Faces are represented holistically in the human occipito-temporal cortex

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See also:

Rossion, B., Dricot, L., De Volder, A., Bodart, J.-M., Crommelinck, M., de Gelder, B., Zoontjes, R., (2000). **Hemispheric asymmetries for whole-based and parts-based face processing in the human fusiform gyrus**. *Journal of Cognitive Neuroscience*, 12, 793-802.

Introduction

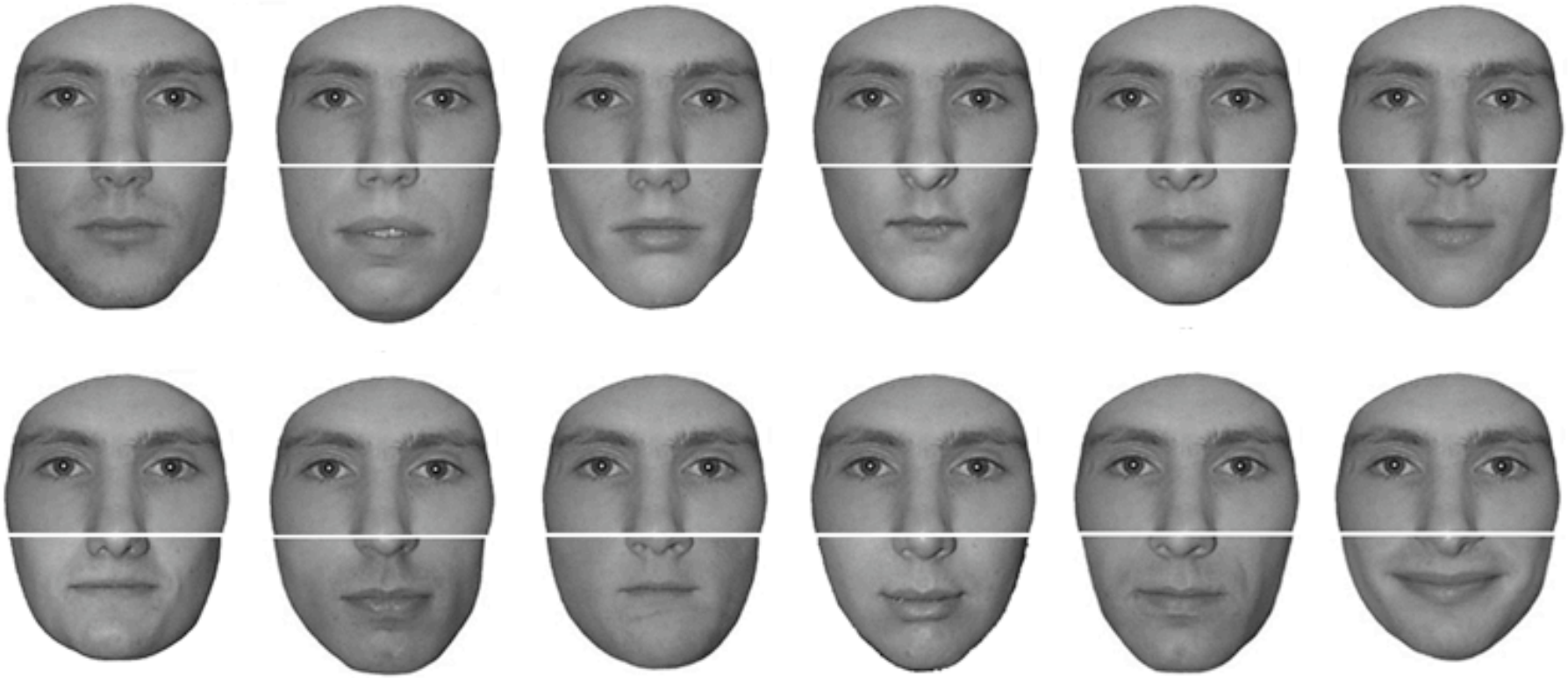
Hypothesis:

- Areas responding preferentially to faces in the human brain represent faces holistically.

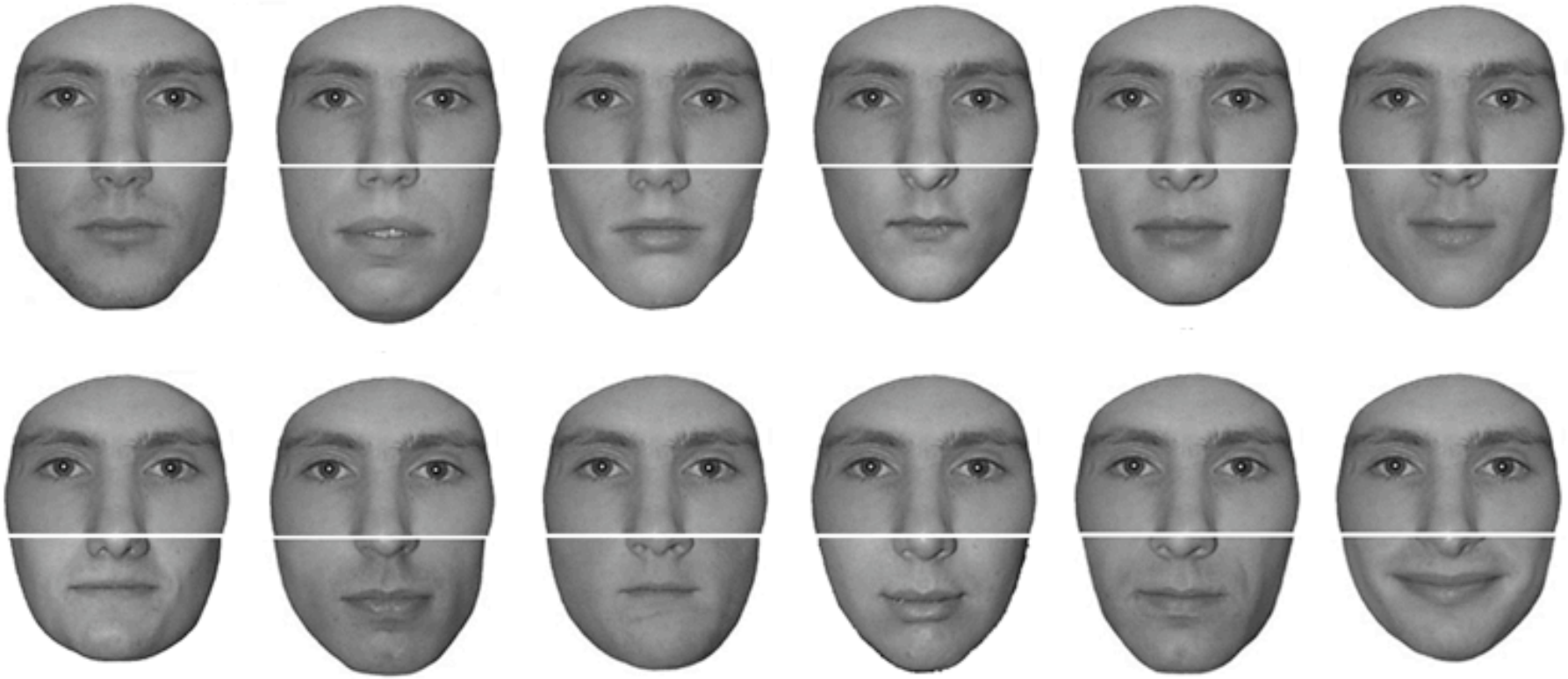
Method:

- Functional magnetic resonance imaging (fMRI) recordings during an adaptation paradigm with the composite face illusion.

