should be learned to minimize representational variability across presentations (e.g., SerreOliva-Poggio07MutchLowe08; although see Foldiak91, for a notable exception). These experimental and computational assumptions stand in contrast to the event structure of the physical world, which is deterministic from one moment to the next.

An equally important question is concerned with how the brain knows when to make its next prediction. Predicting what happens next requires integrating information over some time frame and using the result to drive the actual prediction, but when should integration start? And for how long? Perceptual processing has been shown to undergo temporal fluctuations and in extreme cases, stimuli can be rendered imperceptible if presented during one of these fluctuations (BuschDuboisVanRullen09VanRullenBuschDrewesEtAl11; MathewsonLlerasBeckEtAl11). Again, many laboratory experiments tend not to be concerned with these temporal fluctuations, as they simply add variability to responses that will average out over a large number of trials and can

be mitigated by design decisions such as using a fixation cross to denote the start of a trial. Computational models, similarly, often completely ignore time altogether, although recent advances in spiking models of perceptual processing (e.g., MasquelierThorpe07) are beginning to address this issue.

The goal of the proposed work is to begin systematically investigating the neural mechanisms and circuitry related to prediction and temporal integration. Recently, our lab has developed a theoretical framework and general model for describing how these functions are implemented in the brain. This framework, henceforth referred to as *LeabraTI*,¹ brings together a large number of independent findings from the systems neuroscience literature to describe how multiple interacting mechanisms accomplish prediction and temporal integration in cortex. The fundamental proposal of the LeabraTI theory is that time in the brain is discretized (at least partially) into reference frames that can be associated via general learning mechanisms (e.g., Hebbian and error-driven learning) so that representation of information during one frame can be used to predict what happens during the next. This proposal requires at least two mechanisms: (1.) A mechanism that establishes reference frames over which information is integrated and, (2.) A mechanism that generates the actual prediction itself and validates it against what actually happens.

As will be discussed in detail in Chapter ??, the LeabraTI theory's proposed mechanisms are suggested to be dissociable, generating signatures at distinct spectral frequencies which can be measured physiologically. The potential dissociability of the spatial and temporal components of prediction establishes a number of immediately testable predictions that will form the experimental component of the proposed work.

References

Armstrong-James, M., Fox, K., & Das-Gupta, A. (1992). Flow of excitation within rat barrel cortex on striking a single vibrissa. *Journal of Neurophysiology*, 68(4), 1345–1358.

¹ Leabra refers to a general model of learning in the neocortex (O'ReillyMunakata00O'ReillyMunakataFrankEtAl12); TI to Temporal Integration.

- Balas, B. J., & Sinha, P. (2009). The role of sequence order in determining view canonicity for novel wire-frame objects. Attention, Perception & Psychophysics, 71(4), 712–723.
- Brainard, D. (1997). The Psychophysics Toolbox. Spatial Vision, 10(4), 433–436.
- Buffalo, E. A., Fries, P., Landman, R., Buschman, T. J., & Desimone, R. (2011). Laminar differences in gamma and alpha coherence in the ventral stream. Proceedings of the National Academy of Sciences of the United States of America, 108(27), 11262–11267.
- Bulthoff, H. H., & Edelman, S. (1992). Psychophysical support for a two-dimensional view interpolation theory of object recognition. Proceedings of the National Academy of Sciences of the United States of America, 89(1), 60–64.
- Busch, N. A., Dubois, J., & VanRullen, R. (2009). The phase of ongoing EEG oscillations predicts visual perception. The Journal of Neuroscience, 29(24), 7869–7876.
- Buxhoeveden, D. P., & Casanova, M. F. (2002). The minicolumn hypothesis in neuroscience. Brain, 125(Pt 5), 935–951.
- Connors, B. W., Gutnick, M. J., & Prince, D. A. (1982). Electrophysiological properties of neocortical neurons in vitro. Journal of Neurophysiology, 48(6), 1302–1320.
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. Journal of Neuroscience Methods, 134(1), 9–21.
- Doherty, J. R., Rao, A., Mesulam, M. M., & Nobre, A. C. (2005). Synergistic effect of combined temporal and spatial expectations on visual attention. The Journal of Neuroscience, 25(36), 8259–8266.
- Douglas, R. J., & Martin, K. A. C. (2004). Neuronal circuits of the neocortex. Annual Review of Neuroscience, 27, 419–451.
- Edelman, S., & Bulthoff, H. H. (1992). Orientation dependence in the recognition of familiar and novel views of three-dimensional objects. Vision Research, 32(12), 2385–2400.
- Elman, J. L. (1990). Finding structure in time. Cognitive Science, 14(2), 179–211.
- Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. Cerebral Cortex, 1(1), 1–47.
- Foldiak, P. (1991). Learning invariance from transformation sequences. Neural Computation, 3(2), 194–200.
- Franceschetti, S., Guatteo, E., Panzica, F., Sancini, G., Wanke, E., & Avanzini, G. (1995). Ionic mechanisms underlying burst firing in pyramidal neurons: Intracellular study in rat sensorimotor cortex. Brain Research, 696(1–2), 127–139.
- Hirsch, J. A., & Martinez, L. M. (2006). Laminar processing in the visual cortical column. Current Opinion in Neurobiology, 16(4), 377–384.
- Horton, J. C., & Adams, D. L. (2005). The cortical column: A structure without a function. Philosophical Transactions of the Royal Society B, 360(1456), 837–862.
- Hubel, D. H., & Wiesel, T. N. (1977). Ferrier lecture. Functional architecture of macaque monkey visual cortex. Proceedings of the Royal Society B, 198(1130), 1–59.

- Hughes, S. W., Lorincz, M., Cope, D. W., Blethyn, K. L., Kekesi, K. A., Parri, H. R., Juhasz, G., & Crunelli, V. (2004). Synchronized oscillations at alpha and theta frequencies in the lateral geniculate nucleus. Neuron, 42(2), 253–268.
- Jones, E. G. (2000). Microcolumns in the cerebral cortex. Proceedings of the National Academy of Sciences of the United States of America, 97(10), 5019–5021.
- Lakatos, P., Karmos, G., Mehta, A. D., Ulbert, I., & Schroeder, C. E. (2008). Entrainment of neuronal oscillations as a mechanism of attentional selection. Science, 320(5872), 110–113.
- Logothetis, N., Pauls, J., Bulthoff, H., & Poggio, T. (1994). View-dependent object recognition by monkeys. Current Biology, 4(5), 401–414.
- Logothetis, N. K., Pauls, J., & Poggio, T. (1995). Shape representation in the inferior temporal cortex of monkeys. Current Biology, 5(5), 552–563.
- Lopes da Silva, F. (1991). Neural mechanisms underlying brain waves: from neural membranes to networks. Electroencephalography and Clinical Neurophysiology, 79(2), 81–93.
- Lorincz, M. L., Crunelli, V., & Hughes, S. W. (2008). Cellular dynamics of cholinergically induced alpha (8–13 Hz) rhythms in sensory thalamic nuclei in vitro. The Journal of Neuroscience, 28(3), 660–671.
- Lorincz, M. L., Kekesi, K. A., Juhasz, G., Crunelli, V., & Hughes, S. W. (2009). Temporal framing of thalamic relay-mode firing by phasic inhibition during the alpha rhythm. Neuron, 63(5), 683–696.
- Luczak, A., Bartho, P., & Harris, K. D. (2013). Gating of sensory input by spontaneous cortical activity. The Journal of Neuroscience, 33(4), 1684–1695.
- Lumer, E., Edelman, G., & Tononi, G. (1997). Neural dynamics in a model of the thalamocortical system. I. Layers, loops and the emergence of fast synchronous rhythms. Cerebral Cortex, 7(3), 207–227.
- Masquelier, T., & Thorpe, S. J. (2007). Unsupervised learning of visual features through spike timing dependent plasticity. PLoS Computational Biology, 3(2), 247–257.
- Mathewson, K. E., Lleras, A., Beck, D. M., Fabiani, M., Ro, T., & Gratton, G. (2011). Pulsed out of awareness: EEG alpha oscillations represent a pulsed-inhibition of ongoing cortical processing. Frontiers in Psychology, 2.
- Mountcastle, V. B. (1997). The columnar organization of the neocortex. Brain, 120(Pt 4), 701–722.
- Mutch, J., & Lowe, D. (2008). Object class recognition and localization using sparse features with limited receptive fields. International Journal of Computer Vision, 80(1), 45–57.
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. Computational Intelligence and Neuroscience, 2011.
- O'Reilly, R. C., & Munakata, Y. (2000). Computational Explorations in Cognitive Neuroscience: Understanding the Mind by Simulating the Brain. Cambridge, MA: The MIT Press.

- O'Reilly, R. C., Munakata, Y., Frank, M. J., Hazy, T. E., & Contributors (2012). Computational Cognitive Neuroscience. Wiki Book, 1st Edition, URL: <http://ccnbook.colorado.edu>.
- Pelli, D. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. Spatial Vision, 10(4), 437–442.
- Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. F. (1989). Spherical splines for scalp potential and current density mapping. Electroencephalography and Clinical Neurophysiology, 72(2), 184–187.
- Rockland, K. S., & Pandya, D. N. (1979). Laminar origins and terminations of cortical connections of the occipital lobe in the rhesus monkey. Brain Research, 179(1), 3–20.
- Rohenkohl, G., & Nobre, A. C. (2011). Alpha oscillations related to anticipatory attention follow temporal expectations. The Journal of Neuroscience, 31(40), 14076–14084.
- Schroeder, C. E., & Lakatos, P. (2009). Low-frequency neuronal oscillations as instruments of sensory selection. Trends in Neurosciences, 32(1), 9–18.
- Serre, T., Oliva, A., & Poggio, T. (2007). A feedforward architecture accounts for rapid categorization. Proceedings of the National Academy of Sciences of the United States of America, 104(15), 6424–6429.
- Servan-Schreiber, D., Cleeremans, A., & McClelland, J. L. (1991). Graded state machines: The representation of temporal contingencies in simple recurrent networks. Machine Learning, 7(2–3), 161–193.
- Silva, L. R., Amitai, Y., & Connors, B. W. (1991). Intrinsic oscillations of neocortex generated by layer 5 pyramidal neurons. Science, 251(4992), 432–435.
- Sinha, P., & Poggio, T. (1996). Role of learning in three-dimensional form perception. Nature, 384(6608), 460–463.
- Spaak, E., Bonnefond, M., Maier, A., Leopold, D. A., & Jensen, O. (2012). Layer-specific entrainment of gamma-band neural activity by the alpha rhythm in monkey visual cortex. Current Biology, 22(24), 2313–2318.
- Stefanics, G., Hangya, B., Herndi, I., Winkler, I., Lakatos, P., & Ulbert, I. (2010). Phase entrainment of human delta oscillations can mediate the effects of expectation on reaction speed. The Journal of Neuroscience, 30(41), 13578–13585.
- Thomson, A. M. (2010). Neocortical layer 6, a review. Frontiers in Neuroanatomy, 4.
- Thomson, A. M., & Lamy, C. (2007). Functional maps of neocortical local circuitry. Frontiers in Neuroscience, 1(1), 19–42.
- VanRullen, R., Busch, N. A., Drewes, J., & Dubois, J. (2011). Ongoing EEG phase as a trial-by-trial predictor of perceptual and attentional variability. Frontiers in Psychology, 2.
- Will, U., & Berg, E. (2007). Brain wave synchronization and entrainment to periodic acoustic stimuli. Neuroscience letters, 424(1), 55–60.

