Recovery from adaptation to facial identity is larger for upright than inverted faces in the human occipito-temporal cortex

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Neuropsychologia. 2006, 44, 912-922

See also:

Rossion, B. & Gauthier, I. (2002). **How does the brain process upright and inverted faces?** *Behavioral and Cognitive Neuroscience Reviews*, 1, 63-75.

Yovel, G. & Kanwisher, N. (2005). **The neural basis of the behavioral face inversion effect.** *Current Biology*, 15, 1-7.

Main findings and conclusions

- The differential level of activation to upright and inverted faces in the 'FFA' is largely due to a difference in recovery from adaptation:

differences between individual faces are less well perceived when they are shown upside-down, leading to a stronger adaptation, or reduced recovery from adptation to facial identity

- This phenomenon may account for discrepancies between the results of previous fMRI studies comparing upright and inverted faces.

- The 'FFA' (and to a lesser extent the 'OFA') form the neural basis of the face inversion effect.

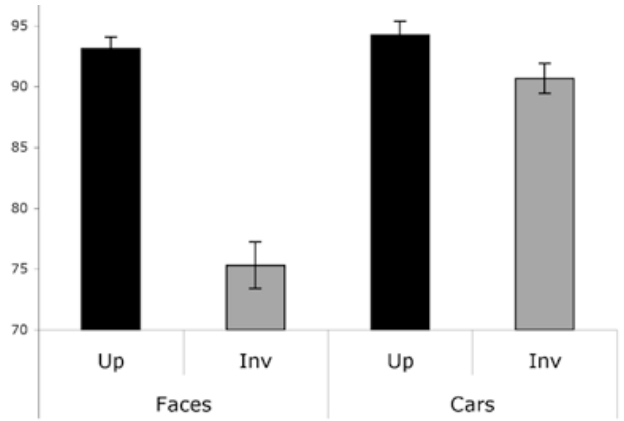
Question: how are upright and inverted faces differentially coded by populations of neurons in these regions?

Introduction

Presenting faces upside-down:

→ Massive drop of recognition or individual discrimination performance

= Much more so than for other object categories (Yin, 1969): *the face inversion effect (FIE)*



- Found for familiar and unfamiliar faces in a variety of tasks

- Inversion affects the perceptual encoding of *multiple cues*, but particularly the relationships between face parts (distances between features, ratio of the face)

Question: What is the neural basis of the drop of performance for inverted faces?

→ *Where* are upright and inverted faces coded differently in the human brain?

5 fMRI studies compared the processing of upright and inverted faces in areas responding preferentially to faces in the occipito-temporal cortex ('FFA', 'OFA', STS)

Two found a *substantial* (0.3 - 0.5% signal change) *reduction* of signal for inverted faces relative to upright faces in the 'FFA'

Kanwisher et al. (1998); Yovel & Kanwisher (2004)

Two found small but significant reduction of signal for inverted faces in the 'FFA'

Gauthier et al. (1999); Haxby et al., (1999)

One did not find differences between upright and inverted faces in the 'FFA'

Aguirre et al., (1999) (event-related fMRI)

For a review, see Rossion & Gauthier, 2002

Why these discrepancies between studies?

Our hypothesis:

Because differences between individual faces are less well perceived when they are shown upside-down, presenting these faces consecutively in a block would lead to less recovery from adaptation than for upright faces

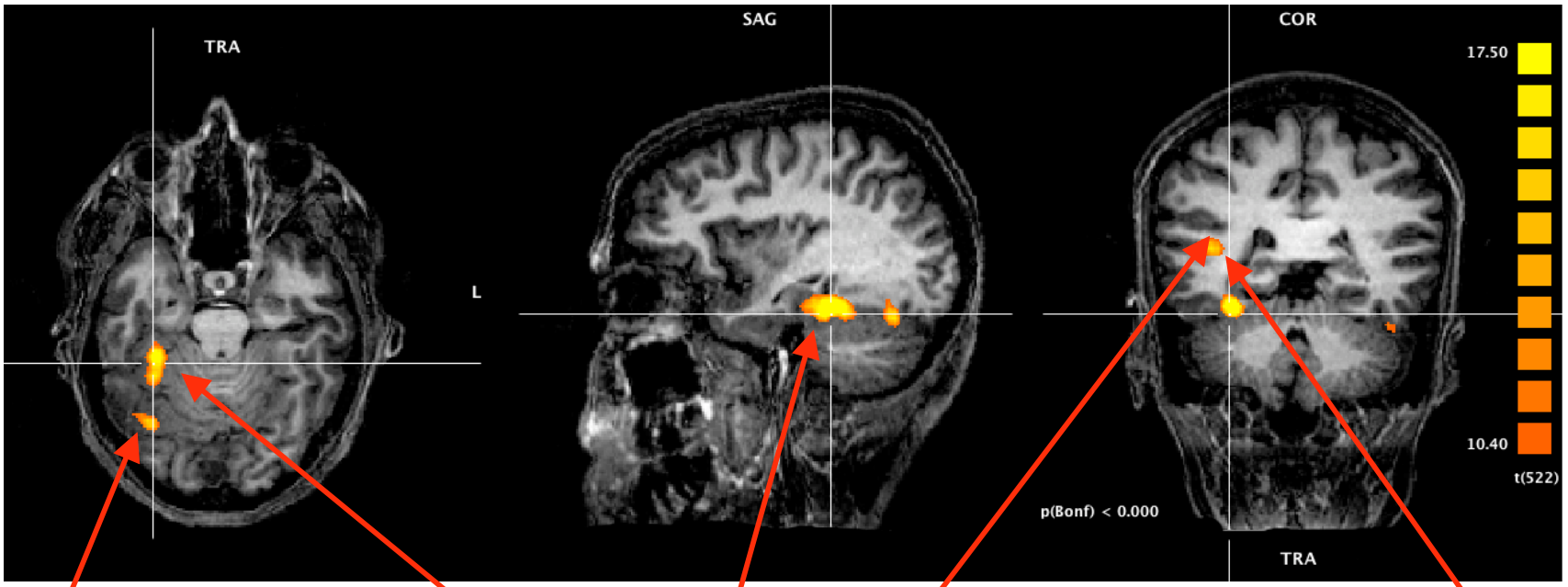
//: there is adaptation to inverted faces, even when different facial identities are presented

Hypothesis tested in areas responding preferentially to faces in the human occipito-temporal cortex

These areas show (recovery from) adaptation to facial identity

= larger signal for blocks of different faces than same faces

(e.g. Gauthier et al., 2000; Grill-Spector & Malach, 2001; Winston et al., 2004)



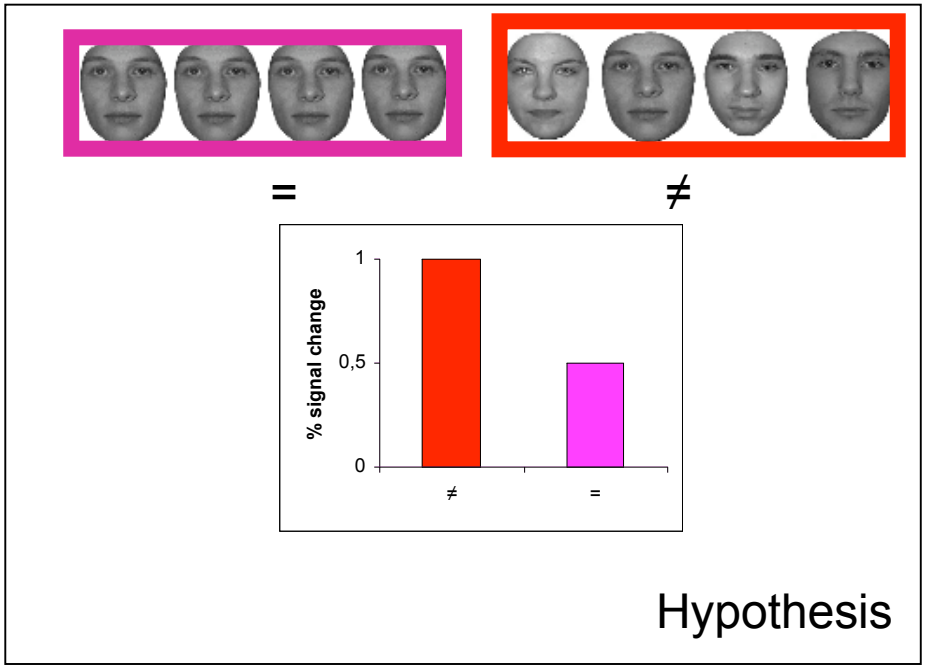
Inferior Occipital Gyrus ('Occipital face area, OFA')

Middle Fusiform Gyrus ('Fusiform face area, FFA')

The Superior Temporal Sulcus (STS)

fMR-adaptation

- See
  - Grill-Spector *et al.*, 1999
  - Grill-Spector & Malach, 2001
  - Henson, 2003
  - Kourtzi and Kanwisher, 2000
  - Grill-Spector et al., 2006



Rationale of the adaptation paradigm:

Specifically the **regions coding facial identity**:

→ yield a **larger** blood oxygenation level-dependent (**BOLD**) signal in response to:

blocks or pairs of trials displaying **different** individual faces as compared >
to blocks or pairs of trials with **identical** faces

In a face-sensitive cortical area:

Recovery from fMR-adaptation to facial identity

is taken as evidence that:

→ different facial identities are represented by distinct neuronal response patterns