The face composite illusion

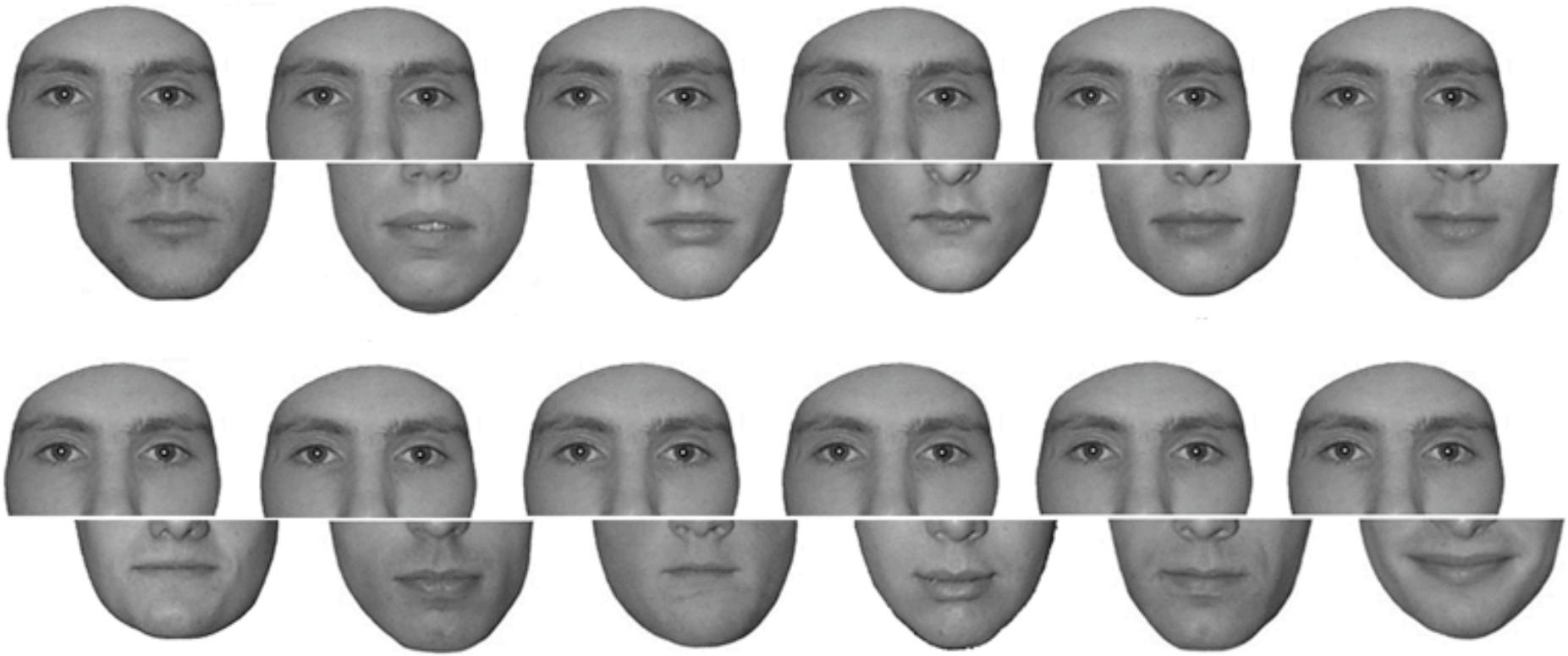


All top parts of the faces are strictly identical



First demonstration of the illusion by Young et al. 1987

The face composite illusion



Theoretical background of the face composite effect

- The 'face composite effect', is taken as strong evidence that faces are processed as a whole rather than as a collection of independent features.

- The composite face effect has been observed for:
  - familiar and unfamiliar faces
  - in recognition experiments
  - in face matching experiments

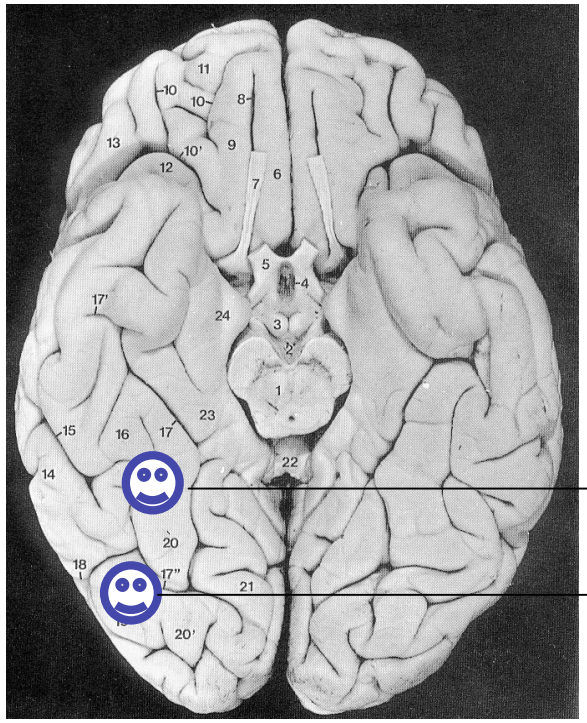
e.g. Young et al., 1987; Le Grand et al., 2004; Goffaux and Rossion, 2006

Areas responding preferentially to faces in humans

- Several occipito-temporal cortical areas respond preferentially to faces in humans, with a right hemispheric dominance

  (e.g. Sergent et al., 1992; Puce et al., 1995; Kanwisher et al., 1997)

- Two of these areas are located in the ventral pathway:



Middle fusiform gyrus (MFG) or ‘FFA’

Inferior occipital gyrus (IOG) or ‘OFA’

Functional role of MFG and IOG

- These two areas play a critical role in the extraction of individual face representations
  (Gauthier et al., 2000; Rossion et al., 2003; Grill-Spector et al., 2004; Schiltz et al., 2006)

- In line with the hierarchical nature of the primate visual system (Felleman and Van Essen, 1991), it has been proposed that:
  - facial features are represented in the IOG
  - whole facial identities are represented in the MFG
  (Haxby et al., 2000)

Note on terminology:

FFA	=	MFG	(middle fusiform gyrus)
OFA	=	IOG	(inferior occipital gyrus)

- The two functional regions are defined by a comparison of faces and nonface stimuli

- Either MFG/IOG terminology is used here, or the terms ‘FFA’ (Kanwisher et al., 1997) and ‘OFA’ (e.g. Gauthier et al., 2000) are used with quotes , since they are somewhat misleading.

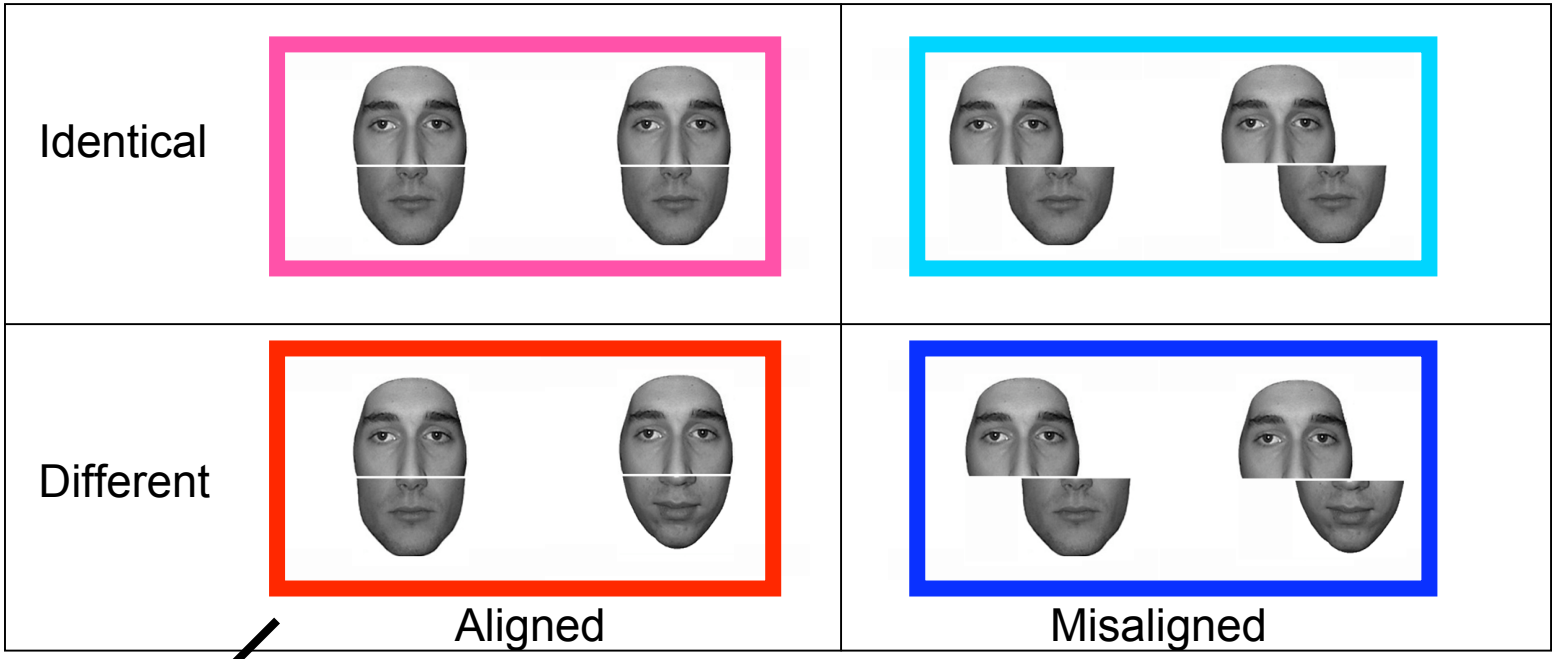
- Indeed

  These regions do respond:
  - to other stimuli than faces
  - to a different level to distinct objects

  (e.g. Ishai et al., 2000; Grill-Spector et al., 2004; 2006)

Experiment 1: Block design fMRI with 4 conditions

TOP part of the face stimulus ALWAYS identical during an epoch

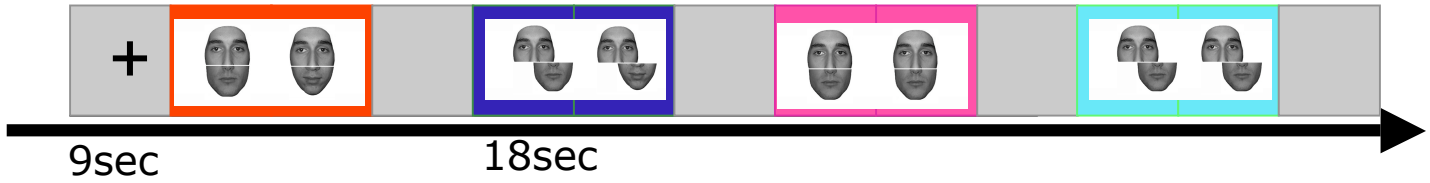


Critical condition: top face parts are perceived as different, release from adaptation to identity should be observed in this condition

Methods

Methods (1)

Paradigm – Experiment 1:



Random order of blocks

Stimuli:	12 stimuli/bloc (500ms+1000ms blank) Faces (grayscale, neutral expression, no external cues, 13 m/f, ±3°)
Task:	Focus on upper face half and detect red colored halves
Imaging:	1.5T, TR:3000ms, 4 runs

6 conditions :

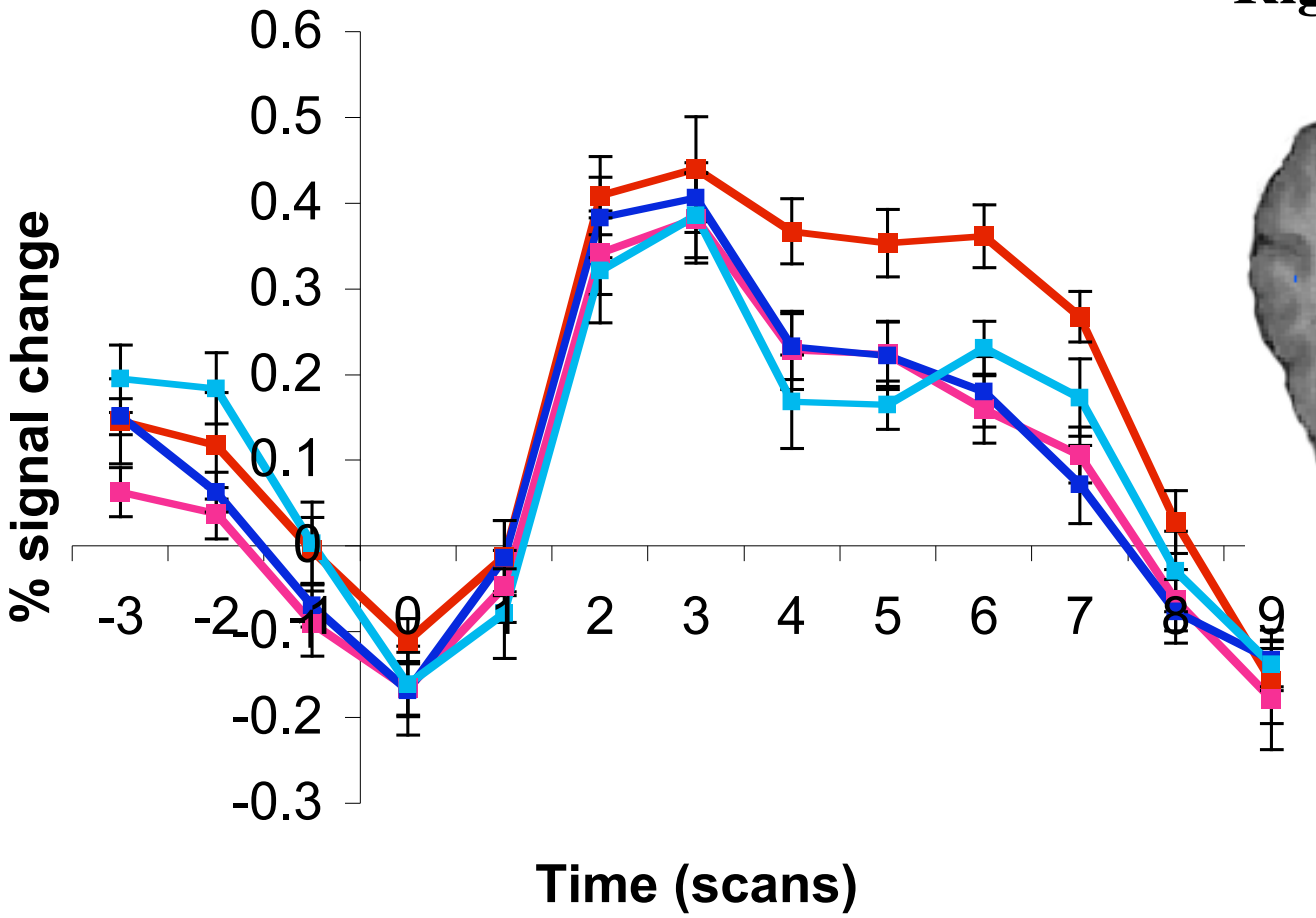
- scrambled faces
- objects, houses

→ localizer

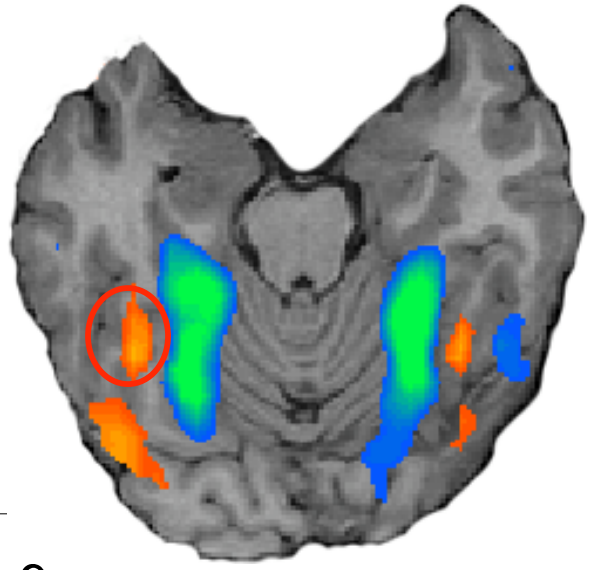
- aligned identical → 12 identical bottom parts per block
- aligned different → 12 different bottom parts per block
- misaligned identical → 12 identical bottom parts per block
- misaligned different → 12 different bottom parts per block

Top parts are always identical!

Results (1)

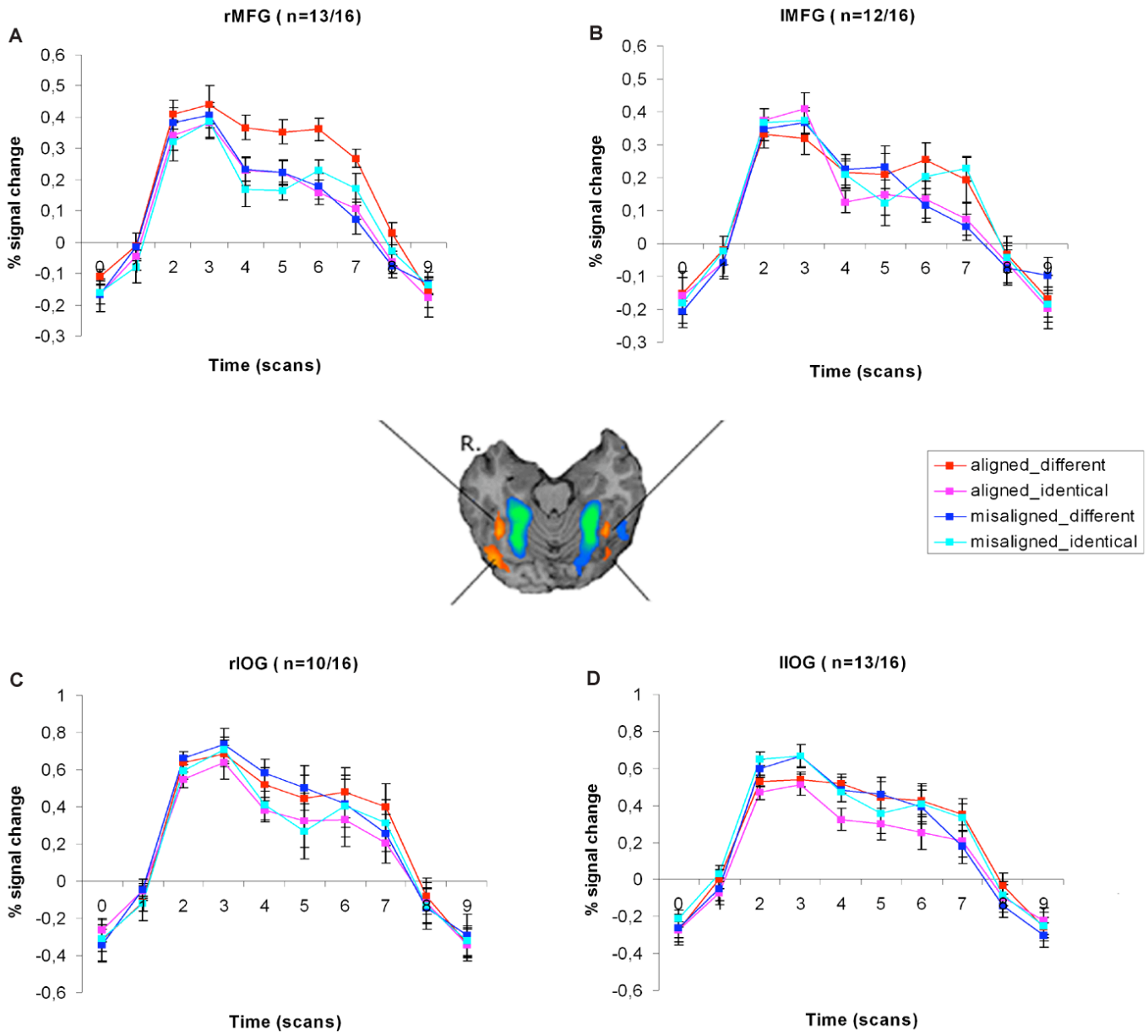


Right fusiform gyrus



Significantly larger BOLD response to different (as compared to identical) bottom parts of faces when the two face halves were aligned than when they were misaligned.

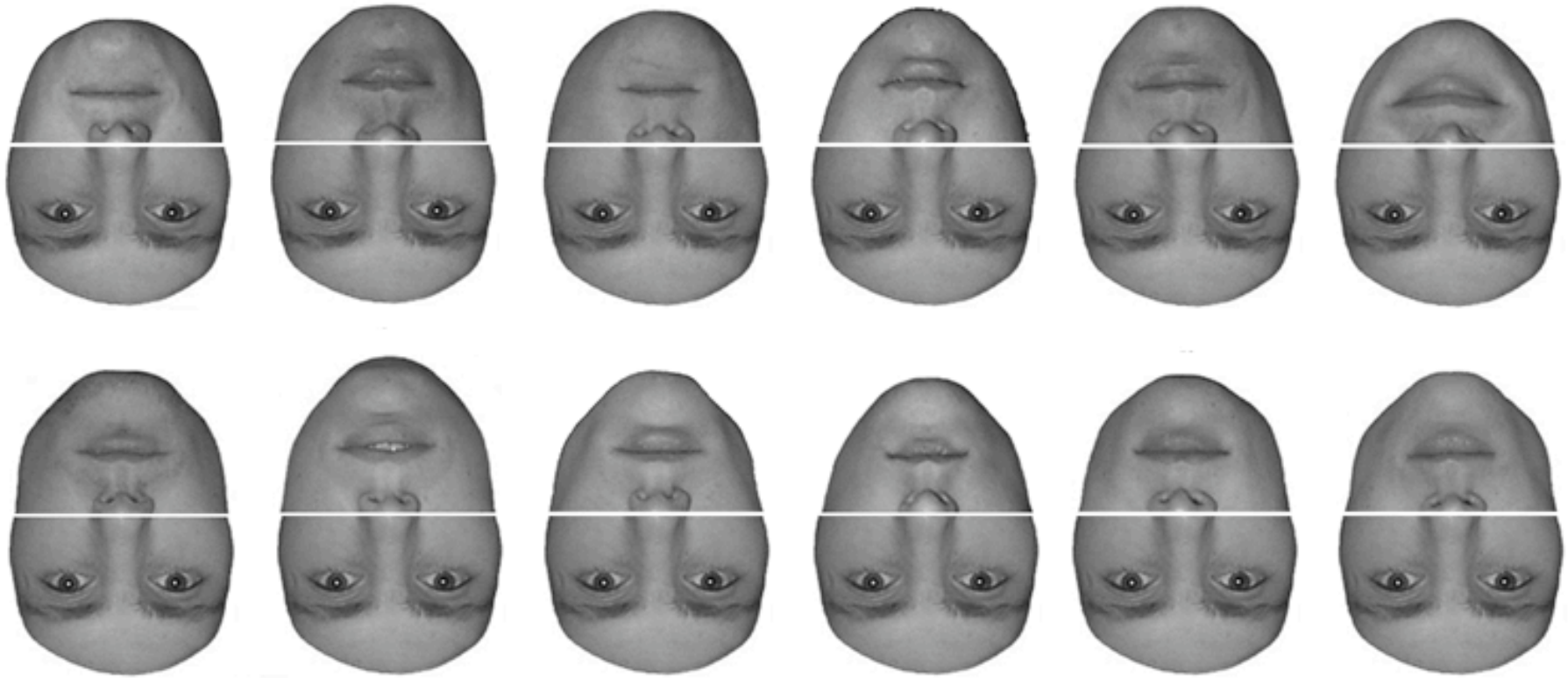
→ In line with the subjective impression of viewing different faces, which occurs exclusively in the 'different' blocks consisting of aligned face parts.



Stronger composite effect (interaction between alignment and identity) observed in the right middle fusiform gyrus, but significant in the 4 areas

Results

The face composite illusion disappears or is reduced when faces are presented upside-down

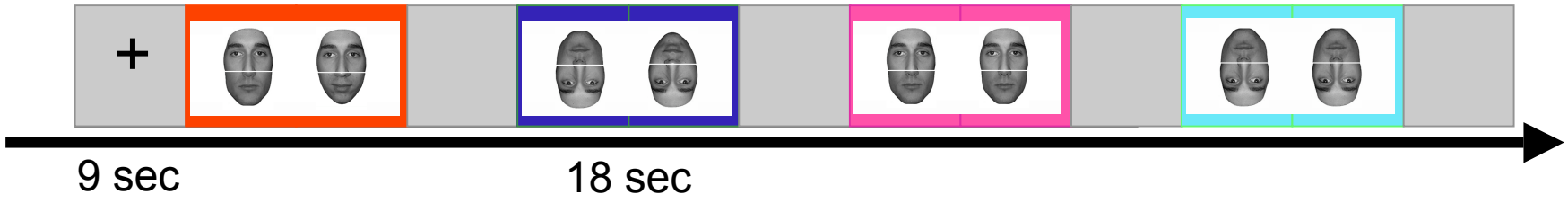


fMRI experiment 2

Methods

Methods (2)

Paradigm – Experiment 2:



Random order of blocks

Stimuli:	12 stimuli/bloc (500ms+1000ms blank) Faces (grayscale, neutral expression, no external cues, 13 m/f, ±3°)
Task:	Focus on upper face half and detect red colored halves
Imaging:	1.5T, TR:3000ms, 4 runs