Chapter 2

2.1 Introduction

The *LeabraTI* framework is a mechanistic description and general model of how prediction and temporal integration might work in the brain. The general idea is closely related to the Simple Recurrent Network (SRN) (Elman90Servan-SchreiberCleeremansMcClelland91) an artificial neural network architecture that explicitly represents temporally lagged information in discrete “context” units whose activity gets integrated with more current information to predict what happens in the next time step (Figure ??a). This method of copying a contextual representation from an intermediate representation at discrete intervals was originally shown to be a robust way to leverage error-driven learning to represent latent temporal structure in auditory streams and artificial grammars. More generally, the SRN’s explicit representation of temporal context can capture the latent structure of any stimulus that varies systematically over time, making it a good basis for a generic prediction and temporal integration mechanism.

However, *LeabraTI* differs in several key ways from the traditional SRN architecture, primarily in the way temporally lagged context is represented and used in neural processing. These differences are due to biological constraints imposed by the circuitry of the neocortex, and thus form a number of testable predictions that can be used to evaluate the validity of the *LeabraTI* framework. The central prediction of *LeabraTI* is that temporal context is updated in a periodic manner, approximately every 100 ms, subserved by deep (Layer 5 and 6) neurons. This periodic updating is suggested to contribute to the brain’s alpha rhythm, which has been studied extensively

using scalp electroencephalography. This chapter **TODO – also need something here about error driven learning**

2.2 LeabraTI biological details

2.2.1 Laminar structure and microcircuitry of the neocortex

A salient feature of the brain, and potential clue in realizing how an SRN-like computation might be carried out in biological neural circuits, is the laminar structure prevalent across the neocortex (Figure ??b). Incoming information from the sensory periphery is transmitted through the thalamus and targets Layer 4 neurons in the primary sensory cortices (e.g., V1). From there, Layer 4 neurons propagate spikes to superficial neurons (Layers 2 and 3) which in turn target Layer 4 neurons of higher-level cortices, forming the prominent corticocortical feedforward pathways that subserve visual and auditory recognition (FellemanVanEssen91). Corticocortical feedback originates in superficial layers or Layer 6 of the higher-level cortex and generally terminates on superficial neurons of the lower-level cortex (RocklandPandya79). In addition to these interareal pathways, there exists a canonical microcircuit of the form Layer 4 \rightarrow Layer 2/3 \rightarrow Layer 5 \rightarrow Layer 6 that routes spike propagation through the local neuronal structure (Douglas-Martin04ThomsonLamy07). This microcircuit forms the core computational unit of LeabraTI, as will be described in this and the following sections.

The importance of the local microcircuit was first suggested by Vernon Mountcastle in his proposal regarding the gross columnar organization of the neocortex (see Mountcastle97, for a comprehensive review). Mountcastle's proposal states that microcolumns composed of around 80-100 neurons extending vertically through all six lamina with canonical circuitry form the core repeating structure of the neocortex. Neurons within a single microcolumnar circuit possess nearly identical receptive field tunings across lamina while neurons in neighboring microcolumns (radial separation greater than 600 μm) possess very different receptive field tunings but contribute to the higher-order macrocolumn (i.e., hypercolumn) structure (HubelWiesel77Jones00). Microcolumns

a)**b)**

Figure 2.1: The Simple Recurrent Network (SRN) and microcircuitry of the neocortex. **a)** The SRN represents temporal information explicitly using discrete context units that are updated once per time step. Context is integrated with more current inputs to predict information at the subsequent time step. Reproduced from Servan-SchreiberCleeremansMcClelland91). **b)** The neocortex is laminated with canonical circuitry between neurons across layers and between areas. Intraareal connections are shown in black with interareal feedforward connections in purple and feedback connections in green.

have been identified in a variety of neural systems with this electrophysiological mapping and are also prominently visible under Nissl staining. Despite this evidence for their structural existence, any function of the microcolumn aside from an organizing principle remains debated (BuxhoevedenCasanova02HortonAdams05).

LeabraTI provides a computational role for the microcolumn, by mapping an SRN-like computation onto their Layer 4 \rightarrow Layer 2/3 \rightarrow Layer 5 \rightarrow Layer 6 circuit. In this mapping, superficial neurons continuously integrate feedforward and feedback interareal synapses to process current information. Layer 2/3 \rightarrow Layer 5 \rightarrow Layer 6 provides an intraareal pathway for explicitly representing temporal context deep layers, which are relatively isolated from nonlocal inputs. There is also appropriate circuitry for recirculating this context through the local microcolumn via Layer 4 to drive the learning of temporal associations. This basic idea provides a concise explanation for the strong degree of isotuning throughout a single microcolumn, as deep neurons need to represent the same information as superficial neurons except at a delayed interval.

More generally, LeabraTI's dichotomy of continuous integration in superficial layers and periodic updating of deep layers receives strong support by the literature. Recent studies that have employed depth electrodes to simultaneously record from multiple layers within a patch of cortex have indicated that superficial layers exhibit spectral power at much higher frequencies than deep layers. BuffaloFriesLandmanEtAl11) recorded responses from ventral visual sites V1, V2, and V4 in awake, behaving monkeys during a simple directed attention task, finding a dissociation in spike coherence frequency in superficial (gamma spectrum, peak ~ 50 Hz) and deep layers (alpha spectrum, peak ~ 10 Hz). A similar experimental paradigm expands on these findings by demonstrating cross-frequency coupling between gamma and alpha spectra localized to superficial and deep layers, respectively (SpaakBonfondMaierEtAl12). The cross-frequency coupling is characterized by a clear nesting of gamma activity within alpha cycles, suggesting that deep neurons' alpha activity might subserve a general pacemaker mechanism. In the context of LeabraTI, this pacemaker property is important to ensure the regular updating of context through deep layers and temporally predictable reintegration with more current information.

In summary, the laminocolumnar organization of the neocortex provides the dual pathways necessary for continuous information processing and the SRN's explicit temporal context representation. One question that remains, however, concerns the 10 Hz alpha periodicity of deep neurons. The Layer 4 → Layer 2/3 → Layer 5 → Layer 6 microcircuit only contains four synapses including the thalamus and intracolumnar monosynaptic latencies for regular spiking neurons are on the order of 5 ms or faster (Armstrong-JamesFoxDas-Gupta92LumerEdelmanTononi97). This relatively small amount of tissue, if driven with constant input, would cause deep neurons to spike at a rate much faster than 10 Hz. How such a circuit could produce the strong alpha power observed in recent depth recordings is described next.

2.2.2 Pacemaker properties of Layer 5 and thalamic bursting neurons

Layer 5 neurons can be roughly divided into 5a and 5b subtypes (ThomsonLamy07). Layer 5a neurons have relatively small cell bodies and exhibit “regular spiking” depolarization responses. They collect input from other Layer 5a neurons and pass it to 5b neurons and thus, likely play a simple information integration role. Layer 5b neurons, in contrast, have larger cell bodies and exhibit “intrinsic bursting” properties at ~10 Hz when over threshold (ConnorsGutnickPrince82SilvaAmitaiConnors91; FranceschettiGuatteoPanzicaEtAl95).

Thalamic neurons...

Layer 5b neurons project to Layer 6 whose neurons can also be roughly divided into corticocortical (CC) and corticothalamic (CT) subtypes (Thomson10).

Both Layer Layer 6 CC neurons have properties similar to Layer 5a neurons – they collect inputs from other Layer 6a neurons and pass it to Layer 6 CT neurons. Layer 6 CT neurons project specifically to the thalamus and also receive direct thalamic input forming a small circuit. They have

This rhythmic firing has been shown to persist even with constant sensory stimulation *in vivo* (LuczakBarthoHarris13), suggesting that Layer 5 neurons' alpha rhythmicity could implement a roughly 10 Hz gating function for spikes relayed to Layer 6 neurons.

Thus, Layer 6 specifically becomes the neural substrate of the SRN's temporally lagged context representation, representing information that is, on average, one alpha cycle (approximately 100 ms) in the past. This contextual storage occurs at an automatic interval due to the intrinsic pacemaking properties of Layer 5 neurons, and might implement a reference frame that essentially would allow the brain to know *when* to anticipate inputs. As such, intrinsic oscillations have been shown to phase lock to environmental stimulation (WillBerg07LakatosKarmosMehtaEtAl08SchroederLakatos09S ensuring environmental events coincide with key events like Layer 5 bursts in cortex.

Layer 6 sends axons toward the thalamus, completing the microcircuit within the local column and allowing the temporally lagged Layer 6 information to integrate with more current Layer 4 inputs. There also exists a direct connection between Layer 6 and Layer 4, that could be used for this purpose, although it has been noted as being weak compared to other intracolumnar connections (HirschMartinez06b). In either case, temporal associations could be created by simple Hebbian learning mechanisms that track high probability co-occurrences across past and present events.

The Leabra algorithm (OReillyMunakata00OReillyMunakataFrankEtAl12), however, also makes use of powerful error-driven learning (in addition to more standard Hebbian learning). In the context of temporal integration, error-driven learning would allow computation of error signals based on the difference between what is predicted to happen at a given moment (given the previous moments context as an input) and what actually happens. However, this computation requires that both the prediction and the actual sensation are represented subsequently within a single alpha cycle, which is not possible if the sensory periphery is always transmitting incoming inputs. To resolve this issue, the LeabraTI framework posits a mechanism to modulate or even block the transmission of inputs from the sensory periphery. A subset of cells in the thalamus exhibit alpha spectrum bursting properties similar to that of Layer 5 neurons (LopesdaSilva91; HughesLorincz-CopeEtAl04; LorinczCrunelliHughes08; LorinczKekesiJuhaszEtAl09), and thus perhaps perform a similar gating function. Specifically, these neurons appear to shift the balance of inputs to Layer 4 and superficial neurons between exogenous environmental inputs and endogenous inputs local to

the microcolumn.

When environmental inputs are downmodulated or blocked, Layer 6 context relayed via the thalamus is the dominant input to the microcolumn, which can be used to predict the incoming sensory event during the latter part of the alpha cycle. Importantly, during both the prediction and sensation phases, feedforward and feedback projections are constantly transmitting between lower and higher cortical areas. As previously mentioned, these projections originate and terminate predominantly in superficial layers, boosting their spike coherence to higher frequency spectra. This could potentially explain the differentially high gamma power in superficial layers compared to deep layers, and provides a compelling link between gamma oscillations and predicting specific details about the next sensory event.

2.2.3 Summary of LeabraTI computation

The overall computation of LeabraTI is shown in Figure ?? and summarized here. When thalamic cells burst (roughly every 100 ms), information from the sensory periphery is the primary driving force for Layer 4 neurons in primary cortex. This information is relayed downstream to higher-level cortical areas via the strong feedforward Layer 4 → Layer 2/3 → Layer 4 pathway (FellemanVanEssen91). Within the local microcolumn, Layer 5 neurons integrate this information, until thalamic bursting quiets (generally around 50 ms). At this point, Layer 5 cells burst, sending outputs to Layer 6 and shifting and inputs to the microcolumn endogenously. The information represented by Layer 6 neurons is temporally lagged (from the previous 50 ms) and is relayed to Layer 4 via non-bursting (regular spiking) thalamic neurons or via the direct Layer 6 → Layer 4 connection (not pictured in Figure ??), and might be maintained by reciprocal thalamocortical drive back to Layer 6. This information can be used as a prediction as to what will happen next when thalamic bursting resumes and veridical sensory information serves as the input once again. In the context of Leabra's error-driven learning these two phases correspond to the plus phase (sensation) and minus phase (prediction), which can be used to compute a sensory prediction error signal. This error signal modifies Layer 5 → Layer 6 synapses to minimize differences between

predictions and sensations over time.

Critically, for the LeabraTI computation to work, thalamic and Layer 5 oscillatory phases need to have an approximately antiphase relationship in order for the error-driven learning scheme described here to work so that Layer 2/3 neurons can represent the current moment's prediction with Layer 6 context as their primary input and then subsequently represent the veridical sensory input while Layer 5 neurons are queuing up the next contextual event. Such a relationship has not yet been shown yet, but very few studies have recorded simultaneously from thalamic and cortical neurons in *in vivo* in the awake behaving animal. It is also possible that the brain implements error-driven learning in such a way that does not require representing predictions and sensations temporally interleaved on the same neural substrate or even that the brain accomplishes temporal integration completely without supervision, which in case thalamic gating is not required.