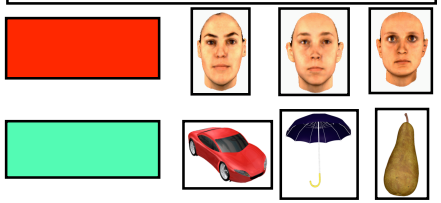
fMRI methods

1.5 T scanner (Philips)
EPI sequence
TR: 100 ms - TE: 40ms - flip: 80°
30 contiguous, near-axial slices (5 mm, 128 x 128)

(1) Classical localizer design

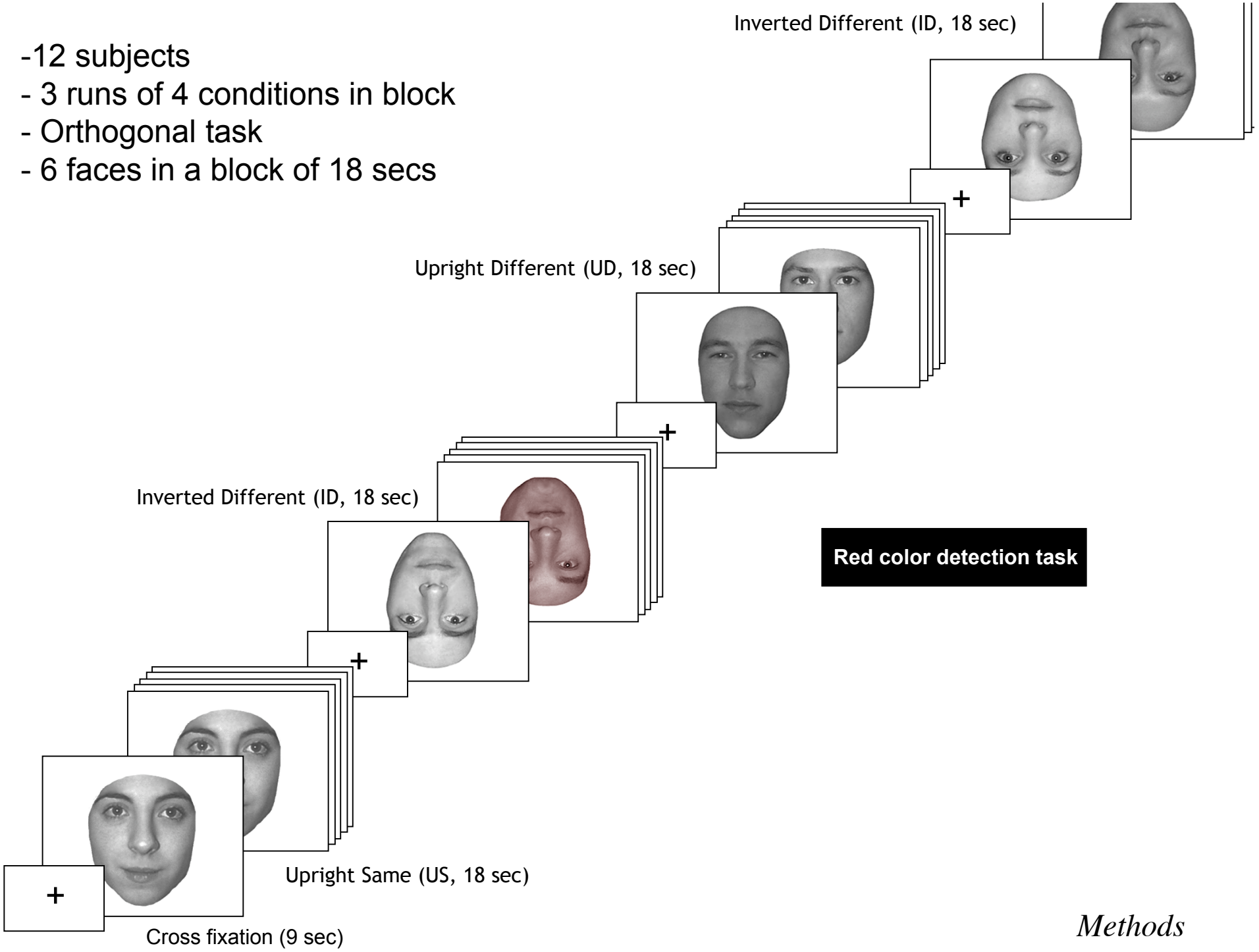
→ Where are the individual 'face areas' located?

(Faces - Objects)



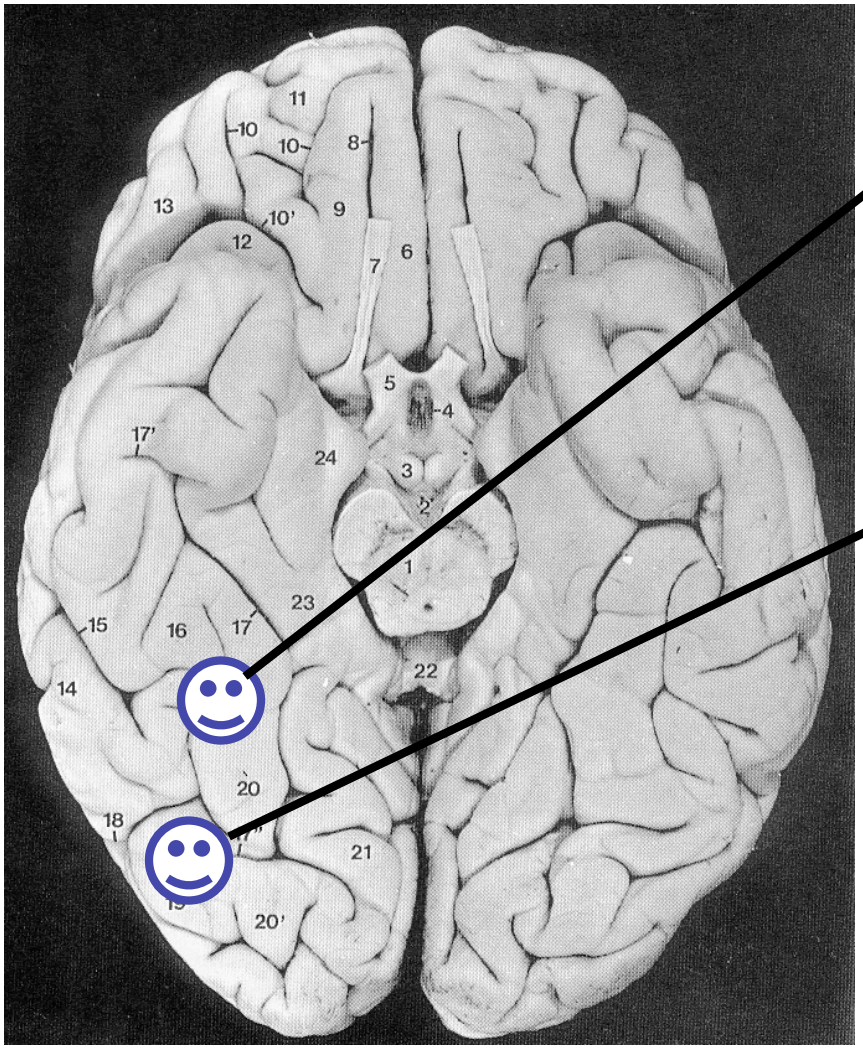
(2) FMR- adaptation design with 4 conditions (orientation x repetition)

-12 subjects
- 3 runs of 4 conditions in block
- Orthogonal task
- 6 faces in a block of 18 secs



Methods

Focus on



‘Fusiform face area’ (‘FFA’)
in the middle fusiform gyrus

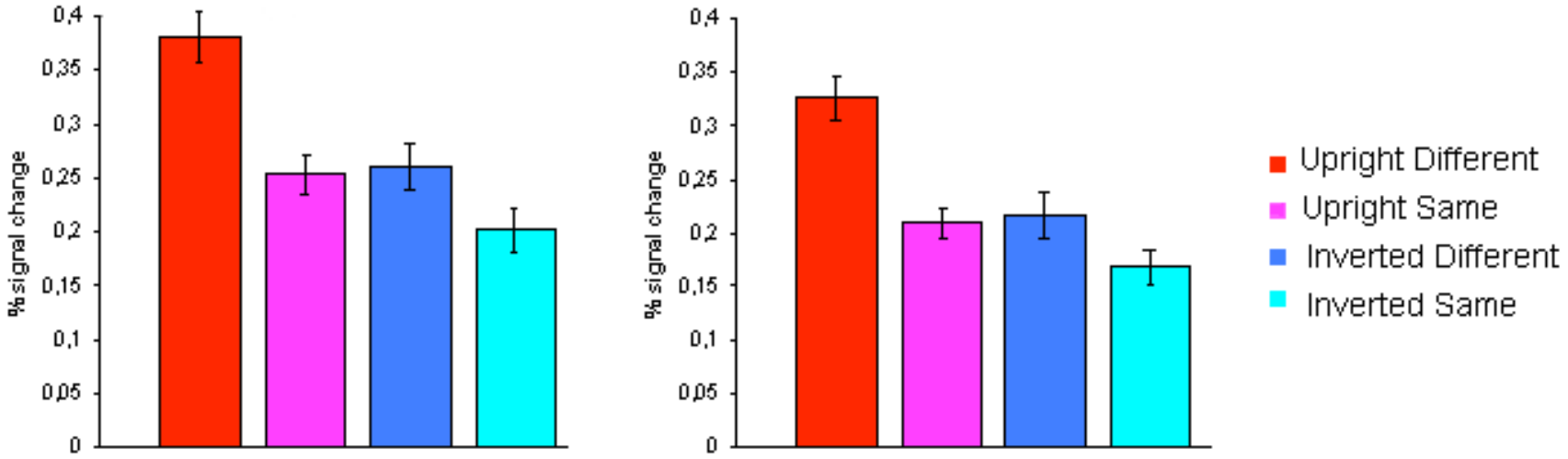
‘Occipital face area’ (‘OFA’)
In the inferior occipital gyrus

Whole time-course analyses

Middle fusiform gyrus

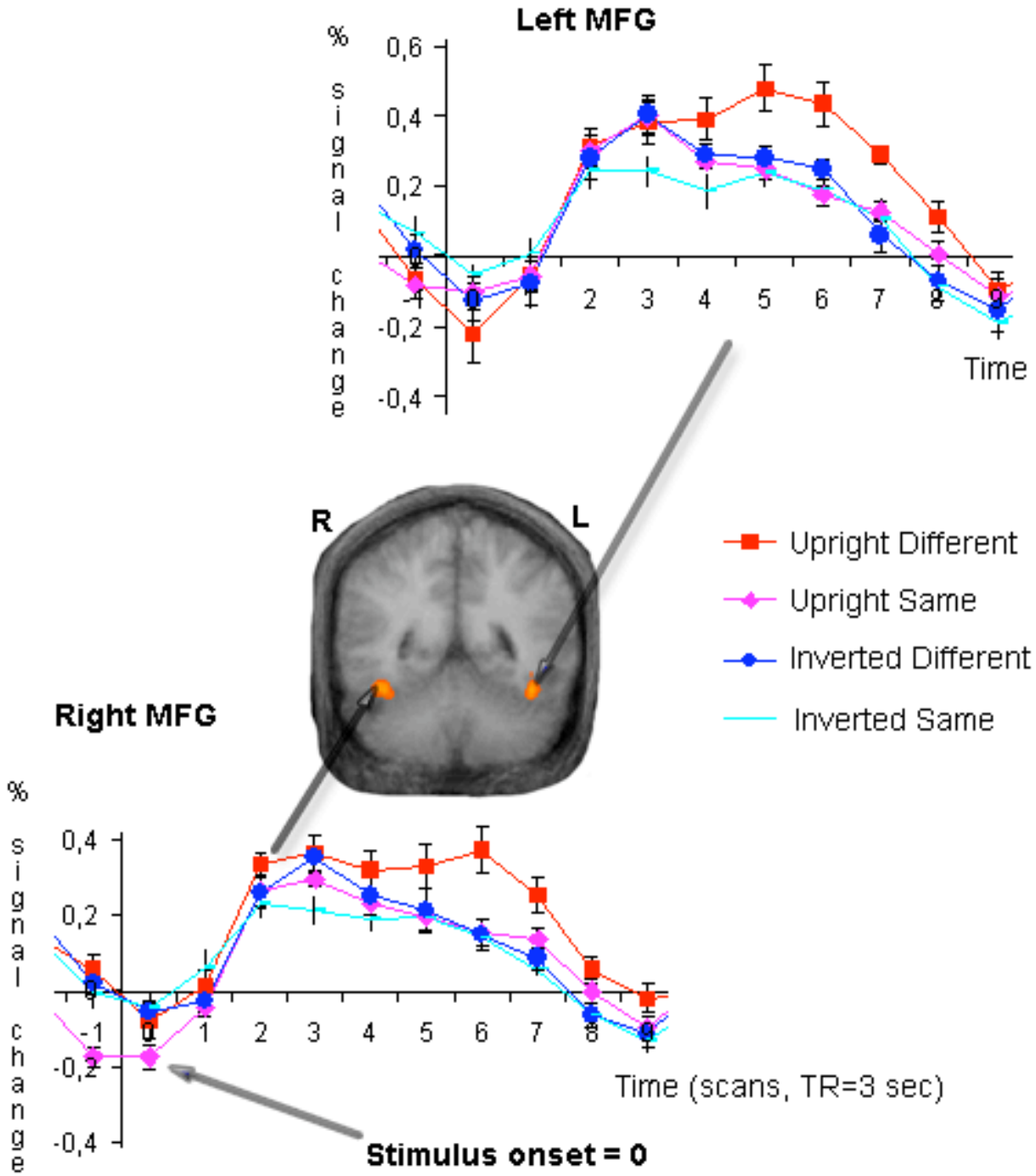
Left ‘FFA’

Right ‘FFA’



Larger recovery from adaptation to upright than inverted faces

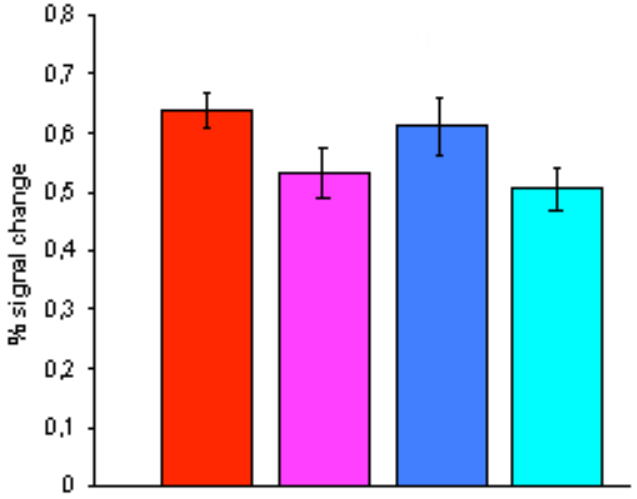
(= interaction between orientation and repetition)


Left MFG
% signal change
0,6
0,4
0,2
-0,2
-0,4
Time
R
L
Upright Different
Upright Same
Inverted Different
Inverted Same
Right MFG
% signal change
0,4
0,2
-0,2
-0,4
-1
1
2
3
4
5
6
7
Time (scans, TR=3 sec)
Stimulus onset = 0

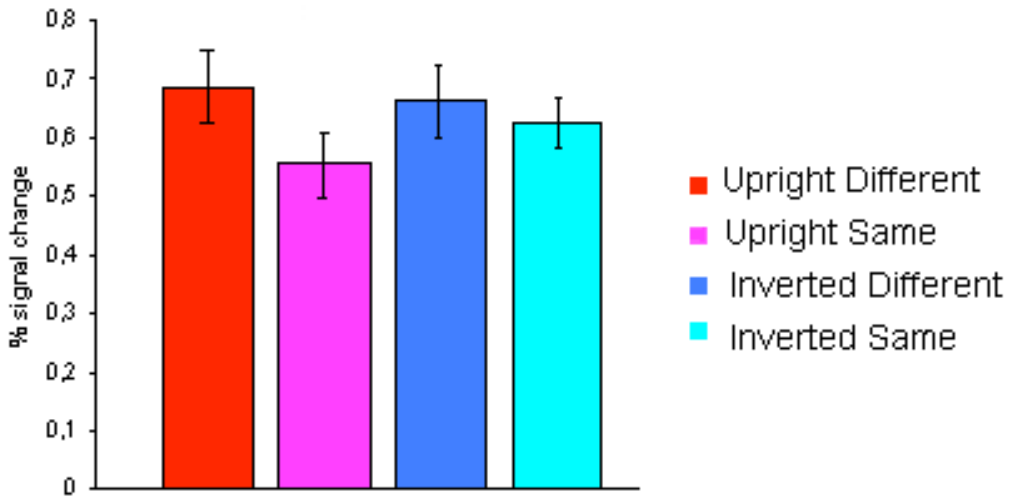
Results

Inferior Occipital Gyrus

Left ‘OFA’



Right ‘OFA’

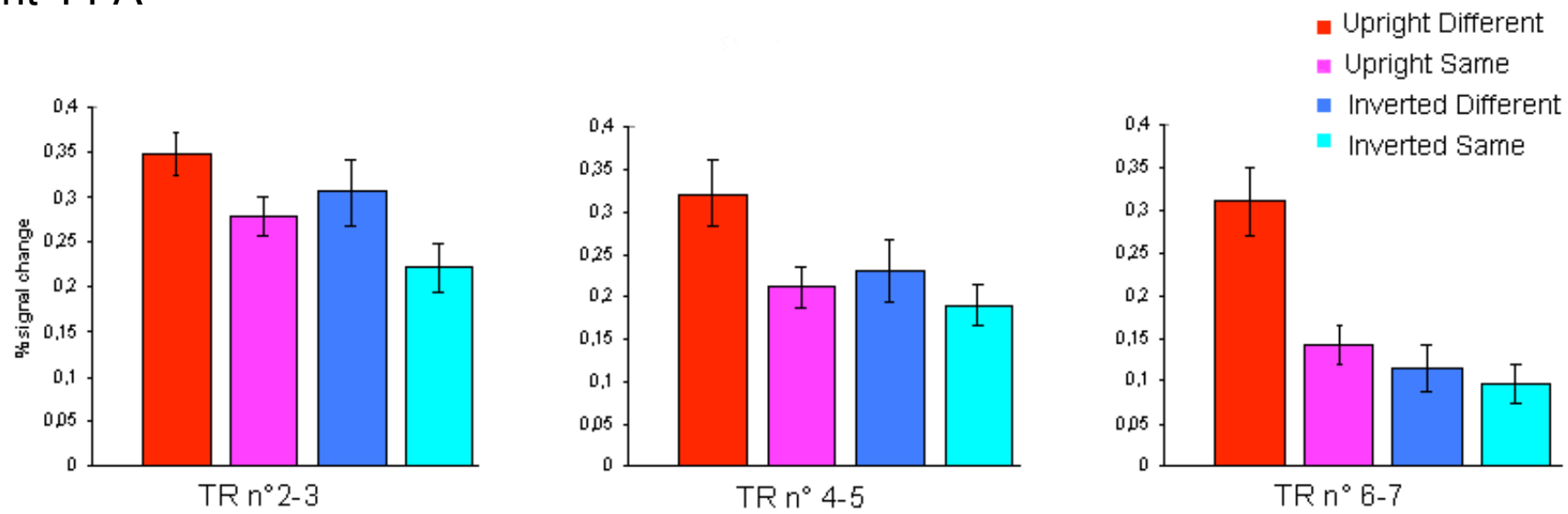


Recovery from adaptation to upright and inverted faces but *no* interaction between orientation and repetition