7 conditions :

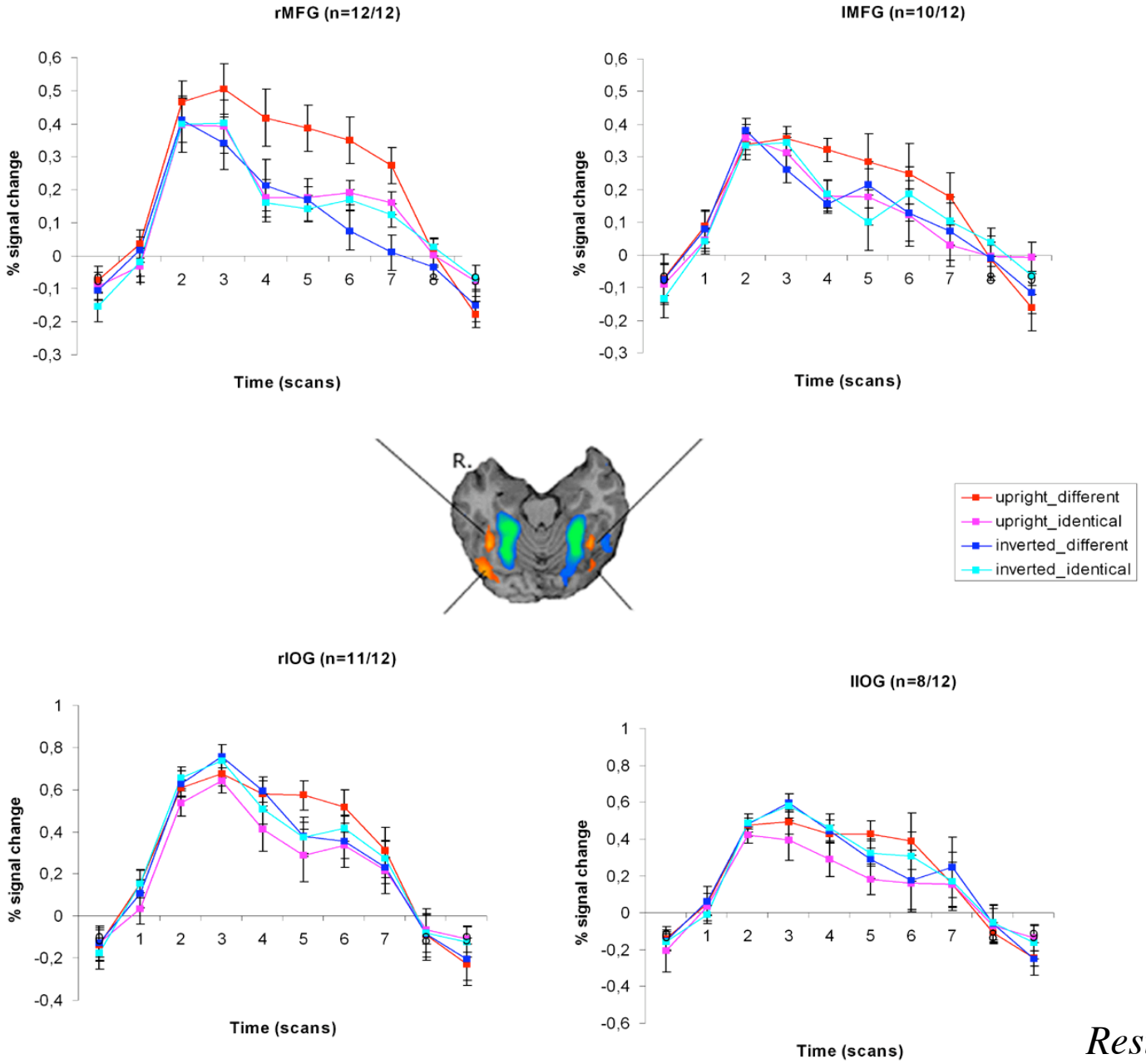
- scrambled
- houses
- different faces

→ localizer

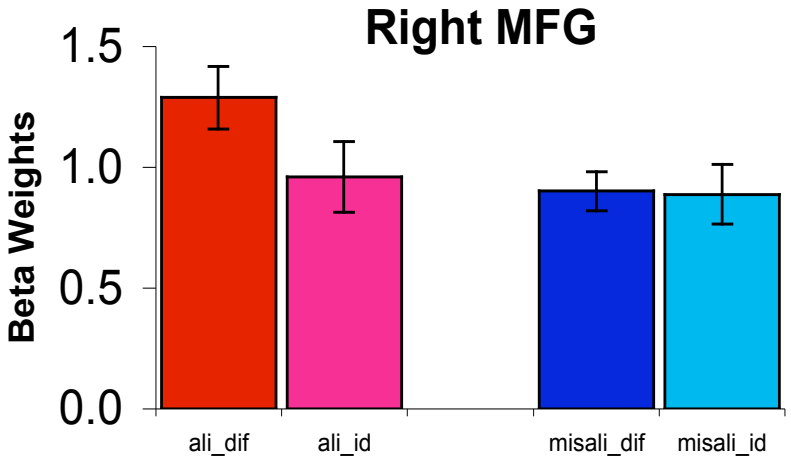
- aligned identical → 12 identical bottom parts per block
- aligned different → 12 different bottom parts per block
- inverted identical → 12 identical bottom parts per block
- inverted different → 12 different bottom parts per block

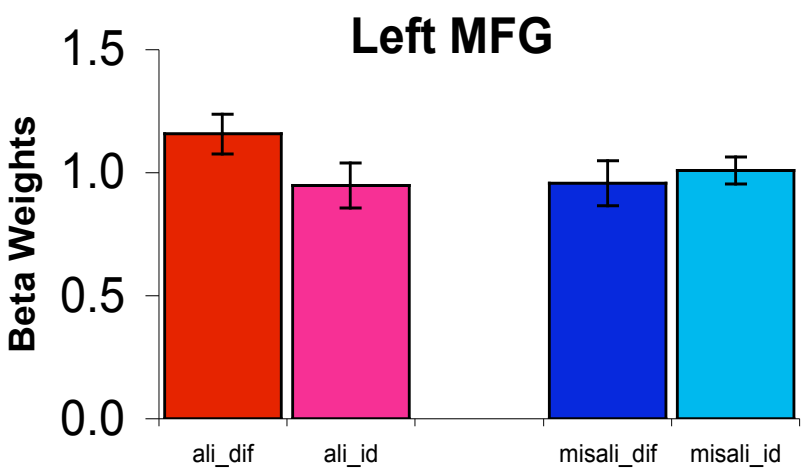
Top parts are always identical!