2.3 LeabraTI predictions

2.3.1 Relation to existing models

2.3.2 Testable predictions

TODO

References

- Armstrong-James, M., Fox, K., & Das-Gupta, A. (1992). Flow of excitation within rat barrel cortex on striking a single vibrissa. *Journal of Neurophysiology*, *68*(4), 1345–1358.
- Balas, B. J., & Sinha, P. (2009). The role of sequence order in determining view canonicity for novel wire-frame objects. *Attention, Perception & Psychophysics*, *71*(4), 712–723.
- Brainard, D. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436.
- Buffalo, E. A., Fries, P., Landman, R., Buschman, T. J., & Desimone, R. (2011). Laminar differences in gamma and alpha coherence in the ventral stream. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(27), 11262–11267.
- Bulthoff, H. H., & Edelman, S. (1992). Psychophysical support for a two-dimensional view interpolation theory of object recognition. *Proceedings of the National Academy of Sciences of the United States of America*, *89*(1), 60–64.
- Busch, N. A., Dubois, J., & VanRullen, R. (2009). The phase of ongoing EEG oscillations predicts visual perception. *The Journal of Neuroscience*, *29*(24), 7869–7876.
- Buxhoeveden, D. P., & Casanova, M. F. (2002). The minicolumn hypothesis in neuroscience. *Brain*, *125*(Pt 5), 935–951.
- Connors, B. W., Gutnick, M. J., & Prince, D. A. (1982). Electrophysiological properties of neocortical neurons in vitro. *Journal of Neurophysiology*, *48*(6), 1302–1320.
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*(1), 9–21.
- Doherty, J. R., Rao, A., Mesulam, M. M., & Nobre, A. C. (2005). Synergistic effect of combined temporal and spatial expectations on visual attention. *The Journal of Neuroscience*, *25*(36), 8259–8266.
- Douglas, R. J., & Martin, K. A. C. (2004). Neuronal circuits of the neocortex. *Annual Review of Neuroscience*, *27*, 419–451.
- Edelman, S., & Bulthoff, H. H. (1992). Orientation dependence in the recognition of familiar and novel views of three-dimensional objects. *Vision Research*, *32*(12), 2385–2400.
- Elman, J. L. (1990). Finding structure in time. *Cognitive Science*, *14*(2), 179–211.
- Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, *1*(1), 1–47.
- Foldiak, P. (1991). Learning invariance from transformation sequences. *Neural Computation*, *3*(2), 194–200.
- Franceschetti, S., Guatteo, E., Panzica, F., Sancini, G., Wanke, E., & Avanzini, G. (1995). Ionic mechanisms underlying burst firing in pyramidal neurons: Intracellular study in rat sensorimotor cortex. *Brain Research*, *696*(1–2), 127–139.
- Hirsch, J. A., & Martinez, L. M. (2006). Laminar processing in the visual cortical column. *Current Opinion in Neurobiology*, *16*(4), 377–384.

- Horton, J. C., & Adams, D. L. (2005). The cortical column: A structure without a function. Philosophical Transactions of the Royal Society B, 360(1456), 837–862.
- Hubel, D. H., & Wiesel, T. N. (1977). Ferrier lecture. Functional architecture of macaque monkey visual cortex. Proceedings of the Royal Society B, 198(1130), 1–59.
- Hughes, S. W., Lorincz, M., Cope, D. W., Blethyn, K. L., Kekesi, K. A., Parri, H. R., Juhasz, G., & Crunelli, V. (2004). Synchronized oscillations at alpha and theta frequencies in the lateral geniculate nucleus. Neuron, 42(2), 253–268.
- Jones, E. G. (2000). Microcolumns in the cerebral cortex. Proceedings of the National Academy of Sciences of the United States of America, 97(10), 5019–5021.
- Lakatos, P., Karmos, G., Mehta, A. D., Ulbert, I., & Schroeder, C. E. (2008). Entrainment of neuronal oscillations as a mechanism of attentional selection. Science, 320(5872), 110–113.
- Logothetis, N., Pauls, J., Bulthoff, H., & Poggio, T. (1994). View-dependent object recognition by monkeys. Current Biology, 4(5), 401–414.
- Logothetis, N. K., Pauls, J., & Poggio, T. (1995). Shape representation in the inferior temporal cortex of monkeys. Current Biology, 5(5), 552–563.
- Lopes da Silva, F. (1991). Neural mechanisms underlying brain waves: from neural membranes to networks. Electroencephalography and Clinical Neurophysiology, 79(2), 81–93.
- Lorincz, M. L., Crunelli, V., & Hughes, S. W. (2008). Cellular dynamics of cholinergically induced alpha (8–13 Hz) rhythms in sensory thalamic nuclei in vitro. The Journal of Neuroscience, 28(3), 660–671.
- Lorincz, M. L., Kekesi, K. A., Juhasz, G., Crunelli, V., & Hughes, S. W. (2009). Temporal framing of thalamic relay-mode firing by phasic inhibition during the alpha rhythm. Neuron, 63(5), 683–696.
- Luczak, A., Bartho, P., & Harris, K. D. (2013). Gating of sensory input by spontaneous cortical activity. The Journal of Neuroscience, 33(4), 1684–1695.
- Lumer, E., Edelman, G., & Tononi, G. (1997). Neural dynamics in a model of the thalamocortical system. I. Layers, loops and the emergence of fast synchronous rhythms. Cerebral Cortex, 7(3), 207–227.
- Masquelier, T., & Thorpe, S. J. (2007). Unsupervised learning of visual features through spike timing dependent plasticity. PLoS Computational Biology, 3(2), 247–257.
- Mathewson, K. E., Lleras, A., Beck, D. M., Fabiani, M., Ro, T., & Gratton, G. (2011). Pulsed out of awareness: EEG alpha oscillations represent a pulsed-inhibition of ongoing cortical processing. Frontiers in Psychology, 2.
- Mountcastle, V. B. (1997). The columnar organization of the neocortex. Brain, 120(Pt 4), 701–722.
- Mutch, J., & Lowe, D. (2008). Object class recognition and localization using sparse features with limited receptive fields. International Journal of Computer Vision, 80(1), 45–57.
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. Computational Intelligence and Neuroscience, 2011.

- O'Reilly, R. C., & Munakata, Y. (2000). Computational Explorations in Cognitive Neuroscience: Understanding the Mind by Simulating the Brain. Cambridge, MA: The MIT Press.
- O'Reilly, R. C., Munakata, Y., Frank, M. J., Hazy, T. E., & Contributors (2012). Computational Cognitive Neuroscience. Wiki Book, 1st Edition, URL: <http://ccnbook.colorado.edu>.
- Pelli, D. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. Spatial Vision, 10(4), 437–442.
- Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. F. (1989). Spherical splines for scalp potential and current density mapping. Electroencephalography and Clinical Neurophysiology, 72(2), 184–187.
- Rockland, K. S., & Pandya, D. N. (1979). Laminar origins and terminations of cortical connections of the occipital lobe in the rhesus monkey. Brain Research, 179(1), 3–20.
- Rohenkohl, G., & Nobre, A. C. (2011). Alpha oscillations related to anticipatory attention follow temporal expectations. The Journal of Neuroscience, 31(40), 14076–14084.
- Schroeder, C. E., & Lakatos, P. (2009). Low-frequency neuronal oscillations as instruments of sensory selection. Trends in Neurosciences, 32(1), 9–18.
- Serre, T., Oliva, A., & Poggio, T. (2007). A feedforward architecture accounts for rapid categorization. Proceedings of the National Academy of Sciences of the United States of America, 104(15), 6424–6429.
- Servan-Schreiber, D., Cleeremans, A., & McClelland, J. L. (1991). Graded state machines: The representation of temporal contingencies in simple recurrent networks. Machine Learning, 7(2–3), 161–193.
- Silva, L. R., Amitai, Y., & Connors, B. W. (1991). Intrinsic oscillations of neocortex generated by layer 5 pyramidal neurons. Science, 251(4992), 432–435.
- Sinha, P., & Poggio, T. (1996). Role of learning in three-dimensional form perception. Nature, 384(6608), 460–463.
- Spaak, E., Bonnefond, M., Maier, A., Leopold, D. A., & Jensen, O. (2012). Layer-specific entrainment of gamma-band neural activity by the alpha rhythm in monkey visual cortex. Current Biology, 22(24), 2313–2318.
- Stefanics, G., Hangya, B., Herndi, I., Winkler, I., Lakatos, P., & Ulbert, I. (2010). Phase entrainment of human delta oscillations can mediate the effects of expectation on reaction speed. The Journal of Neuroscience, 30(41), 13578–13585.
- Thomson, A. M. (2010). Neocortical layer 6, a review. Frontiers in Neuroanatomy, 4.
- Thomson, A. M., & Lamy, C. (2007). Functional maps of neocortical local circuitry. Frontiers in Neuroscience, 1(1), 19–42.
- VanRullen, R., Busch, N. A., Drewes, J., & Dubois, J. (2011). Ongoing EEG phase as a trial-by-trial predictor of perceptual and attentional variability. Frontiers in Psychology, 2.
- Will, U., & Berg, E. (2007). Brain wave synchronization and entrainment to periodic acoustic stimuli. Neuroscience letters, 424(1), 55–60.

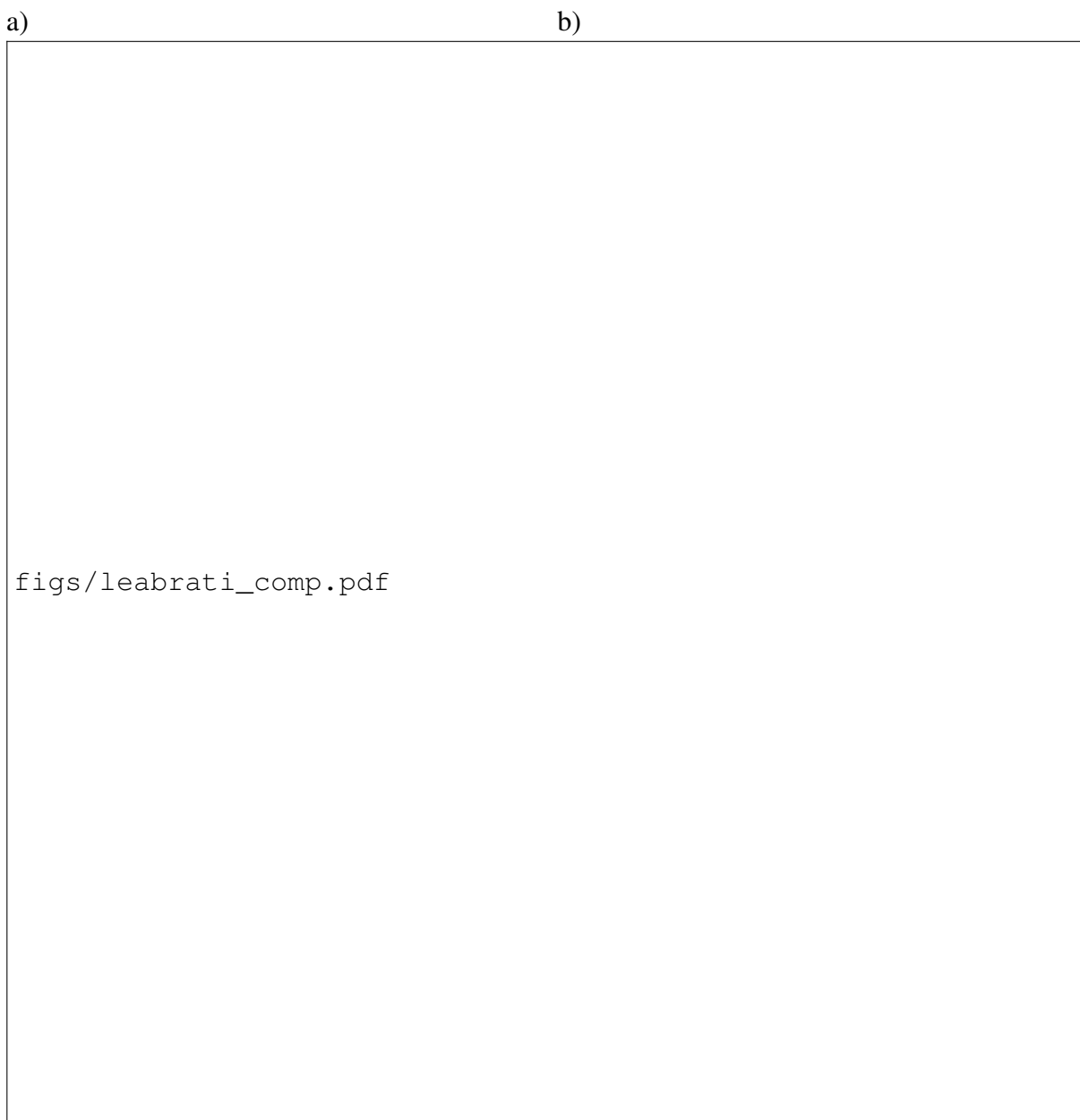


Figure 2.2: The LeabraTI model computation.

