



## Strabismic amblyopia affects relational but not featural and Gestalt processing of faces

Zaira Cattaneo<sup>a,b,\*</sup>, Tomaso Vecchi<sup>b,c</sup>, Maura Monegato<sup>c,d</sup>, Alfredo Pece<sup>d</sup>, Lotfi B. Merabet<sup>e</sup>, Claus-Christian Carbon<sup>f</sup>

<sup>a</sup> Department of Psychology, University of Milano-Bicocca, Milano, Italy

<sup>b</sup> Brain Connectivity Center, IRCCS Mondino, Pavia, Italy

<sup>c</sup> Department of Brain and Behavioral Sciences, University of Pavia, Pavia, Italy

<sup>d</sup> Ophthalmology Unit, Melegnano Hospital, Melegnano, Italy

<sup>e</sup> Department of Ophthalmology, Massachusetts Eye and Ear Infirmary, Harvard Medical School, Boston, USA

<sup>f</sup> Department of General Psychology and Methodology, University of Bamberg, Bamberg, Germany

### ARTICLE INFO

#### Article history:

Received 8 June 2012

Received in revised form 15 January 2013

Available online 31 January 2013

#### Keywords:

Face processing  
Amblyopia  
Relational  
Featural  
Holistic  
Face detection  
Hemisphere  
Laterality  
Recognition  
Strabismus  
Dissociation

### ABSTRACT

The ability to identify faces is of critical importance for normal social interactions. Previous evidence suggests that early visual deprivation may impair certain aspects of face recognition. The effects of strabismic amblyopia on face processing have not been investigated previously. In this study, a group of individuals with amblyopia were administered two tasks known to selectively measure face detection based on a Gestalt representation of a face (Mooney faces task) and featural and relational processing of faces (Jane faces task). Our data show that – when relying on their amblyopic eye only – strabismic amblyopes perform as well as normally sighted individuals in face detection and recognition on the basis of their single features. However, they are significantly impaired in discriminating among different faces on the basis of the spacing of their single features (i.e., configural processing of relational information). Our findings are the first to demonstrate that strabismic amblyopia may cause specific deficits in face recognition, and add to previous reports characterizing visual perceptual deficits associated in amblyopia as high-level and not only as low-level processing.

© 2013 Elsevier Ltd. All rights reserved.

### 1. Introduction

Faces are of capital importance for human social interactions. In fact, faces convey information about individuals' unique identity, but also more general information such as their gender, ethnicity, emotional states, and health status. A deficit in face recognition can therefore be highly detrimental for everyday social interactions (cf. Grüter & Carbon, 2010). A great deal of literature has investigated severe face perception deficits that are due, for instance, to congenital or acquired prosopagnosia (e.g., Avidan, Tanzer, & Behrmann, 2011; Duchaine & Nakayama, 2005). However, there is evidence that more subtle facial processing deficits may be associated with other conditions such as autism (e.g., Simmons et al., 2009, for a review) or visual deficits of various etiologies, such as anisometropic or deprivation amblyopia (e.g., Bankó et al., 2012; Geldart et al., 2002; Le Grand et al., 2001;

Le Grand et al., 2003, 2004; Robbins et al., 2012) or monocular blindness due to enucleation (Kelly, Gallie, & Steeves, 2011). In the last decade, the effects of particular visual deficits on face processing have received increasing attention, as indicated by the increasing number of publications appearing in top scientific journals and linking different areas of research (e.g., Le Grand et al., 2001, 2003, 2004).

Amblyopia is a largely diffused developmental disorder of spatial vision that has been found to affect visual cortical responses to faces (see Bankó et al., 2012). It is characterized by reduced visual acuity and contrast sensitivity usually affecting one eye and is typically associated with an uncorrected ocular misalignment (i.e., strabismic amblyopia) and/or a significant refractive error between the two eyes (i.e., anisometropic amblyopia) occurring early in development. A more rare form of amblyopia is deprivation amblyopia, which occurs when patterned visual input to one or both eyes is reduced due to a congenital dense cataract or to ptosis (drooping of the eyelid that restricts or blocks vision). In association with monocular loss of visual function, amblyopia is also accompanied by impaired or absent binocular vision (Sireteanu, 2000), as a

\* Corresponding author at: Department of Psychology, University of Milano-Bicocca, Milano, Italy.