Results (2)

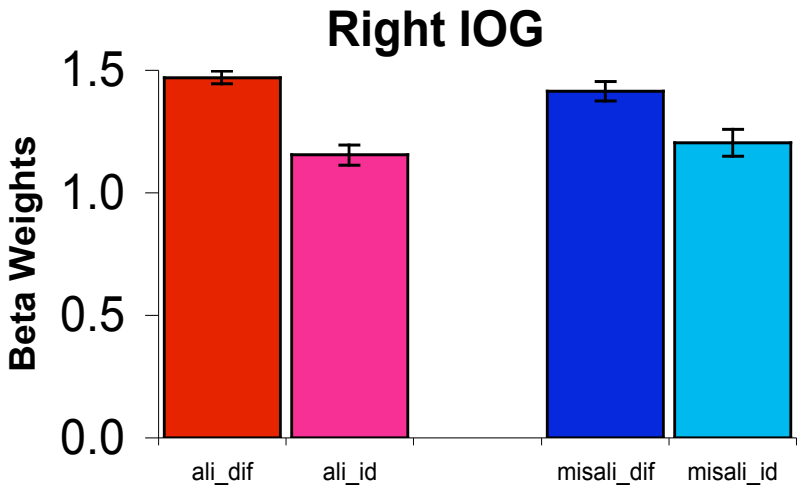


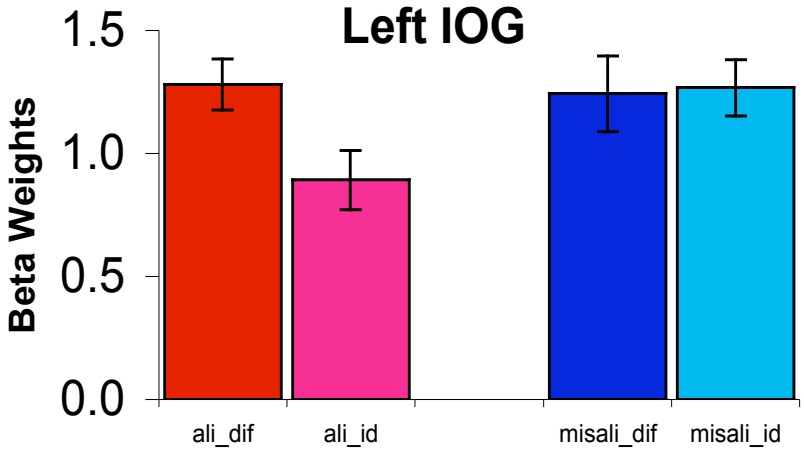
Results

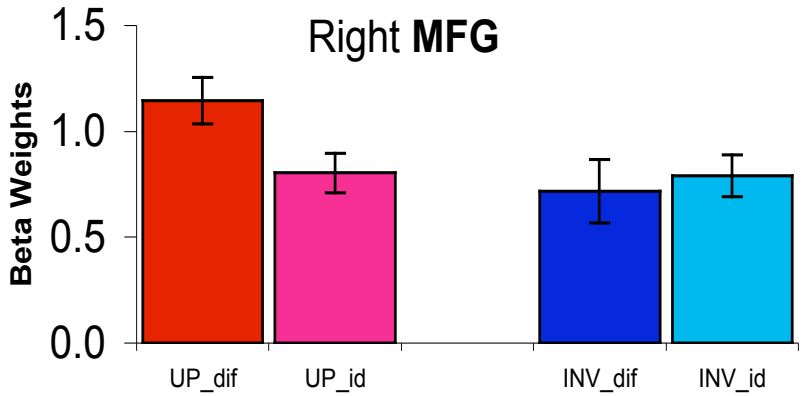


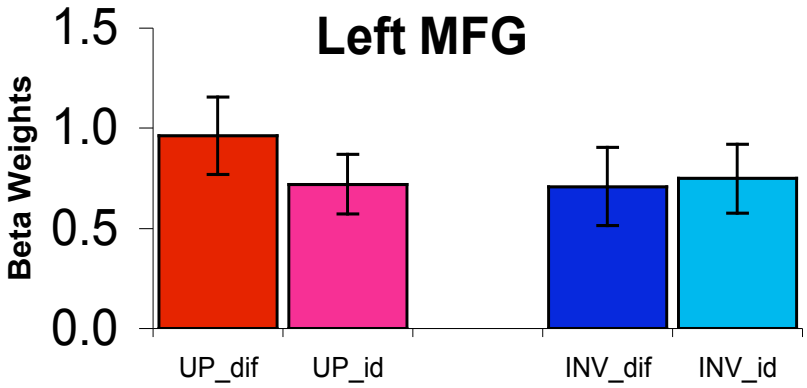


Magnitude of the neural face composite effect (experiment 1)

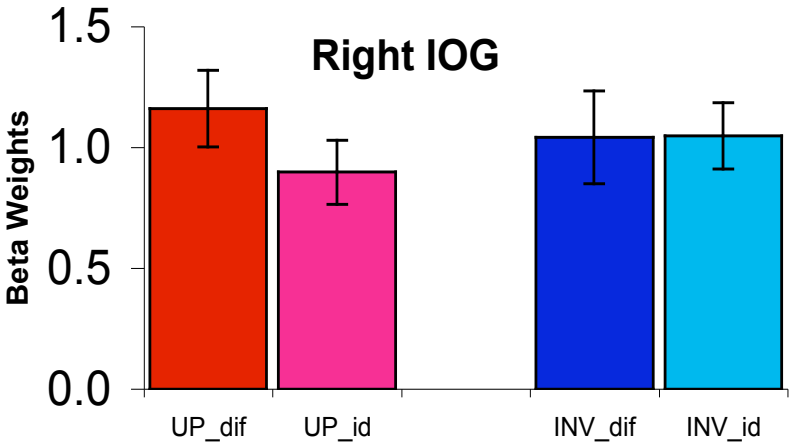


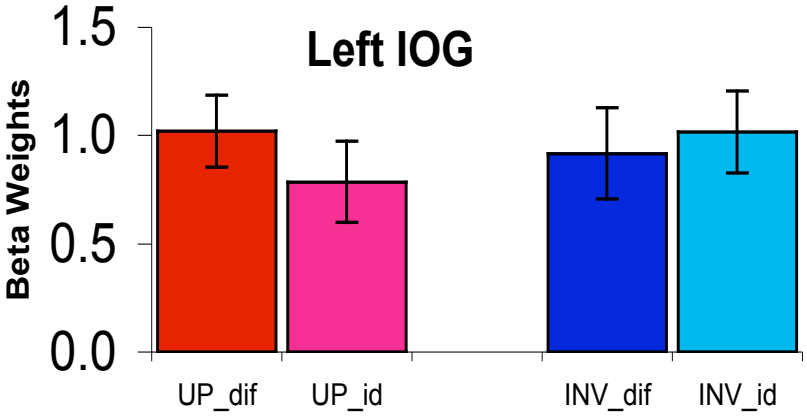






Magnitude of the neural face composite effect (experiment 2)