Results

Temporal evolution of differences during a block (18 seconds - 6 TRs)

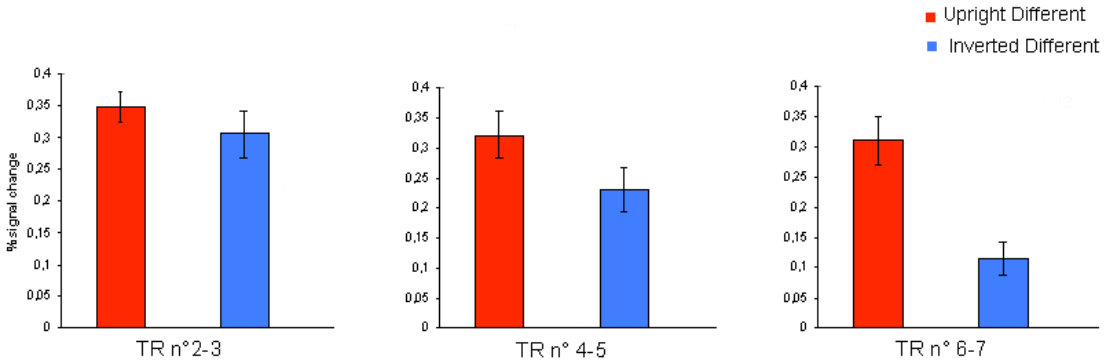
Right ‘FFA’



Initially, larger response to different than same faces of equal magnitude for upright and inverted faces

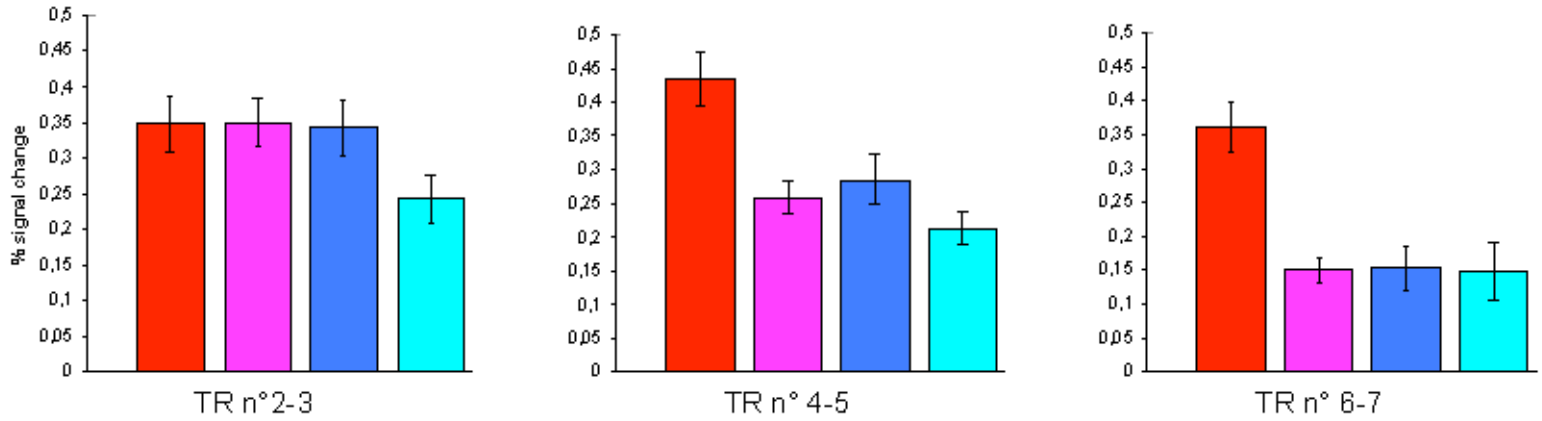
The difference between upright and inverted faces increases with time, reflecting the differential levels of adaptation

Previous block fMRI studies uisng different faces:



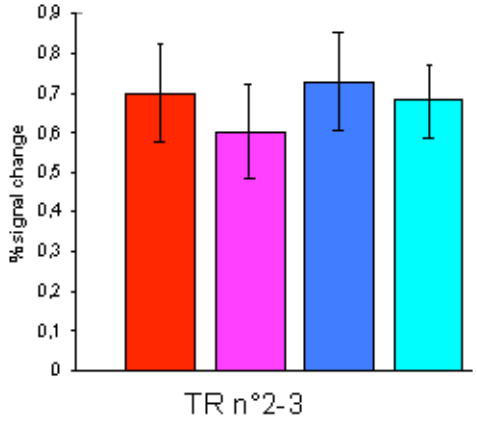
Results

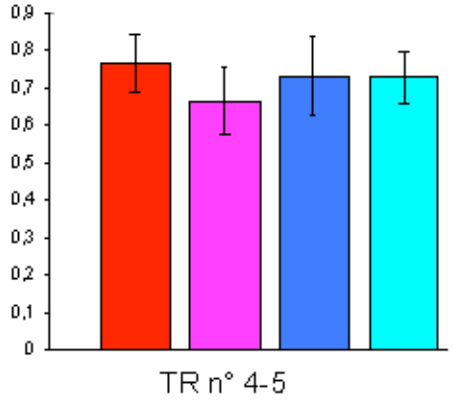
Similar pattern in left ‘FFA’

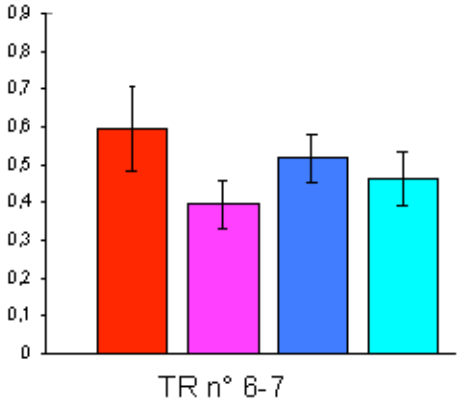


Emergence of an inversion effect in the ‘OFAs’, later in the response

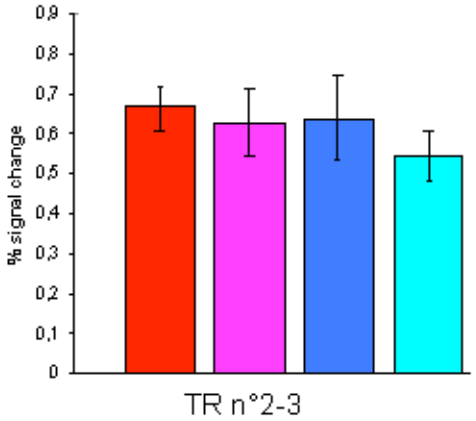
Right H

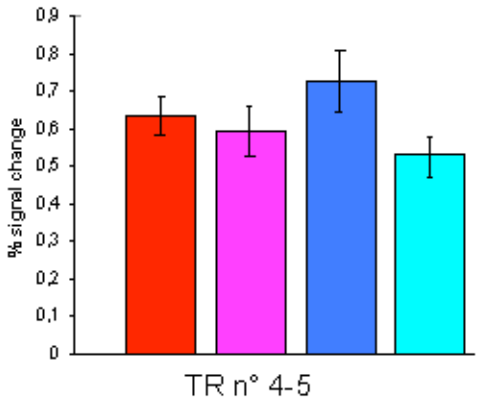


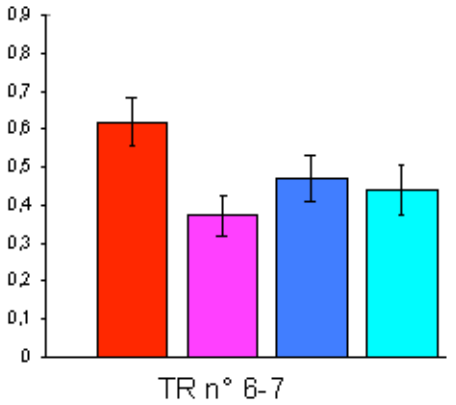




Left H







Discussion

When different faces are presented upside-down consecutively during a block, there is an adaptation of the fMRI signal in occipito-temporal areas coding for facial identity.

or … less recovery from adaptation for different inverted faces than upright faces

The strongest effect is found in areas responding preferentially to faces in the middle fusiform gyrus ('FFA')

This occurs presumably because differences between individual faces are less well perceived when they are shown upside-down

→ The 'FFA' (and the 'OFA' to a lesser extent) form the neural basis of the face inversion effect

Similar findings and conclusions using an active discrimination task in ER and block designs by Yovel & Kanwisher (2005)

Can these observations explain discrepancies between previous fMRI studies comparing upright and inverted faces?

ALL studies using block designs found significant *reduction* of signal for inverted faces relative to upright faces in the 'FFA'

Kanwisher et al. (1998); Yovel & Kanwisher (2004)	*Large effect* (0.3 - 0.5% signal change)
Gauthier et al. (1999); Haxby et al., (1999)	Small *effect*

The only study that did not find differences between upright and inverted faces in the 'FFA' (Aguirre et al., 1999) used an event-related paradigm in which upright and inverted faces were presented one-by-one, interleaved with other pictures

→ No differential adaptation for upright and inverted faces

Factors such as block length, number of different faces in a block …will determine the size of the difference in response between upright and inverted faces