E-mail address: [zaira.cattaneo@unimib.it](mailto:zaira.cattaneo@unimib.it) (Z. Cattaneo).

result of suppression of the amblyopic eye input to the visual cortex. In an extensive study carried out on amblyopic adults (or with risk factors for amblyopia during development because of associated conditions such as strabismus), McKee, Levi, and Movshon (2003) measured visual functions that are known to be abnormal in amblyopia (e.g., *optotype* (Snellen) visual acuity, contrast sensitivity, grating acuity, Vernier acuity, and binocularity) in more than 400 patients that were assigned to different predetermined clinical categories (e.g., Anisometropes, Strabismic-anisometropes, Strabismics, Former Strabismics, Eccentric fixators, Deprivationals, Refractives, and Other abnormal). Interestingly, McKee, Levi, and Movshon (2003)'s findings showed that although *optotype* (Snellen) visual acuity accounted for much of the variance in the other functional measurements, significant differences emerged in the patterns of visual loss among the clinically defined categories of patients, and particularly between strabismic and anisometropic observers, suggesting that reduced resolution and loss of binocularity play a major role in determining the actual pattern of visual deficit. Moreover, the severity of amblyopia depends on the degree of imbalance between the two eyes and to the age at which the amblyogenic factor occurred (McKee, Levi, & Movshon, 2003). Without early corrective intervention (i.e. optical and/or surgical) the impaired visual function of the eye persists given that the neural processing of information from that eye has become impaired (Hess, 2001). Notably, converging findings suggest that amblyopia causes physiological alterations in both early and late visual areas, affecting not only low perceptual functions but also higher visual functions and visuo-spatial attention (e.g., Barnes et al., 2001; Imamura et al., 1997; Muckli et al., 2006). In particular, not only the functioning of the ventral (i.e. "what" object processing) as well as the dorsal (i.e. "where" spatial processing) visual pathways seem to be affected in amblyopia (e.g., Ho & Giaschi, 2006; Simmers et al., 2006), but even parietal and frontal functions may be affected (e.g., Farzin & Norcia, 2011).

Face recognition is a complex process that involves both early and late visual areas, the core face processing network (according to recent models) involving the fusiform face area in the occipito-temporal cortex, the occipital face area in the lateral occipital cortex, and the superior temporal sulcus (see Grill-Spector, Knouf, & Kanwisher, 2004; Haxby, Hoffman, & Gobbini, 2000; Rossion et al., 2003). At the functional level, face recognition appears to rely on multiple parallel processes operating simultaneously (Bruce & Young, 1986). In particular, a face can be recognized mainly on the basis of the global organization of its elements, even when the elementary components cannot be individually recognized as parts of a face (e.g., Leder & Carbon, 2005; Tanaka & Farah, 1993; Taubert et al., 2011). In fact, although the single elements of a face (eyes, nose, mouth, etc.) can occur in different shapes and sizes, their spatial arrangement is fixed (e.g., the mouth is below the nose, the nose is below the eyes, etc.), and individuals are likely to use this "first-order" spatial arrangement (see Maurer, Le Grand, & Mondloch, 2002) to classify an image as a face. A typical example of this strategy is the processing of Mooney faces. Mooney faces are two-tone (thresholded black and white) images first used in the 1950s to measure children's capacity to form a coherent percept or the closure of shape on the basis of global structure missing reliable local details (Mooney, 1956, 1957). In a Mooney face, the single elements are too ambiguous to be identified as parts of a face. Therefore, to find any facial feature (such as an eye or the mouth), one must first detect that the stimulus has the structure of a generic face (e.g., Latinus & Taylor, 2005; McKone, 2004; Rossion et al., 2011).

However, in daily life, we do not just need to recognize a face as a face, but also to recognize that a face belongs to a particular individual, that is, we are continuously required to discriminate between different faces. Several findings suggest that we are able

to discriminate between different faces by mainly relying on relational and featural processing (e.g., Carbon & Leder, 2005; Collishaw & Hole, 2000; Leder & Carbon, 2006; for a review see Maurer, Le Grand, & Mondloch, 2002). Relational (or spacing) information refers to the specific spatial arrangement (a specific distance between the eyes, the eyes and the nose, etc., also referred to as "second-order" spatial relations) that characterizes each single face (see Rhodes, 1988). Featural information refers to featural cues, that is, the shape, or size of individual facial features. Individuals' sensitivity to relational and featural information has been measured in paradigms requiring to discriminate between different faces that only differed in terms of single features (with the spatial arrangement being kept constant) or relational aspects (with single features being kept constant) (for a review, see Maurer, Le Grand, & Mondloch, 2002). Overall, normally sighted adult individuals are quite accurate in deciding whether two faces are identical or different for featural or relational aspects, with accuracy being higher (Freire, Lee, & Symons, 2000; Mondloch, Le Grand, & Maurer, 2002; Mondloch, Robbins, & Maurer, 2010) and speed being faster overall for featural differences (Carbon & