The cultural environment as temporal context for the human brain

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The wise man has eyes in his head.
Ecclesiastes 2.14.

Last minute prologue

- “different learning can produce different connectivity and neural functioning but the same behavior”
  JP Changeux

- “the neurons get active in parts of early visual cortex where the moving stimuli WILL appear later - even prior to stimulation”
  P. Roland

- “the brain gets bored by repeated stimuli”
  Y. Hong.

- “schizophrenia as disconnection syndrome by K.Friston”
  A Chen
Whorf’s principle

- Linguistic relativity
- “How objects look to us depends on how we sort and name them.”
- Speakers of different languages/cultures perceive the world differently
  - Color and categorical perception
  - Other race effect

Temporal context

- Stimuli are not processed in isolation
- Preceding and subsequent stimulation affects neural processing
  - I. Stimuli in pairs
  - II. Stimuli in longer sequences
I. Stimuli in pairs

- Masking
  - Backward
  - Forward
- Adaptation
- Priming
- Cueing

Repetition related response attenuation

- Baylis and Rolls, 1987
  - Repetition of objects in IT
- Haenny and Schiller 1988
  - Repetition of gratings in V4
- Miller Li Desimone 1991
  - Repetition of stimuli actively held in memory in IT
<table>
<thead>
<tr>
<th>EEG/MEG</th>
<th>fMRI: fMRI adaptation</th>
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<tbody>
<tr>
<td>Henson et al, 2004</td>
<td>Grill-Spector et al, 1999</td>
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<td>Schweinberger et al, 1995</td>
<td>Henson, Shallice, Dolan, 2000</td>
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**Repetition related response attenuation**

- Repetition suppression
- Repetition attenuation
- Stimulus specific adaptation
- Adaptation
- Neural priming
- Repetition priming

- Single cell
- ERP
- Fmri-adaptation
- 945 hits in Medline
Adaptation and aftereffects

- A neuron (the entire CNS) adapts to the environment
- Marker of plasticity and learning

Aristoteles, Addams, 1834
Gibson, 1937
Köhler-Wallach, 1944

Motion Aftereffect
Tilt Aftereffect

Face aftereffects

Gradual change of the stimulus: morphing

Leopold et al 2001, Webster et al, 2004
Before adaptation

50%

Fixate ...
After adaptation

Adaptation biases perception/decisions

Category specific face adaptation

- Face adaptation
  - Leopold et al. 2001
- Reflected in the N170
- Category specific

- Kovács, et al. (2006). Cerebral Cortex
II. Stimuli in longer sequences

- Instead of a single prolonged stimulus lets use an array of stimuli:
- Successful recognition depends on the contextual probability of stimulus occurrence
- Prior experiences shape our perception
- Different experiences/environment/culture/learning/etc. lead to different contextual probabilities
- Different predictions about the world

Predictive coding can explain repetition related neural phenomena

Rao and Ballard, 1999; Friston, 2005, 2012
Who is playing in all these movies?

The fugitive
Short cuts
Boogie Nights
Jurassic Park
The big Lebowski
Hannibal
Children of men
A single man.

Repeated stimuli lower neural responses

Predictive coding

\[ Y = w_1 E_{stim,prob} + w_2 R_{stim,prob} \]

Where \( R \) is expectation in the representational units
And \( E \) is error (unexpected occurrence) in the error units

Repeated stimuli lower neural responses
Predictive coding

- Continuous matching of sensory bottom-up and predicted top-down information
- Repetition slowly makes the predicted and incoming stimulus representations more and more similar to each other.
- This attenuates the prediction error in so-called ERROR UNITS of the predictive estimator areas. Leads to reduced response for repeated stimuli
- Requires the top-down connections within a system

Rao and Ballard, 1999; Friston, 2005, 2012

A Neuronal Model of Predictive Coding Accounting for the Mismatch Negativity

- Series of the same sound (frequent) interrupted by another (rare) sound
- MISMATCH NEGATIVITY (MMN)
  - Interpreted as the consequence of predictions (Friston, 2005, Baldeweg, 2007)
  - N1 is a signal of prediction error → reduced by repetitions → disclosing MMN
If MMN is really based on top-down connections:

- Schizophrenia patients who show abnormal experience-dependent plasticity of top-down connection should show impaired MMN: cca 120 studies show that exactly (Todd et al, 2012)

BUT: MMN is automatic → top-down?

BUT: normal RS was found in FFA for faces in SZ (Williams et al, 2013 Schiz.Res):

BUT: perfectly normal predictive processes in SZ patients in another paradigm → Kovács et al (in prep)

BUT: Frequent and expected vs rare and unexpected → predictability and probability are confounded

II. Changing statistical probabilities
So far foveal stimulation. But the eyes move continuously, changing the retinal image.

Also, RS is position independent in FFA/OFA/LO (Kovács et al, 2008 NIMG).

