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Summary

Inferotemporal and prefrontal neurons show response suppression or enhancement with stimulus repetition.

This *stimulus-specific adaptation (SSA)* is used in neuroimaging research to discover the nature of cortical representations, and is thought to be the basis of priming and possibly skill learning.

The goal of our work is to sort through the complex literature from monkey neurophysiology in order to develop a theoretical perspective on stimulus-specific adaptation.

Many factors influence SSA, including brain area, memory span of neuron, the measure of neural activity, and stimulus task relevance.

SSA is not well understood.

How long does suppression last? When is enhancement observed? Can SSA be reconciled with expertise-linked brain activity?

Only a few computational models exist, and they are incomplete or wrong.

We offer a computational framework as an initial step in understanding the role of SSA in learning.

Stimulus-Specific Adaptation of Neural Responses: Insights From Neurophysiology and Computational Models

Michael C. Mozer
Institute of Cognitive Science and Department of Computer Science
University of Colorado

Todd Mytkowicz
Department of Computer Science
University of Colorado

Richard S. Zemel
Department of Computer Science
University of Toronto

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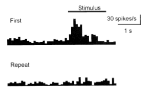
Stimulus-Specific Adaptation

A subset of neurons in temporal and prefrontal areas show response suppression or enhancement with stimulus repetition.

Terms used in literature

- Adaptive filtering (Desimone, 1992)
- Repetition suppression (Li et al., 1993)
- Repetition-sensitive adaptation (Brown & Xiang, 1998)
- Stimulus-specific adaptation (Ringo, 1996)
- Response suppression (Desimone, 1996)
- Decremental responses (Brown et al., 1987; Riches et al., 1991)



Relevance of SSA to Cognitive Neuroscience

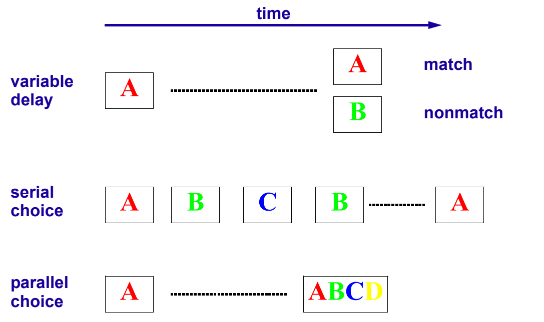
Key tool for discovering the nature of cortical representations in neuroimaging research (e.g., Grill-Spector & Malach, 2001)

If cortical representations are invariant to some dimension of a stimulus, SSA should be observed in that region even when repetitions differ along that dimension.

Thought to mediate psychological phenomenon of priming (e.g., Poldrack & Gabrieli, 2001; Wiggs & Martin, 1998)

Robustness and ubiquity of SSA suggests it may be a fundamental mechanism of learning in neocortex.

Studying SSA via Delayed Match-to-Sample Task

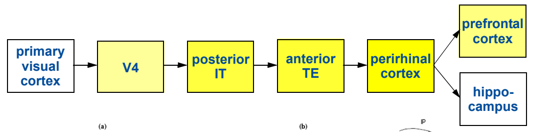


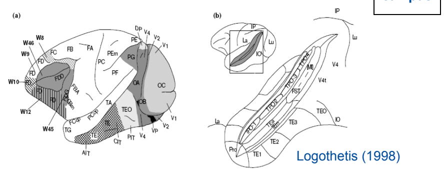
Relevant Dimensions of SSA

Spacing of repetitions

	number of intervening trials	intervening time
short	0–2	0–20 seconds
medium	10–150	.1–72 hours
long	400+	5+ days

Brain regions





Logothetis (1998)

Task relevance of stimulus

- passive viewing
- reward contingency

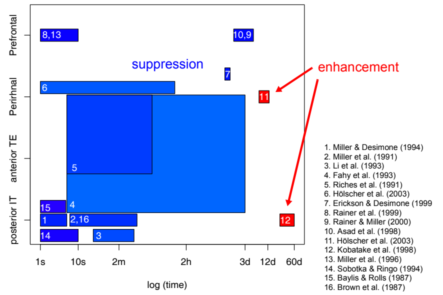
Selection criterion for cells

- all included
- visually responsive only
- only those showing some suppression to a small set of test items

Nature of adaptation

- decreased firing rate of neuron
- increased firing rate of neuron
- increased discriminability of response

Observed Suppression and Enhancement Across Time Scales and Brain Areas



1. Miller & Desimone (1994)
2. Miller et al. (1991)
3. Li et al. (1993)
4. Fahy et al. (1993)
5. Riches et al. (1991)
6. Hölscher et al. (2003)
7. Erickson & Desimone (1999
8. Rainer et al. (1999)
9. Rainer & Miller (2000)
10. Asad et al. (1998)
11. Hölscher et al. (2003)
12. Kobatake et al. (1998)
13. Miller et al. (1996)
14. Sobotka & Ringo (1994)
15. Baylis & Rolls (1987)
16. Brown et al. (1987)

Characteristics of Repetition Suppression

Item specific, not general habituation

Does not depend on behavioral significance of stimulus

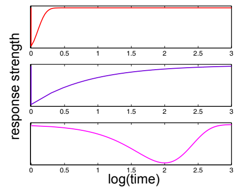
Most active neurons show greatest suppression

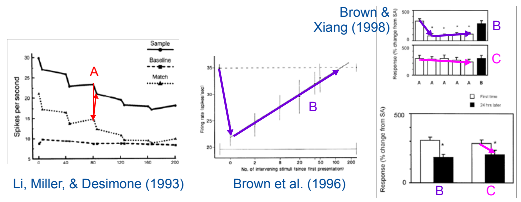
At least three distinct memory spans have been observed

(A) short term: duration 1 intervening trial

(B) medium term ("recency"): immediate suppression, lasting ~ 24 hr

(C) medium term ("familiarity"): 24 hr for suppression, lasting > 72 hr.





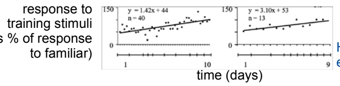
Li, Miller, & Desimone (1993) Brown et al. (1996) Brown & Xiang (1998)

Possibly a continuum of time courses rather than 3 discrete values

Further along the processing hierarchy, memory span increases.

Characteristics of Repetition Enhancement

Occurs on long time scale



Hölscher et al. (2003)

(Also, brief enhancement while item is in working memory.)

Enhancement of discriminability has been observed.

Only a few long-term studies have been conducted; all involve task-relevant stimuli.

- TE (Kobatake et al., 1998)
- perirhinal (Hölscher et al., 2003)
- prefrontal (Rainer & Miller, 2000): *no enhancement*

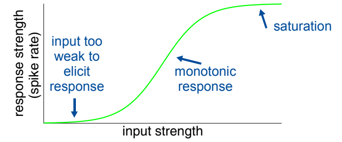
Existing Theories Are Inadequate

theory	proponent	phenomena to be explained: greatest suppression for stimuli that yield the strongest initial response	multiple memory spans for suppression	long-term repetition enhancement	different time courses of suppression and enhancement	priming	other
narrowing of tuning curves	Desimone (1996)	X	?	OK	?	?	
sharpening of neural repre-sentations	Mozer et al., (2004); Norman & O'Reilly (2001); Sohal & Hasselmo (2000)	X	?	OK	X	OK	
familiarity discrimination	Bogacz & Brown (2003)	?	OK	?	?	?	applies only to perirhinal ctx
novelty filter	Li, Miller, & Desi-mone (1993); Ringo (1996)	OK	?	?	?	X	
improved information processing via neural synchrony	Gotts (2003)	OK	X (incompatible with suppression at longer time scales)	?	?	OK	

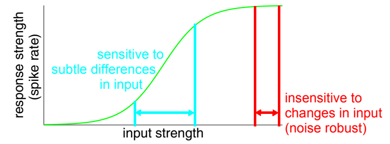
KEY:
OK = consistent with theory
? = not addressed by theory
X = inconsistent with theory

A Computational Hypothesis

A rate-coded neuron has roughly a sigmoidal response function



Trade off between two abilities:
sensitivity to subtle variation in input (necessary for learning)
noise robustness (necessary for performance)

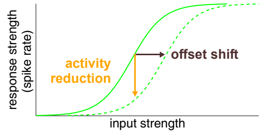


Therefore, operating characteristics of neural response should change over the course of learning.

An Interpretation of SSA

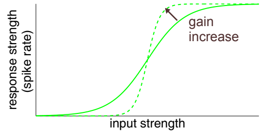
Repetition suppression can be viewed as shifting the offset of the response function.

This shift can lead to greater sensitivity.



Repetition enhancement can be viewed as increasing the gain of the response function.

This increase will lead to greater noise suppression.



How can *stimulus-dependent* adaptation of offset and gain occur?

Self-supervised error-correction learning

error = (target_spike_rate – actual_spike_rate)^2

objective	target_spike_rate
offset shift	*min*
gain increase	*max* if actual_spike_rate > θ, *min* otherwise

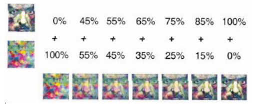
Practice and Noise Robustness (Rainer & Miller, 2000)

DMS paradigm

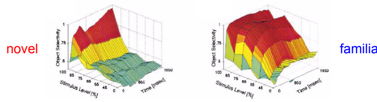
Familiar and novel stimuli

Recording from lateral PFC

Manipulated stimulus noise



Obtained noise-robust neural responses following training



Simulation using same experimental paradigm