Neural model for stimulus-specific adaptation of neurons in area IT

Martin Giese*, Pradeep Kuravi, and Rufin Vogels****

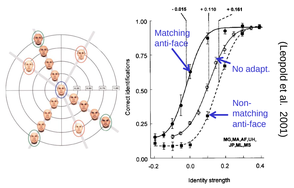
* Section for Computational Sensomotorics, Department of Cognitive Neurology, Hertie Institute for Clinical Brain Research & Centre for Integrative Neuroscience, University Clinic Tübingen, Germany

**Laboratorium voor Neuro- en Psychofysiologie, KU Leuven, Belgium

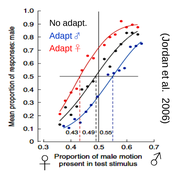
Introduction

- Shape and action perception are associated with high-level adaptation effects.
- Repeated presentation of same stimulus results in after-effects where alternative percepts are preferentially perceived (Leopold et al. 2001; Jordan et al. 2006; Troje al. 2006).
- Adaptation effects have been extensively exploited in fMRI repetition suppression paradigms (e.g. Grill-Spector et a. 1999; Jastorff et al. 2009; Grossman et al., 2010).
- Adaptation of single cell responses in area IT for repetition of shape stimuli (decay of activation by 10-20%) (e.g. Sawamura et al. 2006; de Baene & Vogels, 2011).
- Ambiguous fMRI adaptation results for repetition suppression for action recognition for human mirror neuron system (e.g. Dinstein et al. 2008; Lingnau & Caramazza, 2009).
- No or weak adaptation effects observed in single-cell studies on mirror neurons in area F5 (premotor cortex) and STS neurons (Caggiano et al.2013; Kilner et al. 2014; Kuravi et al. 2016).
- Detailed physiological data available for adaptation effects in area IT that helps to narrow down possible neural mechanisms of adaptation for shape recognition.
- Much less data available for adaptation in action-selective neurons.

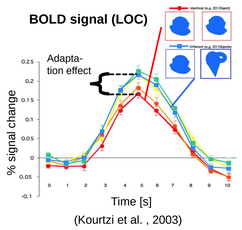
High-level after-effects: faces



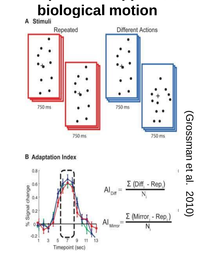
High-level after effect: biological motion



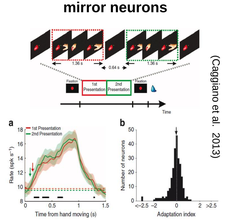
fMRI repetition suppression: shape recognition



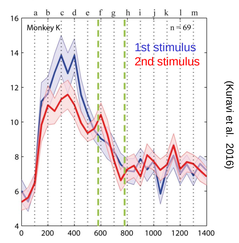
fMRI repetition suppression: biological motion



Adaptation for actions in F5 mirror neurons



Adaptation for actions in STS



Questions / goals

- **Development of a neural model that accounts for critical experiments on the adaptation effects for shape-selective neurons in area IT.**
- **Identification of critical computational mechanisms.**
- **Investigation of possible reasons why adaptation in action-selective neurons might be so much weaker.**

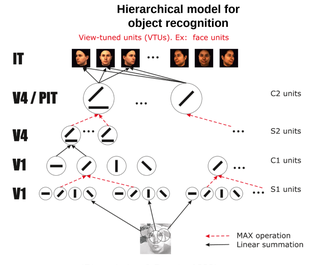
Model

- Hierarchical physiologically-inspired model for object (or action) recognition (Fukushima, 1980; Riesenhuber & Poggio, 1999; Giese & Poggio, 2003); focus on recognition layer.
- Lateral interaction between shape-selective neurons ; results in mutual inhibition or sequence selectivity (Wang et al. 2000; Giese & Poggio, 2003).
- Modelled by two-dimensional neural field (Amari, 1977):