Chapter 3

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3.1 Introduction

TODO, pull from proposal and proposal-r1.

3.2 Methods

3.2.1 Participants

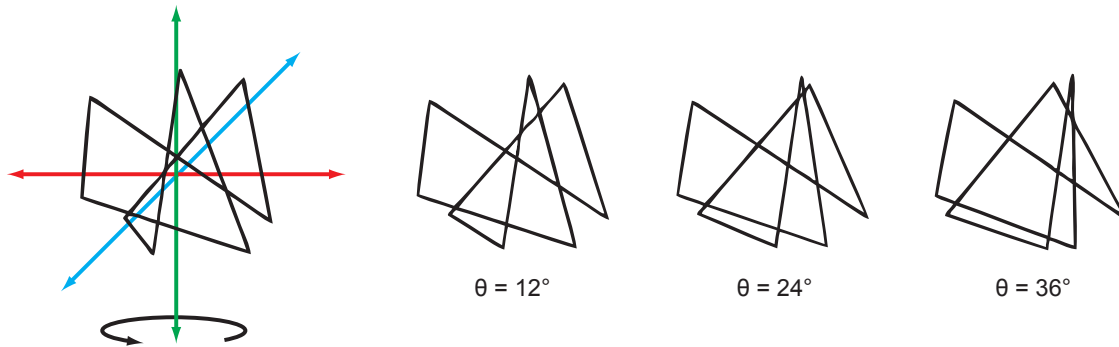
A total of 58 students from the University of Colorado Boulder participated in the experiment (ages 18-28 years, mean=21; 31 male, 27 female). EEG was recorded from 29 of the participants while they completed the experiment. The remaining 29 participants completed a solely behavioral experiment without EEG recording. All participants were right-handed and reported normal or corrected-to-normal vision. Participants either received course credit or payment of \$15 per hour as compensation for their participation. Informed consent was obtained from each participant prior to the experiment in accordance with Institutional Review Board policy at the University of Colorado.

3.2.2 Stimuli

Novel “paper clip” objects similar to those used in previous studies (BulthoffEdelman92EdelmanBulthoff92) were created using MATLAB. Eight vertices were placed randomly on the surface of a sphere of unit radius and then joined together with line segments. The last and first vertex were also joined

to form a closed loop so that line segment terminations were not a salient feature (BalasSinha09b). Objects were constrained to exclude extremely acute angles between successive segments (less than 20 degrees) and were approximately rotationally balanced (center of mass within 10% of the origin). Objects were rotated completely about their vertical axis in steps of 12 degrees and rendered to bitmap images under an orthographic projection. A total of 16 objects were created using this procedure, yielding 480 images (30 images per object). Object examples are shown in Figure ??.

A



B

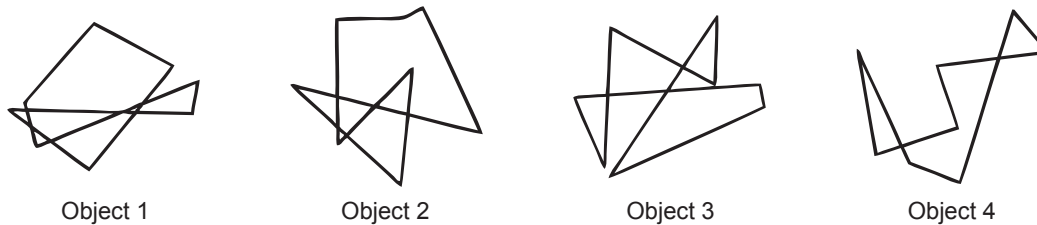


Figure 3.1: Novel “paper clip” objects

A: Objects were composed of eight three-dimensional vertices joined together with line segments. To render the objects to bitmap images, each object was rotated completely about its vertical axis in steps of 12 degrees and reduced to an orthographic projection. **B:** Four of the 16 objects used in the experiment.

3.2.3 Procedure

Participants observed an entraining sequence of rotated views of a random object and performed a same-different judgement about a probe stimulus. On each trial, a view was randomly

selected as the initial view of the sequence followed by seven additional views spaced 24 degrees apart (Figure ??A, blue tick marks). Thus, the eight view entraining sequence spanned 168 degrees of the object. The entraining sequence was either presented in order (i.e., spatially predictable) or randomized. Following the entraining sequence after a 200 ms blank was a probe stimulus consisting of either an unseen view from the entraining object or a novel distractor. Unseen views were randomly sampled from the 12 degree interpolations between views of the entraining sequence (Figure ??A, magenta tick marks) and from outside of the span of the entraining sequence in increments of 24 degrees (Figure ??A, green tick marks).

Distractors were created from the original target objects by randomly selecting new spherical coordinates for six of the eight vertices and re-rendering them to bitmap images using the same method as the original target objects (12 degree steps about the vertical axis). Distractors conformed to the same constraints as the original target objects (no extremely acute angles, approximately rotationally balanced). Participants were instructed to respond “same” if they believed the probe depicted the same object as the entraining sequence or “different” if it depicted a distractor object. Participants received feedback after each trial according to whether their response was correct or incorrect.

During the entraining sequence, object views were presented for 50 ms at either 10 Hz (i.e., temporally predictable) or at a variable rate by manipulating the interstimulus interval (ISI) between subsequent views. Temporally predictable ISIs were 50 ms, totaling 350 ms across the entraining sequence. Variable ISIs were selected by randomly generating seven ISIs that also summed to 350 ms (Figure ??B). ISIs were in the range of 16.67 ms (minimum) to 216.67 ms (maximum) in increments of 16.67 ms. Temporal unpredictability was maximized by generating 400 such ISI sequences, calculating the summed squared error (SSE) across subsequent ISIs in a sequence, and selecting the 100 sequences with the highest SSE for use during the experiment.

The experiment was displayed on an LCD monitor with a native resolution of 1280x1024 operating at 60 Hz using the Psychophysics Toolbox Version 3 (Brainard97Pelli97). Stimuli were presented on an isoluminant 50% gray background and subtended approximately 5 degrees of

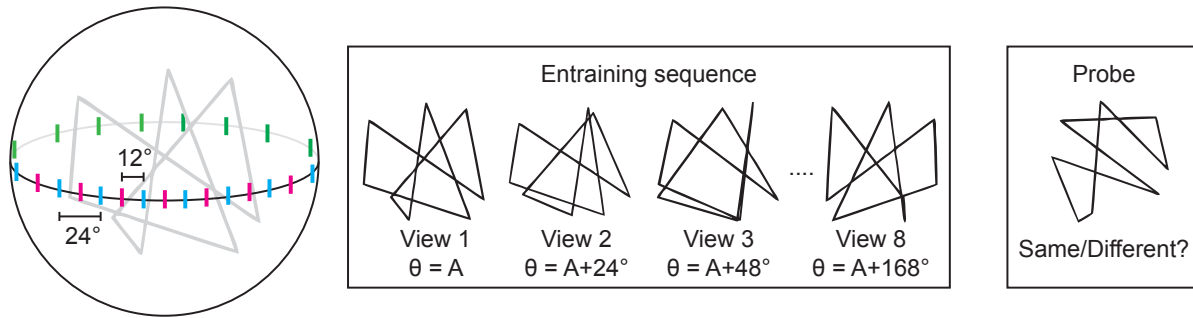
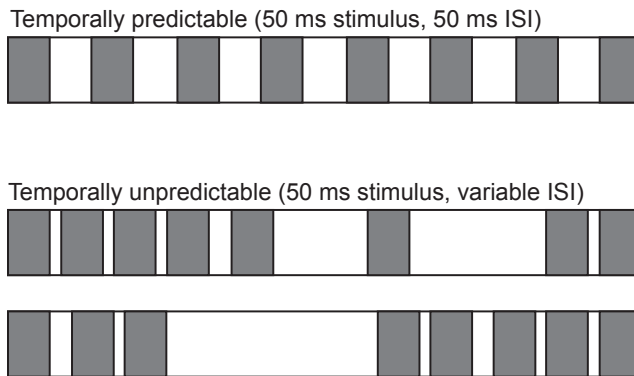
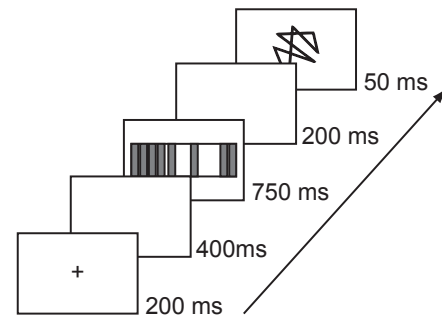
A**B****C**

Figure 3.2: Experimental procedure

A: Experimental trials contained an entraining sequence composed of eight views of a single object, followed by a probe stimulus. Entraining views were spaced 24 degrees apart (blue tick marks). The probe depicted an unseen view from the 12 degree interpolations between views of the entraining sequence (magenta tick marks) or from outside the span of the entraining sequence in increments of 24 degrees (green tick marks). **B:** Entraining views were either presented at 10 Hz with a 50 ms on time and 50 ms off time or in a temporally unpredictable manner with a 50 ms on time (gray segments) and variable off time (white segments). In both cases, the duration of the total entraining sequence was held constant at 750 ms. **C:** Order and timing of events within a single trial.

visual angle. Trials began with a fixation cross (200 ms) followed by a blank (400 ms), the entraining sequence (750 ms total), a second blank (200 ms), and ended with the probe stimulus (50 ms) (Figure ??C). Participants were required to respond within 2000 ms. Trials were separated by a variable intertrial interval of 2000-2400 ms. The experiment contained 500 trials with an additional 20 practice trials that contained a longer blank (1000 ms) between the entraining sequence and the

probe to familiarize participants with the order of events during trials. Participants completed the 20 practice trials (which were discarded from analysis) prior to performing the 500 experimental trials.

3.2.4 EEG recording and preprocessing

The EEG was recorded using an Electrical Geodesics, Inc. (EGI) system composed of a 128 channel net (HCGSN 130) amplified through 200 M Ω amplifiers (Net Amps 200). The signal was sampled at 250 Hz with impedances for each electrode were adjusted to less than 40 k Ω before and during the recording. Stimulus and response trigger onsets were measured via the Psychophysics Toolbox using a high precision realtime clock that was synchronized within 2.5 ms of the EEG system's clock before every trial during the experiment.

EEG data were preprocessed using the FieldTrip toolbox (OostenveldFriesMarisEtAl11). Raw data were first band-pass filtered between 1 Hz and 100 Hz with a 59-61 Hz band-stop and then epoched into 2350 ms segments that spanned the start of the pre-trial blank to 1000 ms after the probe stimulus. Individual segments were visually inspected and rejected if found to contain muscle artifacts or atypical noise. Bad channels were also identified and temporarily removed from the data before performing ICA decomposition (DelormeMakeig04) to remove of ocular artifacts. Components related to ocular artifacts were identified based on their topographical distribution across electrodes. The data were reconstructed without the ocular components and any bad channels were replaced using spherical spline interpolation (PerrinPernierBertrandEtAl89). The resulting segments were re-referenced to the average reference.

3.2.5 Event-related averaging

Event-related averaging was performed separately for the entraining sequence and the subsequent probe. For the entraining sequence, data were aligned to the onset of entraining views 2 through 8 and averaged from the period beginning 50 ms before each entrainer and ending 50 ms after. Baseline correction was performed using the first 50 ms of this period. For the probe, data

were aligned to the probe onset and averaged from the period beginning 200 ms before the probe and ending 400 ms after. This allowed detection of predictability effects during the blank period elicited by the entraining sequence as well as probe-evoked predictability effects.

All waveforms were averaged over a montage of 23 electrodes that covered the occipital and parietal cortices (Figure ??). The montage included locations from the 10-10 system that are commonly associated with perceptual processing (Oz, O1/O2, PO3/PO4, and PO7/PO8) (e.g., DohertyRaoMesulamEtAl05RohenkohlNobre11FahrenfortScholteLamme07).

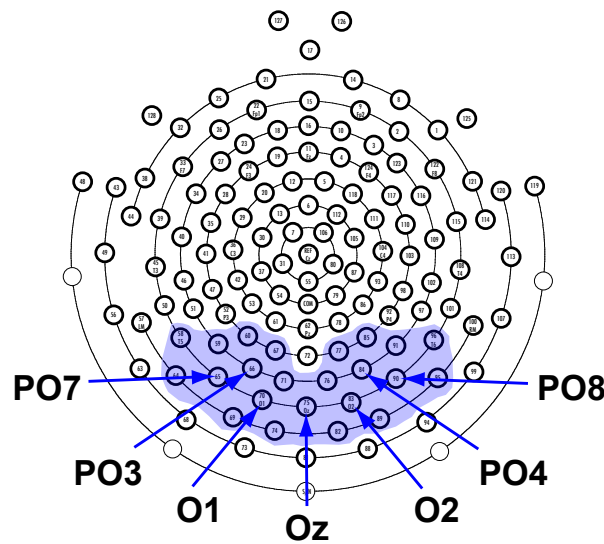


Figure 3.3: Electrode pooling

3.2.6 Time-frequency analysis

$$ITC(f, t) = \left| \frac{1}{N} \sum_{n=1}^N \frac{F_n(f, t)}{|F_n(f, t)|} \right|$$

3.3 Results

3.3.1 Behavioral measures of spatial and temporal predictability

Five subjects were excluded from behavioral analyses for accuracy 2.7σ (or further) below mean accuracy across subjects. The remaining 53 subjects were submitted to a 2x2 ANOVA with spatial and temporal predictability as within-subjects factors. Experiment type (EEG or behavioral only) was included as an additional between-subjects factor to ensure that it did not interact with any of the within-subjects factors. Accuracy and reaction times were collected during the experiment and were used to compute d' , a measure of sensitivity that takes into account response bias, and inverse efficiency, a measure that combines accuracy and reaction times (TownshendAshby78). These behavioral measures are plotted in Figure ??.

Subjects that completed the full EEG experiment were on average less accurate ($F(1, 51) = 4.80, p = 0.033$) but responded more quickly ($F(1, 51) = 10.05, p = 0.003$) than subjects that completed the solely behavioral experiment. These differences reflect a speed-accuracy tradeoff, likely due to differences in instructions given to subjects by experimenters or motivational differences between subject groups. Importantly, experiment type did not interact with any within-subjects factors (all p 's > 0.05) indicating that the behavioral measures of interest were not dependent on which type of experiment subjects completed.

Overall, subjects were more accurate when the entraining sequence was temporally predictable ($F(1, 51) = 17.84, p < 0.001$). A similar effect for spatial predictability failed to reach significance ($F(1, 51) = 1.85, p = 0.18$). The interaction between spatial and temporal predictability, however, was significant ($F(1, 51) = 6.13, p = 0.017$). LeabraTI as well as previous investigations of predictability (e.g., DohertyRaoMesulamEtAl05) suggest that spatial and temporal predictability should have an additive effect on behavioral outcomes. However, the combined spatial and temporal predictability condition here (denoted S+T+ in Figure ??) does not exhibit this pattern. Although not significantly different from spatial predictability alone ($t(52) = 1.29, p = 0.204$) or from temporal predictability alone ($t(52) = 0.45, p = 0.652$), this result merits further investigation.

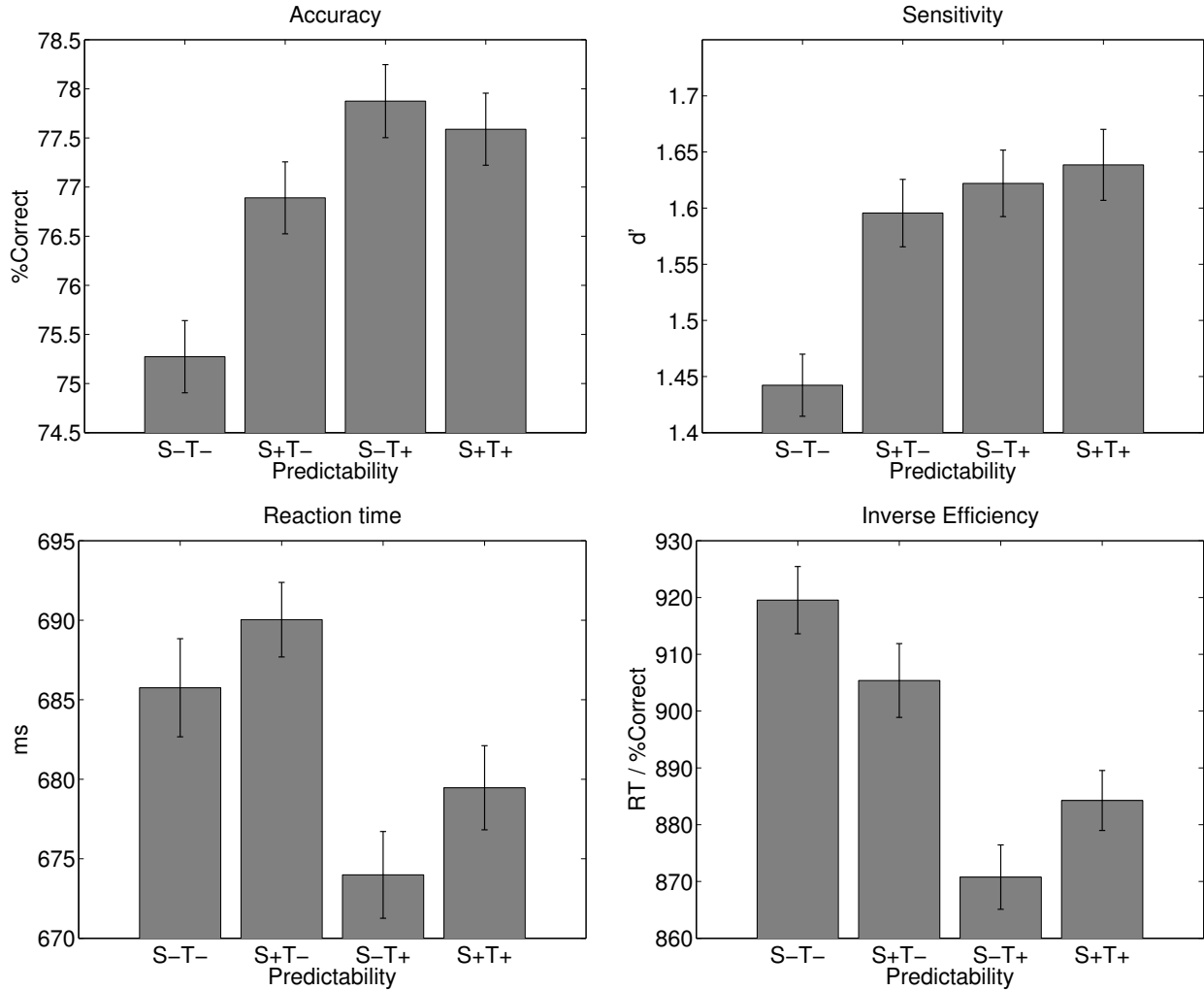


Figure 3.4: Behavioral measures of spatial and temporal predictability

Accuracy, d' (sensitivity), reaction time, and inverse efficiency (reaction time divided by percent correct) as a function of entrainment condition. S-/± refers to spatially unpredictable and predictable, T-/± to temporally unpredictable and predictable. Error bars depict within-subjects error using the method described in Cousineau05) adapted for standard error.

When responses are transformed into d' , there is a significant effect of both spatial ($F(1, 51) = 4.71, p = 0.035$) and temporal predictability ($F(1, 51) = 11.99, p < 0.001$). This result suggests that response bias can partially explain why spatial predictability failed to reach significance for raw accuracy. Other potential reasons for this result are discussed later. The interaction between spatial and temporal predictability remained significant for d' ($F(1, 51) = 4.49, p = 0.039$). The

interaction is additive, but is driven primarily by the strong effect of introducing spatial or temporal predictability over complete unpredictability (S-T- versus S+T-, $t(52) = 3.19, p = 0.002$; S-T- versus S+T+, $t(52) = 4.26, p < 0.001$) opposed to any synergistic effect of combined spatial and temporal predictability (S+T+ versus S+T-, $t(52) = 0.90$; S+T+ versus S-T+, $t(52) = 0.31$; both p 's > 0.05).

Reaction times were significantly faster when the entraining sequence was temporally predictable ($F(1, 51) = 12.38, p < 0.001$). A similar effect for spatial predictability failed to reach significance ($F(1, 51) = 1.96, p = 0.168$) nor did the interaction term ($F(1, 51) = 0.05, p = 0.83$).

Inverse efficiency, which considers reaction time as a function of accuracy (defined as reaction time divided by percent correct) can be thought of as the amount of energy consumed by the system to produce a behavioral outcome (TownshendAshby83). It is often used to remove non-monotonicities present in accuracy or reaction times alone, although that effect is not observed here. Nevertheless, it provides another lens under which to interpret the results, and thus it is considered here. Inverse efficiency was significantly lower when the entraining sequence was temporally predictable ($F(1, 51) = 23.31, p < 0.001$), but not when it was spatially predictability ($F(1, 51) = 0.002, p = 0.963$). Inverse efficiency is characterized by a significant cross-over interaction ($F(1, 51) = 5.85, p = 0.019$). Spatial predictability of the entraining sequence produces lowers inverse efficiency over complete unpredictability. Inverse efficiency is lowest on average when stimuli are temporally predictable, but the addition of spatial predictability causes an increase in inverse efficiency. These results suggest... **TODO**

3.3.2 Time course of spatial and temporal predictability

A total of five subjects were excluded from EEG analyses – three for an overabundance of artifacts in the EEG recording resulting in low trial counts after rejection and two for accuracy 2.7σ (or further) below mean accuracy across subjects (these two subjects were also excluded from behavioral analyses, see preceding section). The remaining 24 subjects were included in all EEG analyses.

A 2x2 ANOVA with spatial and temporal predictability as within-subjects factors was used

to assess statistical significance at each time bin of event-related averages. *p*-values were corrected for a maximum false discovery rate (FDR) of 5% using the method described in BenjaminiYekutieli01). Additionally, effects were only considered significant if they persisted for at least 16 ms.

To investigate the build-up of spatial and temporal predictability over the entraining sequence, activity from the second through final entraining views was averaged for each condition (the first entraining view is unpredictable, so it is omitted from the average). The results of this analysis are plotted in Figure???. The first thing worth noting is that a large 10 Hz periodicity is present for the temporally predictable conditions (S-T+ and S+T+), phase aligned approximately to the onset of each entrainer. Temporally unpredictable entrainers (S-T- and S+T-) are also approximately periodic. The reason for the 10 Hz periodicity in these conditions despite being temporally unpredictable is likely due to the 750 ms constant duration of the entraining sequence regardless of condition (Figure ??B). Presenting eight stimuli in 750 ms with a variable ISI is a 10 Hz presentation rate on average. Still, the temporally unpredictable entrainers exhibit markedly weaker amplitude and are approximately 180 degrees out of phase with the the temporally predictable entrainers.

The effect of spatial predictability manifested 26 ms after the onset of the entrainer and persisted for at least another 24 ms (one quarter of the 10 Hz period). Temporal predictability, in contrast, manifested prior to (-38 through -22 ms pre-stimulus) and at the onset of the entrainer (-6 ms pre-stimulus through 18 ms post-stimulus). The effect of temporal predictability appears to be driven by the anti phase relationship between T- and T+ conditions at these time points. Together, these effects demonstrate differential time courses for spatial and temporal predictability. Spatial predictability is a post-stimulus process and might represent a comparison computation between the previous stimulus and the currently presented one. Temporal predictability, in contrast, is a truly anticipatory process, occurring before (and at) the onset of each stimulus.

Spatial predictability was enhanced when stimuli were temporally predictable. This effect is characterized by the significant interaction between spatial and temporal predictability starting 14 ms after the onset of the entrainer and persisting for at least another 36 ms. This result indicates

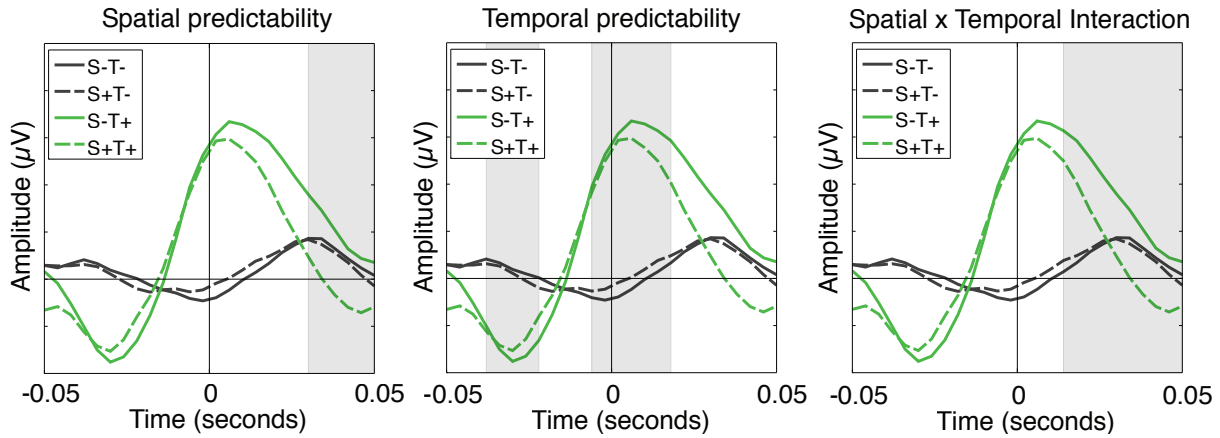


Figure 3.5: Entrainment-evoked activity

Grand averages for entrainers 2 through 8 as a function of entrainment condition. S-/± refers to spatially unpredictable and predictable, T-/± to temporally unpredictable and predictable. All plots depict the grand average with gray shaded regions denoting significant effects of spatial predictability (left), temporal predictability (center), and the interaction between these terms controlling for a maximum false discovery rate (FDR) of 5%.

that the brain is more capable of differentiating between spatially coherent and random sequences of stimuli when it can properly anticipate the presentation of each stimulus (S-T+ versus S+T+) compared to when the onset is unpredictable.

To investigate the effect of spatial and temporal predictability on perception of the probe, waveforms were aligned to the probe onset averaged from 200 ms before through 400 ms after (Figure ??). The results of this analysis basically mirror the entrainer-evoked effects albeit with a few key differences. Temporal predictability was again a purely anticipatory process, manifesting within the pre-stimulus period (-184 ms through -160 ms and -132 ms through -108 ms pre-stimulus). Spatial predictability also manifested briefly within the pre-stimulus period (-128 ms through -80 ms pre-stimulus), which was not seen for spatially predictable entrainers. The post-stimulus effects of spatial predictability occurred much earlier than for entrainers and persisted much longer, beginning approximately at the onset of the probe (-12 ms pre-stimulus) and lasting 136 ms through the P1 response with several transient effects after.

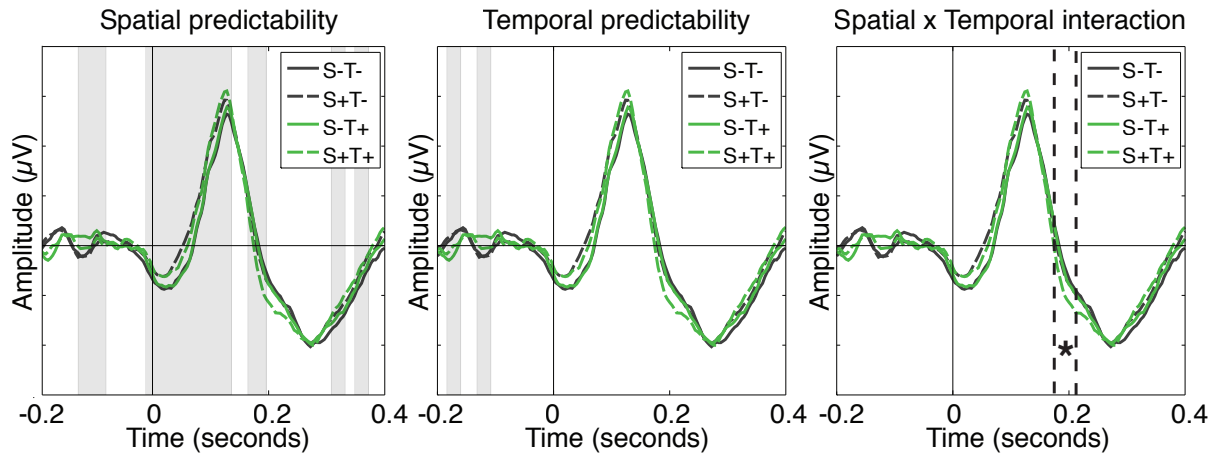


Figure 3.6: Probe-evoked activity

Grand averages for the probe stimulus, including the preceding 200 ms blank. S-/± refers to spatially unpredictable and predictable, T-/± to temporally unpredictable and predictable. All plots depict the grand average with gray shaded regions denoting significant effects of spatial predictability (left), temporal predictability (center), and the interaction between these terms controlling for a maximum false discovery rate (FDR) of 5%. The asterisk in the interaction plot denotes significance at the 5% level using amplitude averaged within the window defined by the dotted lines.

3.3.3 Entrainment of 10 Hz oscillations

3.3.4 Alpha phase at probe onset

3.4 Discussion

References

- Armstrong-James, M., Fox, K., & Das-Gupta, A. (1992). Flow of excitation within rat barrel cortex on striking a single vibrissa. *Journal of Neurophysiology*, *68*(4), 1345–1358.
- Balas, B. J., & Sinha, P. (2009). The role of sequence order in determining view canonicity for novel wire-frame objects. *Attention, Perception & Psychophysics*, *71*(4), 712–723.
- Brainard, D. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436.
- Buffalo, E. A., Fries, P., Landman, R., Buschman, T. J., & Desimone, R. (2011). Laminar differences in gamma and alpha coherence in the ventral stream. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(27), 11262–11267.
- Bulthoff, H. H., & Edelman, S. (1992). Psychophysical support for a two-dimensional view inter-

- polation theory of object recognition. Proceedings of the National Academy of Sciences of the United States of America, 89(1), 60–64.
- Busch, N. A., Dubois, J., & VanRullen, R. (2009). The phase of ongoing EEG oscillations predicts visual perception. The Journal of Neuroscience, 29(24), 7869–7876.
- Buxhoeveden, D. P., & Casanova, M. F. (2002). The minicolumn hypothesis in neuroscience. Brain, 125(Pt 5), 935–951.
- Connors, B. W., Gutnick, M. J., & Prince, D. A. (1982). Electrophysiological properties of neocortical neurons in vitro. Journal of Neurophysiology, 48(6), 1302–1320.
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. Journal of Neuroscience Methods, 134(1), 9–21.
- Doherty, J. R., Rao, A., Mesulam, M. M., & Nobre, A. C. (2005). Synergistic effect of combined temporal and spatial expectations on visual attention. The Journal of Neuroscience, 25(36), 8259–8266.
- Douglas, R. J., & Martin, K. A. C. (2004). Neuronal circuits of the neocortex. Annual Review of Neuroscience, 27, 419–451.
- Edelman, S., & Bulthoff, H. H. (1992). Orientation dependence in the recognition of familiar and novel views of three-dimensional objects. Vision Research, 32(12), 2385–2400.
- Elman, J. L. (1990). Finding structure in time. Cognitive Science, 14(2), 179–211.
- Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. Cerebral Cortex, 1(1), 1–47.
- Foldiak, P. (1991). Learning invariance from transformation sequences. Neural Computation, 3(2), 194–200.
- Franceschetti, S., Guatteo, E., Panzica, F., Sancini, G., Wanke, E., & Avanzini, G. (1995). Ionic mechanisms underlying burst firing in pyramidal neurons: Intracellular study in rat sensorimotor cortex. Brain Research, 696(1–2), 127–139.
- Hirsch, J. A., & Martinez, L. M. (2006). Laminar processing in the visual cortical column. Current Opinion in Neurobiology, 16(4), 377–384.
- Horton, J. C., & Adams, D. L. (2005). The cortical column: A structure without a function. Philosophical Transactions of the Royal Society B, 360(1456), 837–862.
- Hubel, D. H., & Wiesel, T. N. (1977). Ferrier lecture. Functional architecture of macaque monkey visual cortex. Proceedings of the Royal Society B, 198(1130), 1–59.
- Hughes, S. W., Lorincz, M., Cope, D. W., Blethyn, K. L., Kekesi, K. A., Parri, H. R., Juhasz, G., & Crunelli, V. (2004). Synchronized oscillations at alpha and theta frequencies in the lateral geniculate nucleus. Neuron, 42(2), 253–268.
- Jones, E. G. (2000). Microcolumns in the cerebral cortex. Proceedings of the National Academy of Sciences of the United States of America, 97(10), 5019–5021.
- Lakatos, P., Karmos, G., Mehta, A. D., Ulbert, I., & Schroeder, C. E. (2008). Entrainment of neuronal oscillations as a mechanism of attentional selection. Science, 320(5872), 110–113.