If top-down effects (P$_{rep}$) determine RS it should be independent of the relative position of objects.

P$_{rep}$ modulation of RS is independent of the relative position in FFA/OFA/LO

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Inversion interrupts configural/holistic processing of faces

If P$_{rep}$ originates from these steps inversion should eliminate it.

Grotheer and Kovács (2014) NIMG
$P_{\text{rep}}$ effects for inverted faces

$P_{\text{rep}}$ is the function of the post-configural stages of face processing.

- Grotheer and Kovacs (2014) NIMG

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Single-cell evidences

- Macaques
- Local field potentials and spiking activity
- Inferior temporal cortex
- Repeated and alternating trials in two blocks (75% or 25% repeated trials)
- Object and fractals as stimuli

- Kaliukhovich and Vogels, 2010
No effect of repetition probability for objects/fractals

Kaliukhovich and Vogels, 2010

No effect of \( P_{\text{rep}} \) for either spiking or local field potentials

Supports simpler, bottom-up local mechanisms.

\( P_{\text{rep}} \) effects for objects

- Object stimuli of the Kaliukhovich Vogels study
- fMRIa/RS as before
- Concentrate on LO (assumed homologue area of macaque IT)
P\(_{(\text{rep})}\) effects for objects

LO:
- RS in both blocks similarly
- No effect of P\(_{\text{rep}}\)

Face stimuli in FFA

Is it due to the different variance of face / object stimuli?
LO:

- RS in both blocks similarly
- No effect of $P_{\text{rep}}$

Is the probability modulation of RS specific to faces?

- Why?
  - "Faces are (always) special"

- Experience
- Expertise
- Frequency of exposure
- Saliency, importance
**P\textsubscript{(rep)} effects for letter strings**

- Letter Form Area (LFA; Thesen et al, 2012)
- LH mid-fusiform (-45, -66, -14)
- Posterior to VWFA
- Letters of the familiar script vs. false fonts.

**P\textsubscript{(rep)} effects for letters**

- Roman letters:
  - Strong RS in LFA/LO
  - Restricted to REPEATED Block
  - Strong P\textsubscript{rep} modulation alike to faces.
- False fonts:
  - Strong RS in LFA/LO
  - No effect of P\textsubscript{rep}
- P\textsubscript{(rep)} effect depends on prior experiences

Grotheer and Kovács, 2014 J Neuosci
Expectation suppression (ES) vs. Repetition suppression (RS)

- Repetition and expectation suppression might be of different time scales (e.g., Friston, 2005)
  - RS: earlier, due to immediate repetitions
  - ES: later, due to learnt statistical regularities
- Attention affects more ES than RS (Larsson and Smith, 2012)
- Manipulate repetition and expectation orthogonally

Expectation vs. repetition suppression

<table>
<thead>
<tr>
<th></th>
<th>Repeated</th>
<th>Alternating</th>
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<tbody>
<tr>
<td>expected</td>
<td><img src="image1.png" alt="Graph" /></td>
<td><img src="image2.png" alt="Graph" /></td>
</tr>
<tr>
<td>Unexpected</td>
<td><img src="image3.png" alt="Graph" /></td>
<td><img src="image4.png" alt="Graph" /></td>
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</tbody>
</table>

- Only RS
- ES adds to RS
- RS and ES are independent
Expectation vs. repetition suppression

- Manipulate repetition and expectation orthogonally
- Gender predicts Rep/Alt

<table>
<thead>
<tr>
<th>Repetition (Rep)</th>
<th>Alternation (Alt)</th>
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<tbody>
<tr>
<td>Expected Rep</td>
<td>37.5%</td>
</tr>
<tr>
<td>Unexpected Rep</td>
<td>12.5%</td>
</tr>
<tr>
<td>Expected Alt</td>
<td>37.5%</td>
</tr>
<tr>
<td>Unexpected Alt</td>
<td>12.5%</td>
</tr>
</tbody>
</table>

FFA & OFA:
- RS
- ES
- No interaction

LO:
- RS
- NO ES
- RS precedes ES

Grotheer and Kovács, in rev
Summary

- Repetition probability effects on RS are present in humans for non-face stimuli as well
- It is present in every studied cortical area, usually higher-level
- The effect is not face or area-specific
- Learning/experience determine the predictive modulation of RS.
- ES and RS are separate phenomena

Outlook

- Whorf's principle: Linguistic relativity: Speakers of different languages perceive the world differently
  - Color and categorical perception
  - Other race effect
- Is it merely a probability issue due to different expectation/prediction processes?
- How the different contextual probabilities in different cultures determine repetition related neural phenomena?
  - Faces (and bodies) of persons
  - Letters of the familiar/unfamiliar scripts
  - Role of variability: different multicultural environments may be volatile or stable
Thank you for your attention