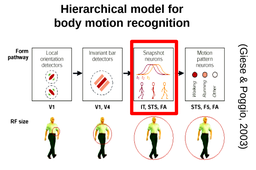
$$\tau \frac{\mathrm{d}}{\mathrm{d}t} u(\mathbf{x},t) = -u(\mathbf{x},t) + \int w(\mathbf{x}-\mathbf{x}') H(u(\mathbf{x}',t))\,\mathrm{d}\mathbf{x}' - h + \underbrace{\int m(\mathbf{x},\mathbf{y},t) v(\mathbf{y},t))\,\mathrm{d}\mathbf{y}}_{s(\mathbf{x},t)} - F(a(\mathbf{x},t)) + k_c c(\mathbf{x},t)$$

$\mathbf{x} = [\phi, \theta]$
θ: shape no.
ϕ: view
H: step threshold

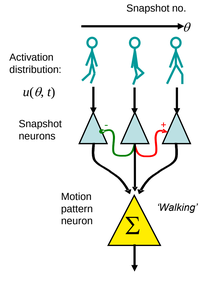
Hierarchical model for object recognition



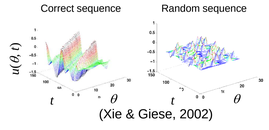
Hierarchical model for body motion recognition



Circuit for sequence selectivity



Sequence-selective neural field



- Extension by four necessary **adaptation mechanisms**:

a) ***Firing rate (FR) fatigue**:* Spike rate-dependent adaptation:

$$\tau_a \frac{\mathrm{d}}{\mathrm{d}t} a(\mathbf{x},t) = -a(\mathbf{x},t) + H(u(\mathbf{x},t)) \qquad a\text{: adaptation level}$$

Saturating function $F(a)$ limits the amount of adaptation.

b) ***Input fatigue (IF):*** Gain of synaptic inputs of field neurons adapts dependent on negative flanks of input signal $v(x, t)$:

$$\tau_b \frac{\mathrm{d}}{\mathrm{d}t} b(\mathbf{y},t) = -b(\mathbf{y},t) + \left[-\frac{\partial}{\partial t} v(\mathbf{y},t))\right]_+ \qquad b\text{: adaptation level}$$

$$m(\mathbf{x},\mathbf{y},t) = m(\mathbf{x},\mathbf{y}) \cdot \left(\frac{1}{b(\mathbf{y},t)/c_b + 1}\right)$$

(Multiplicative gain control of synaptic gain m)

c) *Spike rate adaptation:* required to model shape of the PSTH of neurons in area IT; depends on pos. flanks of effective input:

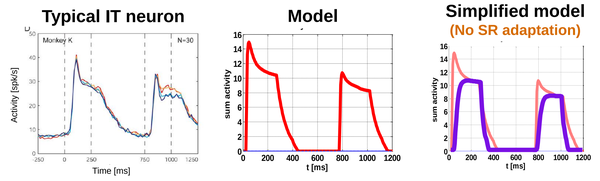
$$\tau_c \frac{\mathrm{d}}{\mathrm{d}t} c(\mathbf{x},t) = -c(\mathbf{c},t) + \left[\frac{\partial}{\partial t} s(\mathbf{x},t))\right]_+$$

c: adaptation level
s: effective input signal

- All components are required for the detailed reproduction of adaptation effects of neurons in area IT (see Results).

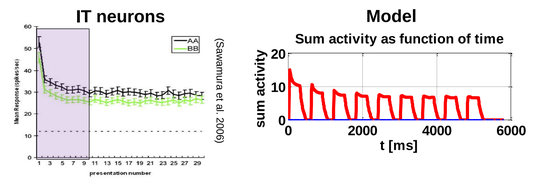
Simulation results

Response: single stimulus repetition



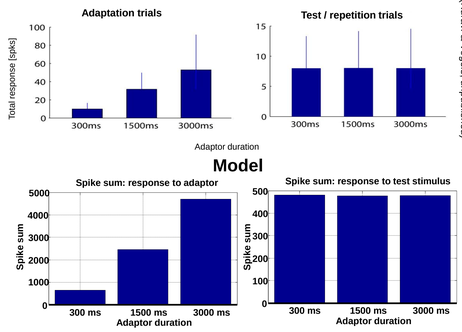
- Reproduction of the shape of the PSTH of typical IT neurons.
- The fast overshoot after stimulus onset requires SR adaptation; otherwise, signal shape not reproduced.
- No influence of this model component on accuracy of modelling of the other results.