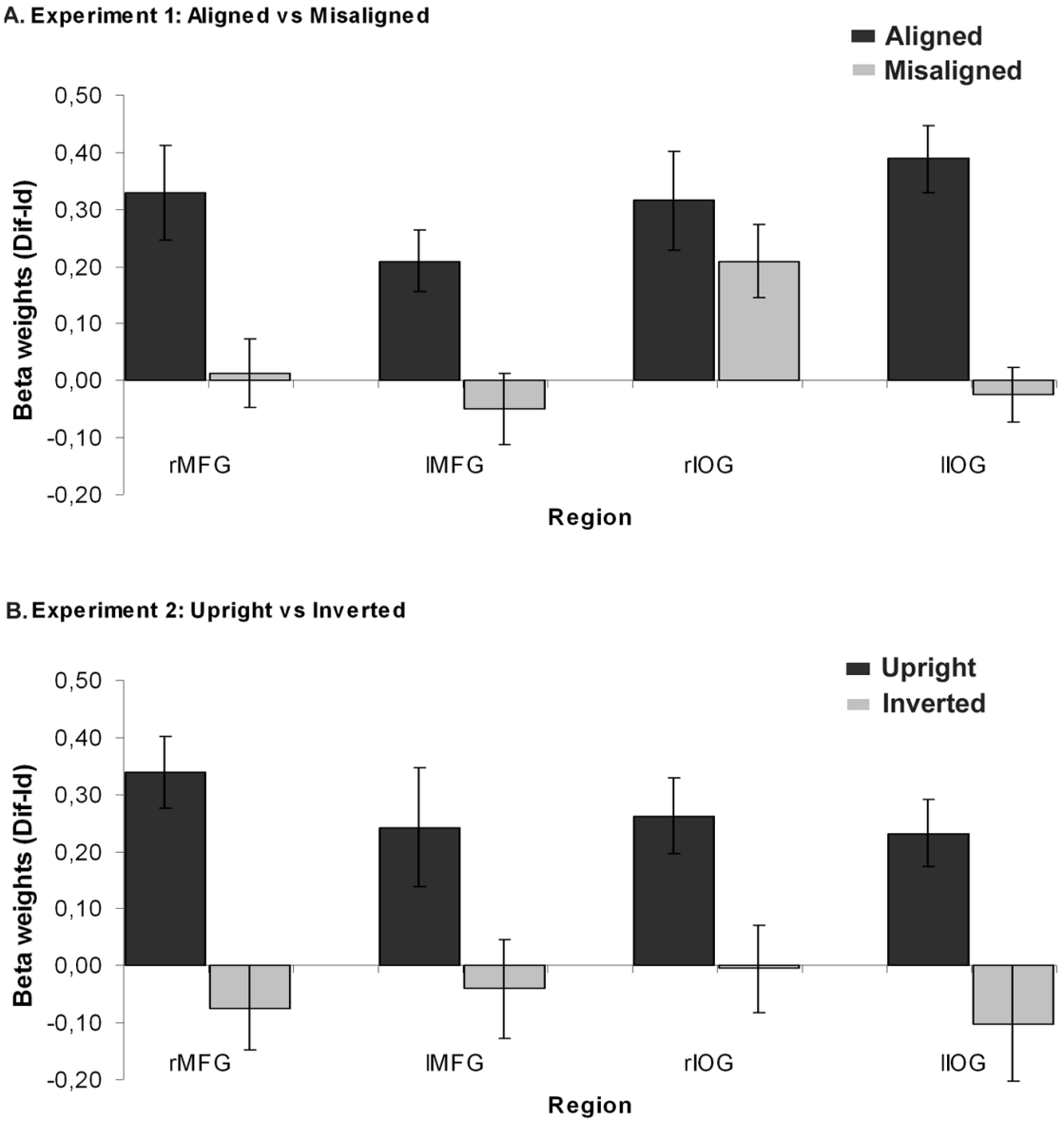




(A) In experiment 1 differential fMR-adaptation (different vs. identical bottom parts) was significantly larger for aligned than for misaligned faces in the four regions.

(B) In experiment 2 a significantly higher BOLD response level for 'different' compared to 'identical' upright face stimuli was found in combination with the absence of such a difference for inverted face stimuli in the four regions.

fMR-adaptation indexes



fMR-adaptation indexes are computed by subtracting of the beta weights of the GLM for 'same' from 'different' conditions)

Results

Results - Summary

In our two fMR-adaptation experiments we observed:

- A significantly larger response to the same top face when it was aligned with different bottom parts than with the same bottom part

- This difference was not found when the top and the bottom face parts were spatially misaligned, or when the faces were presented upside-down.
- Over the two experiments, the effects were stronger in the right middle fusiform gyrus than in the other face regions.

Discussion and Conclusions (1)

- The finding that faces are represented holistically in the fusiform and inferior occipital areas responding preferentially to faces is consistent with:
  - Neurophysiological experiments showing that a large proportion of face-selective cells in the monkey infero-temporal cortex (IT) are sensitive to the whole facial organization:
    - removal of a part of the face (Tsunoda et al., 2001)
    - scrambling the parts (Desimone et al., 1984)

      → causes a marked reduction in neuronal response strength
  - The observation in positron emission tomography (PET) of a reduced right fusiform activation when human subjects have to discriminate faces on specific facial features (Rossion et al., 2000).
  - Evidence that face recognition deficits in brain-damaged patients (prosopagnosia (Bodamer, 1947)) following lesions of the bilateral or right occipito-temporal cortex concern the ability to process faces holistically (Sergent and Signoret, 1992; Farah et al., 1998; Barton et al., 2002; Boutsen and Humphreys, 2002)

Discussion and Conclusions (2)

- The integration of face parts into a holistic representation was more robust in the middle fusiform gyrus.
- The differential fMR-adaptation to identity was less specific in the inferior occipital gyrus for aligned as compared to misaligned face stimuli.
- Behavioral studies suggest that the extraction of a holistic face representation perceptually dominates the analysis of detailed features (Tanaka and Farah, 1993) and may have a temporal precedence during the microgenesis of face perception (Sergent, 1986; Goffaux and Rossion, 2006).
- Holistic representations of faces might thus be initially extracted in the middle fusiform gyrus and call upon processes in a lower-level face visual area to extract detailed information about facial features and build robust individual representations of faces

  → see discussion in Rossion et al., 2003 and Schiltz et al., 2006