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The neural correlates of change detection in the face perception network

Mary-Ellen Large[a,*], Cristiana Cavina-Pratesi[a], Tutis Vilis[b], Jody C. Culham[a]

[a] Department of Psychology, CIHR Group for Action and Perception, University of Western Ontario, Ontario, Canada
[b] Department of Physiology and Pharmacology, CIHR Group for Action and Perception, University of Western Ontario, Ontario, Canada

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ABSTRACT

A common view is that visual processing within the ventral visual stream is modulated by attention and awareness. We used fMRI adaptation to investigate whether activation in a network of brain regions involved with face recognition – namely the fusiform face area (FFA), occipital face area (OFA) and right superior temporal sulcus (rSTS) – was modulated by physical changes to face stimuli or by observers' awareness of the changes. We sequentially presented two matrices of four faces. In two thirds of the trials one of the faces changed. We compared activations generated in three conditions (i) change detected trials, (ii) change blind trials, and (iii) no change trials. If face areas were sensitive to physical changes then we expected similar levels of activation for face changes regardless of change detection. If face areas were sensitive to levels of awareness of change then we expected greater levels of activation for detected changes compared to no change detection. We found that all three-face regions recovered from adaptation when subjects were aware of changes, but only OFA recovered from adaptation when subjects were not aware of the changes. These results suggest that within the face network OFA is involved in representing information that has not yet entered awareness and that consciousness is not an all-or-none phenomenon throughout the ventral stream.

1. Introduction

The argument that the ventral (occipitotemporal) pathway supports conscious perception has received considerable support from neuroimaging studies. Activation in intermediate-level visual areas of the ventral stream, such as the fusiform face area and parahippocampal place area, have been found to be modulated by visual attention (Wojciulik, Kanwisher, & Driver, 1998) and conscious awareness (Beck, Rees, Frith, & Lavie, 2001; Tong, Nakayama, Vaughan, & Kanwisher, 1998). In contrast, category-selective areas within the dorsal stream appear to be insensitive to whether stimuli are consciously perceived or not (Fang & He, 2005). However, many of these neuroimaging studies have focused on single category-specific areas or used experimental paradigms that may utilize sub-cortical routes bypassing ventral structures. We were interested in finding out how awareness of change would modulate a network of ventral stream regions involved in processing a specific type of stimulus, namely faces.

Faces are a particularly useful stimulus that activate several brain areas within the occipitotemporal cortex: in addition to FFA (Kanwisher, McDermott, & Chun, 1997), face-selectivity has also been characterized in OFA (Haxby, Hoffman, & Gobbini, 2000; Rossion, Schiltz, & Crommelinck, 2003b; Rotshtein, Henson, Treves, Driver, & Dolan, 2005) and the superior temporal sulcus (Andrews & Ewbank, 2004). Though the importance of the FFA in face processing has been most strongly touted, a growing body of neuropsychological evidence suggests that accurate face recognition requires that the OFA be intact and connected to the FFA (Rossion et al., 2003a; Steeves et al., 2006). In addition, the STS is also responsive to the changeable aspects of faces such as expression and eye gaze (Andrews & Ewbank, 2004).

We used fMRI adaptation techniques (Grill-Spector, Henson, & Martin, 2006) to assess the responses of a network of regions involved in face processing to varying levels of change awareness. The level of awareness was manipulated by applying a change detection paradigm (Simons, 1996) that induced change blindness in 50% of the trials. We measured the response of face areas to awareness (or lack of awareness) of change by calculating the reduction of the fMRI signal produced by repeating four faces and comparing it to the same measure when one of the four faces changed, both when the change was detected and when it was not. We expected to find a decrease in brain activity (adaptation) in all face areas for trials where no change occurred compared to trials in which a change in face identity occurred and was detected.

Abbreviations: FFA, fusiform face area; OFA, occipital face area; LO, lateral occipital area; rSTS, right superior temporal sulcus; %BSC, percent BOLD signal change; ROI, region of interest.

* Corresponding author at: Department of Psychology, University of Hull, Cottingham Road, Hull HU6 7RX, UK. Tel.: +44 1482 466711; fax: +44 1482 465599.
E-mail address: M.Large@hull.ac.uk (M.-E. Large).

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The more interesting question was how each region would respond to changes that occurred but were not detected. If the face area responds only to changes that reach awareness then we expected activation to be higher for detected changes compared to repeated identical faces and that there would be little difference in activation between repeated identical faces and the change blindness. Conversely, if the face area was sensitive to physical changes then we expected greater activation for change trials that were detected compared to no change trials, regardless of levels of awareness. We found that FFA and the right superior temporal sulcus (rSTS) responded to undetected changes in face identity with reduced activation as if identical faces had been repeated. In contrast, OFA responded similarly to detected changes and undetected changes in face identity, suggesting that OFA plays a role in the unconscious processing of faces.

2. Materials and methods

2.1. Participants

Nine university students (6 male; age range: 24–38) with normal or corrected-to-normal vision participated in this study. They were all right handed as measured by the Edinburgh Handedness Inventory (Oldfield, 1971). All participants gave written consent and all procedures were approved by the University of Western Ontario Health Sciences Review Ethics Board. All nine participants performed repeated functional runs for two experiments.

2.2. Experimental procedures

In all experiments, participants viewed images back-projected onto a screen that was located approximately 50 cm from the participant's eyes and reflected through a mirror. Participants were required to fixate centrally for the duration of the experiment. All participants held a button box in their right hand and they were asked to respond using the index and the middle fingers. Stimulus presentation and response collection were controlled by a PC laptop using Macromedia Flash MX 2004, version 7.0 (Macromedia, US).