Responses: many stimulus repetitions

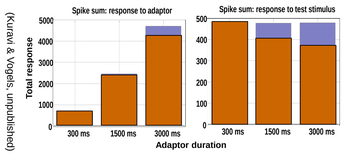


- Response decays until after about 9 stimulus repetitions.
- Constraint for time scale of major adaptation mechanism.
- Can be reproduced with many different models; no strong constraint for computational mechanisms.

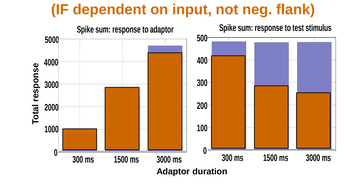
Spike sum for adaptor and test stimulus (IT neurons)



Simplified models
(No saturation of FR fatigue)

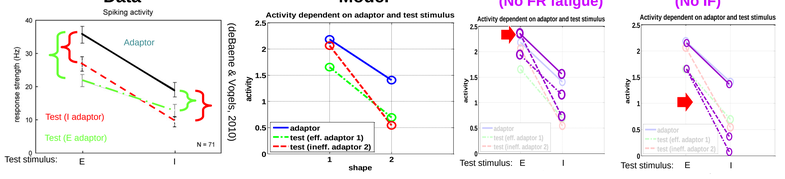


(IF dependent on input, not neg. flank)



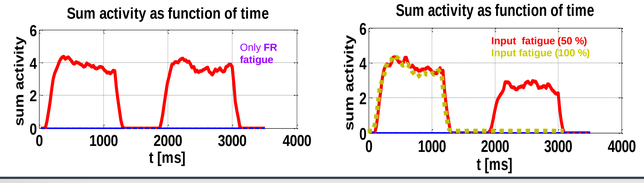
- IT neuron activity during testing is **in**dependent of the duration of the adaptor stimulus.
- Spike sum during adaptor depends on adaptor duration; spike sum during test stimulus (200 ms) is not dependent on adaptor duration.
- Highly constraining result for the modelling; not reproduced by many standard adaptation models.
- Model reproduces effect by bounding firing rate adaptation through nonlinearity $F(a)$, and assuming that IF process that depends on negative stimulus flank.
- Both mechanisms necessary; models without this fail to reproduce data.

Adaptation to effective and ineffective stimuli



- Adaptation and testing with effective and ineffective stimuli.
- **Interaction**: Ineffective adaptors lead to stronger adaptation effects for ineffective test stimulus than effective adaptor.
- This effect cannot be reproduced with models without IF adaptation.
- Full reproduction of data requires both, IF and FR fatigue.

Prediction of adaptation effects for action-selective neurons



- To test reasons for weak adaptation in action-selective neurons we transferred adaptation mechanisms from IT model to action recognition model.
- Model with only FR fatigue reproduces the weak exp. observed adaptation effects.
- Model even with weak with IF leads to strong adaptation effetcs opposite to experimental results.

Conclusions

- Set of highly constraining experiments on adaptation of neurons in area IT reproduced by a single physiologically-inspired neural model.
- Both, **firing rate fatigue** and **input fatigue** are necessary to account for results.
- Model reproduces the independence of adaptation effects from adaptor duration (critical: saturation of adaptation, dependence of IF on falling input flanks ⇒ rebound bursting activity?).
- Transfer to action recognition model reproduces weak adaptation effects only for model without input fatigue.
  ➔ Different dominance of adaptation mechanisms for action and shape-selective areas?

References

Amari S. (1977) Dynamics of pattern formation in lateral inhibition type neural fields. *Biol Cyb*, 27:77–87.
Barraclough N.E., Keith R.H., Xiao D., Oram M.W., Perrett D.I.,(2009) Visual adaptation to goal-directed hand actions. *J Cogn Neurosci*. 21(9), 1806-1820.
de Baene W., Vogels R.(2010). Effects of adaptation on the stimulus selectivity of macaque inferior temporal spiking activity and local field potentials. *Cer Cortex 20(9)*, 2145-2165.
Caggiano V, Pomper JK, Fleischer F, Fogassi L, Giese M, Thier P. (2013) Mirror neurons in monkey area F5 do not adapt to the observation of repeated actions. *Nat Commun*. 4:1433.
Dinstein I. (2008) Human cortex: reflections of mirror neurons. *Curr Biol*.18(20):R956-9.
Fukushima K. (1980) Neocognitron: a self organizing neural network model for a mechanism of pattern recognition unaffected by shift in position. *Biol Cybern*. 36(4):193-202.
Giese M.A., Poggio T. (2003). Neural mechanisms for the recognition of biological movements and action. *Nat Rev Neurosci*, *4*, 179-192.
Grill-Spector K1, Kushnir T, Edelman S, Avidan G, Itzchak Y, Malach R. (1999) Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron* 24(1):187-203.
Grossman E.D., Jardine N.L., Pyles J.A. (2010) fMR-Adaptation Reveals Invariant Coding of Biological Motion on the Human STS. *Front Hum Neurosci*. 23;4:15.
Jastorff J., Kourtzi Z., Giese M.A. (2009) Visual learning shapes the processing of complex movement stimuli in the human brain.*J Neurosci*. 29(44):14026-38.
Jordan H., Fallah M., Stoner G.R. (2006) Adaptation of gender derived from biological motion. Nat Neurosci. 9(6):738-9.
Kaliukhovich D.A, Vogels R. (2011) Stimulus repetition probability does not affect repetition suppression in macaque inferior temporal cortex. *Cereb Cortex*. 21(7):1547-58.
Kilner J.M., Kraskov A., Lemon R.N. (2014) Do monkey F5 mirror neurons show changes in firing rate during repeated observation of natural actions? *J Neurophysiol*. 111(6):1214-26.
Kuravi P, Caggiano V, Giese M., Vogels R. (2016) Repetition suppression for visual actions in the macaque superior temporal sulcus. J Neurophysiol. 115(3):1324-37.
Leopold, D ., O'Toole AJ, Vetter T, Blanz V. (2001) Prototype-referenced shape encoding revealed by high-level aftereffects. *Nat Neurosci*. 4(1):89-94.
Lingnau A., Gesierich B., Caramazza A. (2009) Asymmetric fMRI adaptation reveals no evidence for mirror neurons in humans. *Proc Natl Acad Sci U S A*. 106(24):9925-30.
Riesenhuber M, Poggio T. (1999) Hierarchical models of object recognition in cortex. *Nat Neurosci*. 2(11):1019-25.
Sawamura H., Orban G.A., Vogels R. (2006) Selectivity of neuronal adaptation does not match response selectivity: a single-cell study of the FMRI adaptation paradigm. *Neuron* 49(2):307-18.
Singer J.M., Sheinberg D.L.(2010) Temporal cortex neurons encode articulated actions as slow.sequences of integrated poses. *J Neurosci*. 30(8),3133-3145.
Troje NF, Sadr J, Geyer H, Nakayama K. (2006) Adaptation aftereffects in the perception of gender from biological motion. *J Vis*. 6(8):850-7.
Wang, Y., Fujita, I., Murayama, Y. (2000) Neuronal mechanisms of selectivity for object features revealed by blocking inhibition in infrotemporal cortex. *Nat. Neurosc*. 3(8), 807-813.
Xie X., Giese M. (2002). Nonlinear dynamics of direction-selective recurrent neural media. *Phys Rev E Stat Nonlin Soft Matter Phys*. 65 (5 Pt 1):051904 (2002)., 65(5, Pt. 1).
Zhang K. (1996). Representation of spatial orientation by the intrinsic dynamics of the head-direction cell ensemble: A theory. *J Neurosci* 16: 2112-2126.

Support

This work was supported by the EU projects ABC: PEOPLE-2011-ITN PITN-GA-011-290011; HBP: FP7-ICT-2013-FET-F/ 604102; Koroibot FP7-ICT-2013-10/ 611909, and by DFG GI 305/4-1, DFG GZ: KA 1258/15-1, and BMBF, FKZ: 01GQ1002A; CogIMon H2020 ICT-644727.