- Logothetis, N., Pauls, J., Bulthoff, H., & Poggio, T. (1994). View-dependent object recognition by monkeys. Current Biology, 4(5), 401–414.
- Logothetis, N. K., Pauls, J., & Poggio, T. (1995). Shape representation in the inferior temporal cortex of monkeys. Current Biology, 5(5), 552–563.
- Lopes da Silva, F. (1991). Neural mechanisms underlying brain waves: from neural membranes to networks. Electroencephalography and Clinical Neurophysiology, 79(2), 81–93.
- Lorincz, M. L., Crunelli, V., & Hughes, S. W. (2008). Cellular dynamics of cholinergically induced alpha (8–13 Hz) rhythms in sensory thalamic nuclei in vitro. The Journal of Neuroscience, 28(3), 660–671.
- Lorincz, M. L., Kekesi, K. A., Juhasz, G., Crunelli, V., & Hughes, S. W. (2009). Temporal framing of thalamic relay-mode firing by phasic inhibition during the alpha rhythm. Neuron, 63(5), 683–696.
- Luczak, A., Bartho, P., & Harris, K. D. (2013). Gating of sensory input by spontaneous cortical activity. The Journal of Neuroscience, 33(4), 1684–1695.
- Lumer, E., Edelman, G., & Tononi, G. (1997). Neural dynamics in a model of the thalamocortical system. I. Layers, loops and the emergence of fast synchronous rhythms. Cerebral Cortex, 7(3), 207–227.
- Masquelier, T., & Thorpe, S. J. (2007). Unsupervised learning of visual features through spike timing dependent plasticity. PLoS Computational Biology, 3(2), 247–257.
- Mathewson, K. E., Lleras, A., Beck, D. M., Fabiani, M., Ro, T., & Gratton, G. (2011). Pulsed out of awareness: EEG alpha oscillations represent a pulsed-inhibition of ongoing cortical processing. Frontiers in Psychology, 2.
- Mountcastle, V. B. (1997). The columnar organization of the neocortex. Brain, 120(Pt 4), 701–722.
- Mutch, J., & Lowe, D. (2008). Object class recognition and localization using sparse features with limited receptive fields. International Journal of Computer Vision, 80(1), 45–57.
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. Computational Intelligence and Neuroscience, 2011.
- O'Reilly, R. C., & Munakata, Y. (2000). Computational Explorations in Cognitive Neuroscience: Understanding the Mind by Simulating the Brain. Cambridge, MA: The MIT Press.
- O'Reilly, R. C., Munakata, Y., Frank, M. J., Hazy, T. E., & Contributors (2012). Computational Cognitive Neuroscience. Wiki Book, 1st Edition, URL: <http://ccnbook.colorado.edu>.
- Pelli, D. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. Spatial Vision, 10(4), 437–442.
- Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. F. (1989). Spherical splines for scalp potential and current density mapping. Electroencephalography and Clinical Neurophysiology, 72(2), 184–187.

- Rockland, K. S., & Pandya, D. N. (1979). Laminar origins and terminations of cortical connections of the occipital lobe in the rhesus monkey. Brain Research, 179(1), 3–20.
- Rohenkohl, G., & Nobre, A. C. (2011). Alpha oscillations related to anticipatory attention follow temporal expectations. The Journal of Neuroscience, 31(40), 14076–14084.
- Schroeder, C. E., & Lakatos, P. (2009). Low-frequency neuronal oscillations as instruments of sensory selection. Trends in Neurosciences, 32(1), 9–18.
- Serre, T., Oliva, A., & Poggio, T. (2007). A feedforward architecture accounts for rapid categorization. Proceedings of the National Academy of Sciences of the United States of America, 104(15), 6424–6429.
- Servan-Schreiber, D., Cleeremans, A., & McClelland, J. L. (1991). Graded state machines: The representation of temporal contingencies in simple recurrent networks. Machine Learning, 7(2–3), 161–193.
- Silva, L. R., Amitai, Y., & Connors, B. W. (1991). Intrinsic oscillations of neocortex generated by layer 5 pyramidal neurons. Science, 251(4992), 432–435.
- Sinha, P., & Poggio, T. (1996). Role of learning in three-dimensional form perception. Nature, 384(6608), 460–463.
- Spaak, E., Bonnefond, M., Maier, A., Leopold, D. A., & Jensen, O. (2012). Layer-specific entrainment of gamma-band neural activity by the alpha rhythm in monkey visual cortex. Current Biology, 22(24), 2313–2318.
- Stefanics, G., Hangya, B., Herndi, I., Winkler, I., Lakatos, P., & Ulbert, I. (2010). Phase entrainment of human delta oscillations can mediate the effects of expectation on reaction speed. The Journal of Neuroscience, 30(41), 13578–13585.
- Thomson, A. M. (2010). Neocortical layer 6, a review. Frontiers in Neuroanatomy, 4.
- Thomson, A. M., & Lamy, C. (2007). Functional maps of neocortical local circuitry. Frontiers in Neuroscience, 1(1), 19–42.
- VanRullen, R., Busch, N. A., Drewes, J., & Dubois, J. (2011). Ongoing EEG phase as a trial-by-trial predictor of perceptual and attentional variability. Frontiers in Psychology, 2.
- Will, U., & Berg, E. (2007). Brain wave synchronization and entrainment to periodic acoustic stimuli. Neuroscience letters, 424(1), 55–60.

Chapter 4

4.1 Introduction

TODO

4.2 Methods

4.2.1 Participants

A total of NN students from the University of Colorado Boulder participated in the experiment (ages NN-NN, mean=NN.NN years; NN male, NN female). All participants reported normal or corrected-to-normal vision and received course credit as compensation for their participation. Informed consent was obtained from each participant prior to the experiment in accordance with Institutional Review Board policy at the University of Colorado.

4.2.2 Stimuli

Novel “paper clip” objects (see REF PLEAST) were used as stimuli. A total of eight objects were created using the same method as in Experiment PLEAST. Four of the objects were target objects from Experiment PLEAST.

4.2.3 Procedure

References

- Armstrong-James, M., Fox, K., & Das-Gupta, A. (1992). Flow of excitation within rat barrel cortex on striking a single vibrissa. *Journal of Neurophysiology*, *68*(4), 1345–1358.
- Balas, B. J., & Sinha, P. (2009). The role of sequence order in determining view canonicity for novel wire-frame objects. *Attention, Perception & Psychophysics*, *71*(4), 712–723.
- Brainard, D. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436.
- Buffalo, E. A., Fries, P., Landman, R., Buschman, T. J., & Desimone, R. (2011). Laminar differences in gamma and alpha coherence in the ventral stream. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(27), 11262–11267.
- Bulthoff, H. H., & Edelman, S. (1992). Psychophysical support for a two-dimensional view interpolation theory of object recognition. *Proceedings of the National Academy of Sciences of the United States of America*, *89*(1), 60–64.
- Busch, N. A., Dubois, J., & VanRullen, R. (2009). The phase of ongoing EEG oscillations predicts visual perception. *The Journal of Neuroscience*, *29*(24), 7869–7876.
- Buxhoeveden, D. P., & Casanova, M. F. (2002). The minicolumn hypothesis in neuroscience. *Brain*, *125*(Pt 5), 935–951.
- Connors, B. W., Gutnick, M. J., & Prince, D. A. (1982). Electrophysiological properties of neocortical neurons in vitro. *Journal of Neurophysiology*, *48*(6), 1302–1320.
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*(1), 9–21.
- Doherty, J. R., Rao, A., Mesulam, M. M., & Nobre, A. C. (2005). Synergistic effect of combined temporal and spatial expectations on visual attention. *The Journal of Neuroscience*, *25*(36), 8259–8266.
- Douglas, R. J., & Martin, K. A. C. (2004). Neuronal circuits of the neocortex. *Annual Review of Neuroscience*, *27*, 419–451.
- Edelman, S., & Bulthoff, H. H. (1992). Orientation dependence in the recognition of familiar and novel views of three-dimensional objects. *Vision Research*, *32*(12), 2385–2400.
- Elman, J. L. (1990). Finding structure in time. *Cognitive Science*, *14*(2), 179–211.
- Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, *1*(1), 1–47.
- Foldiak, P. (1991). Learning invariance from transformation sequences. *Neural Computation*, *3*(2), 194–200.
- Franceschetti, S., Guatteo, E., Panzica, F., Sancini, G., Wanke, E., & Avanzini, G. (1995). Ionic mechanisms underlying burst firing in pyramidal neurons: Intracellular study in rat sensorimotor cortex. *Brain Research*, *696*(1–2), 127–139.

- Hirsch, J. A., & Martinez, L. M. (2006). Laminar processing in the visual cortical column. Current Opinion in Neurobiology, 16(4), 377–384.
- Horton, J. C., & Adams, D. L. (2005). The cortical column: A structure without a function. Philosophical Transactions of the Royal Society B, 360(1456), 837–862.
- Hubel, D. H., & Wiesel, T. N. (1977). Ferrier lecture. Functional architecture of macaque monkey visual cortex. Proceedings of the Royal Society B, 198(1130), 1–59.
- Hughes, S. W., Lorincz, M., Cope, D. W., Blethyn, K. L., Kekesi, K. A., Parri, H. R., Juhasz, G., & Crunelli, V. (2004). Synchronized oscillations at alpha and theta frequencies in the lateral geniculate nucleus. Neuron, 42(2), 253–268.
- Jones, E. G. (2000). Microcolumns in the cerebral cortex. Proceedings of the National Academy of Sciences of the United States of America, 97(10), 5019–5021.
- Lakatos, P., Karmos, G., Mehta, A. D., Ulbert, I., & Schroeder, C. E. (2008). Entrainment of neuronal oscillations as a mechanism of attentional selection. Science, 320(5872), 110–113.
- Logothetis, N., Pauls, J., Bulthoff, H., & Poggio, T. (1994). View-dependent object recognition by monkeys. Current Biology, 4(5), 401–414.
- Logothetis, N. K., Pauls, J., & Poggio, T. (1995). Shape representation in the inferior temporal cortex of monkeys. Current Biology, 5(5), 552–563.
- Lopes da Silva, F. (1991). Neural mechanisms underlying brain waves: from neural membranes to networks. Electroencephalography and Clinical Neurophysiology, 79(2), 81–93.
- Lorincz, M. L., Crunelli, V., & Hughes, S. W. (2008). Cellular dynamics of cholinergically induced alpha (8–13 Hz) rhythms in sensory thalamic nuclei in vitro. The Journal of Neuroscience, 28(3), 660–671.
- Lorincz, M. L., Kekesi, K. A., Juhasz, G., Crunelli, V., & Hughes, S. W. (2009). Temporal framing of thalamic relay-mode firing by phasic inhibition during the alpha rhythm. Neuron, 63(5), 683–696.
- Luczak, A., Bartho, P., & Harris, K. D. (2013). Gating of sensory input by spontaneous cortical activity. The Journal of Neuroscience, 33(4), 1684–1695.
- Lumer, E., Edelman, G., & Tononi, G. (1997). Neural dynamics in a model of the thalamocortical system. I. Layers, loops and the emergence of fast synchronous rhythms. Cerebral Cortex, 7(3), 207–227.
- Masquelier, T., & Thorpe, S. J. (2007). Unsupervised learning of visual features through spike timing dependent plasticity. PLoS Computational Biology, 3(2), 247–257.
- Mathewson, K. E., Lleras, A., Beck, D. M., Fabiani, M., Ro, T., & Gratton, G. (2011). Pulsed out of awareness: EEG alpha oscillations represent a pulsed-inhibition of ongoing cortical processing. Frontiers in Psychology, 2.
- Mountcastle, V. B. (1997). The columnar organization of the neocortex. Brain, 120(Pt 4), 701–722.
- Mutch, J., & Lowe, D. (2008). Object class recognition and localization using sparse features with limited receptive fields. International Journal of Computer Vision, 80(1), 45–57.

- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. Computational Intelligence and Neuroscience, 2011.
- O'Reilly, R. C., & Munakata, Y. (2000). Computational Explorations in Cognitive Neuroscience: Understanding the Mind by Simulating the Brain. Cambridge, MA: The MIT Press.
- O'Reilly, R. C., Munakata, Y., Frank, M. J., Hazy, T. E., & Contributors (2012). Computational Cognitive Neuroscience. Wiki Book, 1st Edition, URL: <http://ccnbook.colorado.edu>.
- Pelli, D. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. Spatial Vision, 10(4), 437–442.
- Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. F. (1989). Spherical splines for scalp potential and current density mapping. Electroencephalography and Clinical Neurophysiology, 72(2), 184–187.
- Rockland, K. S., & Pandya, D. N. (1979). Laminar origins and terminations of cortical connections of the occipital lobe in the rhesus monkey. Brain Research, 179(1), 3–20.
- Rohenkohl, G., & Nobre, A. C. (2011). Alpha oscillations related to anticipatory attention follow temporal expectations. The Journal of Neuroscience, 31(40), 14076–14084.
- Schroeder, C. E., & Lakatos, P. (2009). Low-frequency neuronal oscillations as instruments of sensory selection. Trends in Neurosciences, 32(1), 9–18.
- Serre, T., Oliva, A., & Poggio, T. (2007). A feedforward architecture accounts for rapid categorization. Proceedings of the National Academy of Sciences of the United States of America, 104(15), 6424–6429.
- Servan-Schreiber, D., Cleeremans, A., & McClelland, J. L. (1991). Graded state machines: The representation of temporal contingencies in simple recurrent networks. Machine Learning, 7(2–3), 161–193.
- Silva, L. R., Amitai, Y., & Connors, B. W. (1991). Intrinsic oscillations of neocortex generated by layer 5 pyramidal neurons. Science, 251(4992), 432–435.
- Sinha, P., & Poggio, T. (1996). Role of learning in three-dimensional form perception. Nature, 384(6608), 460–463.
- Spaak, E., Bonnefond, M., Maier, A., Leopold, D. A., & Jensen, O. (2012). Layer-specific entrainment of gamma-band neural activity by the alpha rhythm in monkey visual cortex. Current Biology, 22(24), 2313–2318.
- Stefanics, G., Hangya, B., Herndi, I., Winkler, I., Lakatos, P., & Ulbert, I. (2010). Phase entrainment of human delta oscillations can mediate the effects of expectation on reaction speed. The Journal of Neuroscience, 30(41), 13578–13585.
- Thomson, A. M. (2010). Neocortical layer 6, a review. Frontiers in Neuroanatomy, 4.
- Thomson, A. M., & Lamy, C. (2007). Functional maps of neocortical local circuitry. Frontiers in Neuroscience, 1(1), 19–42.

- VanRullen, R., Busch, N. A., Drewes, J., & Dubois, J. (2011). Ongoing EEG phase as a trial-by-trial predictor of perceptual and attentional variability. Frontiers in Psychology, 2.
- Will, U., & Berg, E. (2007). Brain wave synchronization and entrainment to periodic acoustic stimuli. Neuroscience letters, 424(1), 55–60.

References

- Armstrong-James, M., Fox, K., & Das-Gupta, A. (1992). Flow of excitation within rat barrel cortex on striking a single vibrissa. Journal of Neurophysiology, 68(4), 1345–1358.
- Balas, B. J., & Sinha, P. (2009). The role of sequence order in determining view canonicity for novel wire-frame objects. Attention, Perception & Psychophysics, 71(4), 712–723.
- Brainard, D. (1997). The Psychophysics Toolbox. Spatial Vision, 10(4), 433–436.
- Buffalo, E. A., Fries, P., Landman, R., Buschman, T. J., & Desimone, R. (2011). Laminar differences in gamma and alpha coherence in the ventral stream. Proceedings of the National Academy of Sciences of the United States of America, 108(27), 11262–11267.
- Bulthoff, H. H., & Edelman, S. (1992). Psychophysical support for a two-dimensional view interpolation theory of object recognition. Proceedings of the National Academy of Sciences of the United States of America, 89(1), 60–64.
- Busch, N. A., Dubois, J., & VanRullen, R. (2009). The phase of ongoing EEG oscillations predicts visual perception. The Journal of Neuroscience, 29(24), 7869–7876.
- Buxhoeveden, D. P., & Casanova, M. F. (2002). The minicolumn hypothesis in neuroscience. Brain, 125(Pt 5), 935–951.
- Connors, B. W., Gutnick, M. J., & Prince, D. A. (1982). Electrophysiological properties of neocortical neurons in vitro. Journal of Neurophysiology, 48(6), 1302–1320.
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. Journal of Neuroscience Methods, 134(1), 9–21.
- Doherty, J. R., Rao, A., Mesulam, M. M., & Nobre, A. C. (2005). Synergistic effect of combined temporal and spatial expectations on visual attention. The Journal of Neuroscience, 25(36), 8259–8266.
- Douglas, R. J., & Martin, K. A. C. (2004). Neuronal circuits of the neocortex. Annual Review of Neuroscience, 27, 419–451.
- Edelman, S., & Bulthoff, H. H. (1992). Orientation dependence in the recognition of familiar and novel views of three-dimensional objects. Vision Research, 32(12), 2385–2400.
- Elman, J. L. (1990). Finding structure in time. Cognitive Science, 14(2), 179–211.
- Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. Cerebral Cortex, 1(1), 1–47.

- Foldiak, P. (1991). Learning invariance from transformation sequences. Neural Computation, 3(2), 194–200.
- Franceschetti, S., Guatteo, E., Panzica, F., Sancini, G., Wanke, E., & Avanzini, G. (1995). Ionic mechanisms underlying burst firing in pyramidal neurons: Intracellular study in rat sensorimotor cortex. Brain Research, 696(1–2), 127–139.
- Hirsch, J. A., & Martinez, L. M. (2006). Laminar processing in the visual cortical column. Current Opinion in Neurobiology, 16(4), 377–384.
- Horton, J. C., & Adams, D. L. (2005). The cortical column: A structure without a function. Philosophical Transactions of the Royal Society B, 360(1456), 837–862.
- Hubel, D. H., & Wiesel, T. N. (1977). Ferrier lecture. Functional architecture of macaque monkey visual cortex. Proceedings of the Royal Society B, 198(1130), 1–59.
- Hughes, S. W., Lorincz, M., Cope, D. W., Blethyn, K. L., Kekesi, K. A., Parri, H. R., Juhasz, G., & Crunelli, V. (2004). Synchronized oscillations at alpha and theta frequencies in the lateral geniculate nucleus. Neuron, 42(2), 253–268.
- Jones, E. G. (2000). Microcolumns in the cerebral cortex. Proceedings of the National Academy of Sciences of the United States of America, 97(10), 5019–5021.
- Lakatos, P., Karmos, G., Mehta, A. D., Ulbert, I., & Schroeder, C. E. (2008). Entrainment of neuronal oscillations as a mechanism of attentional selection. Science, 320(5872), 110–113.
- Logothetis, N., Pauls, J., Bulthoff, H., & Poggio, T. (1994). View-dependent object recognition by monkeys. Current Biology, 4(5), 401–414.
- Logothetis, N. K., Pauls, J., & Poggio, T. (1995). Shape representation in the inferior temporal cortex of monkeys. Current Biology, 5(5), 552–563.
- Lopes da Silva, F. (1991). Neural mechanisms underlying brain waves: from neural membranes to networks. Electroencephalography and Clinical Neurophysiology, 79(2), 81–93.
- Lorincz, M. L., Crunelli, V., & Hughes, S. W. (2008). Cellular dynamics of cholinergically induced alpha (8–13 Hz) rhythms in sensory thalamic nuclei in vitro. The Journal of Neuroscience, 28(3), 660–671.
- Lorincz, M. L., Kekesi, K. A., Juhasz, G., Crunelli, V., & Hughes, S. W. (2009). Temporal framing of thalamic relay-mode firing by phasic inhibition during the alpha rhythm. Neuron, 63(5), 683–696.
- Luczak, A., Bartho, P., & Harris, K. D. (2013). Gating of sensory input by spontaneous cortical activity. The Journal of Neuroscience, 33(4), 1684–1695.
- Lumer, E., Edelman, G., & Tononi, G. (1997). Neural dynamics in a model of the thalamocortical system. I. Layers, loops and the emergence of fast synchronous rhythms. Cerebral Cortex, 7(3), 207–227.
- Masquelier, T., & Thorpe, S. J. (2007). Unsupervised learning of visual features through spike timing dependent plasticity. PLoS Computational Biology, 3(2), 247–257.

- Mathewson, K. E., Lleras, A., Beck, D. M., Fabiani, M., Ro, T., & Gratton, G. (2011). Pulsed out of awareness: EEG alpha oscillations represent a pulsed-inhibition of ongoing cortical processing. Frontiers in Psychology, 2.
- Mountcastle, V. B. (1997). The columnar organization of the neocortex. Brain, 120(Pt 4), 701–722.
- Mutch, J., & Lowe, D. (2008). Object class recognition and localization using sparse features with limited receptive fields. International Journal of Computer Vision, 80(1), 45–57.
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. Computational Intelligence and Neuroscience, 2011.
- O'Reilly, R. C., & Munakata, Y. (2000). Computational Explorations in Cognitive Neuroscience: Understanding the Mind by Simulating the Brain. Cambridge, MA: The MIT Press.
- O'Reilly, R. C., Munakata, Y., Frank, M. J., Hazy, T. E., & Contributors (2012). Computational Cognitive Neuroscience. Wiki Book, 1st Edition, URL: <http://ccnbook.colorado.edu>.
- Pelli, D. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. Spatial Vision, 10(4), 437–442.
- Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. F. (1989). Spherical splines for scalp potential and current density mapping. Electroencephalography and Clinical Neurophysiology, 72(2), 184–187.
- Rockland, K. S., & Pandya, D. N. (1979). Laminar origins and terminations of cortical connections of the occipital lobe in the rhesus monkey. Brain Research, 179(1), 3–20.
- Rohenkohl, G., & Nobre, A. C. (2011). Alpha oscillations related to anticipatory attention follow temporal expectations. The Journal of Neuroscience, 31(40), 14076–14084.
- Schroeder, C. E., & Lakatos, P. (2009). Low-frequency neuronal oscillations as instruments of sensory selection. Trends in Neurosciences, 32(1), 9–18.
- Serre, T., Oliva, A., & Poggio, T. (2007). A feedforward architecture accounts for rapid categorization. Proceedings of the National Academy of Sciences of the United States of America, 104(15), 6424–6429.
- Servan-Schreiber, D., Cleeremans, A., & McClelland, J. L. (1991). Graded state machines: The representation of temporal contingencies in simple recurrent networks. Machine Learning, 7(2–3), 161–193.
- Silva, L. R., Amitai, Y., & Connors, B. W. (1991). Intrinsic oscillations of neocortex generated by layer 5 pyramidal neurons. Science, 251(4992), 432–435.
- Sinha, P., & Poggio, T. (1996). Role of learning in three-dimensional form perception. Nature, 384(6608), 460–463.
- Spaak, E., Bonnefond, M., Maier, A., Leopold, D. A., & Jensen, O. (2012). Layer-specific entrainment of gamma-band neural activity by the alpha rhythm in monkey visual cortex. Current Biology, 22(24), 2313–2318.

- Stefanics, G., Hangya, B., Herndi, I., Winkler, I., Lakatos, P., & Ulbert, I. (2010). Phase entrainment of human delta oscillations can mediate the effects of expectation on reaction speed. The Journal of Neuroscience, 30(41), 13578–13585.
- Thomson, A. M. (2010). Neocortical layer 6, a review. Frontiers in Neuroanatomy, 4.
- Thomson, A. M., & Lamy, C. (2007). Functional maps of neocortical local circuitry. Frontiers in Neuroscience, 1(1), 19–42.
- VanRullen, R., Busch, N. A., Drewes, J., & Dubois, J. (2011). Ongoing EEG phase as a trial-by-trial predictor of perceptual and attentional variability. Frontiers in Psychology, 2.
- Will, U., & Berg, E. (2007). Brain wave synchronization and entrainment to periodic acoustic stimuli. Neuroscience letters, 424(1), 55–60.