2.3. Change detection experiment

We presented participants with a matrix consisting of four faces followed by a second matrix of four faces, in which one face changed (see Fig. 1). There were an equal number of changes in each of the four positions in the matrix, which occurred in a random order. The aim of the change detection task was to equalize, as far as possible, the number of trials falling into the following three categories according to participants' responses: change trials in which the participants detected the change (change detected trials), change trials in which the participants *did not* detect a change (change blind trials), and no change trials in which the participants correctly determined there was no change (no change trials). During behavioural piloting, we determined that there were too few trials in which subjects reported a change when there was no change (i.e. false alarms) to include this condition in the fMRI analyses.

A total of 300 greyscale photographs of faces were collected from the web, from the CVL Face Database (Peter Peer; http://www.lrv.fri.uni-lj.si/facedb.html) and from *The AR Face Database* (Martinez & Benavente, 1998; http://rvl1.ecn.purdue.edu/(aleix/aleix_face_DB.html). There were 150 male faces and 150 female faces – approximately half were neutral and the other half were expressive (smiling, angry, surprised, and sad). The face stimuli were digitally processed by graphics software so that each face had the same oval shape (with visual angles approximately 2° wide × 2.7° high). In each trial two stimulus displays were presented sequentially (see Fig. 1). The displays were a matrix of four faces located above, below and to left and right of a central fixation point at a constant distance of 2° visual angle from the centre of each face and fixation (Simons, 1996). Face stimuli only repeated within a trial from array one to array two. In one third of the trials all faces in the array repeated (no change trials = 100% repetition) and in two thirds of the trials one face changed (change trials = 75% repetition). No face stimuli were repeated between trials to prevent effects of adaptation in one trial carrying over to subsequent trials.

The experiment consisted of four runs with 27 experimental trials per run and a control period lasting 15 s at the beginning and end of each run. On each trial the two matrices of faces were presented for 1400 ms each separated by a 200 ms grey masking box. The inter-trial interval was 12 s. In nine trials, the faces in the two matrices were identical (no change trials). In the remaining 18 trials one of the four faces changed either its identity (single dimension change), or its identity and

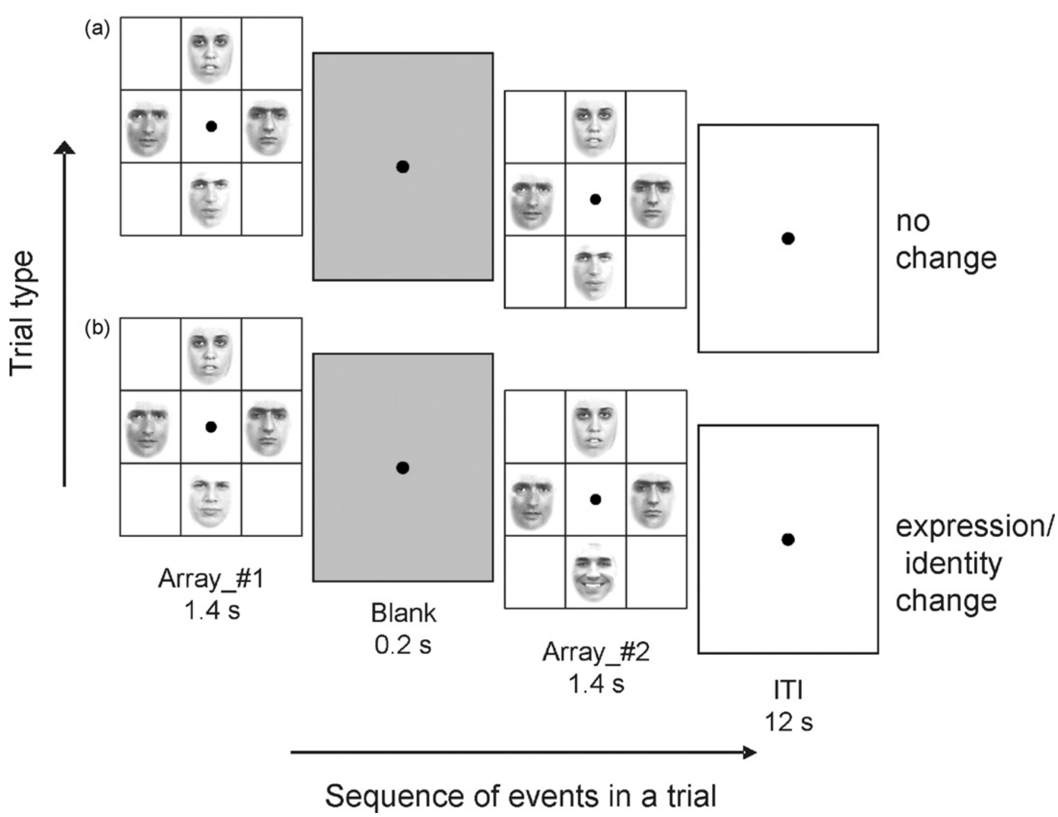

Fig. 1. Change detection task: (a) no change trials: two identical matrices of four faces were sequentially presented, interposed by a grey masking box. (b) Change identity/expression trials: two matrices were presented sequentially and one of the four faces changed identity or identity and expression in the second matrix. Subjects were required to press one of two buttons to indicate whether they detected a change or no change.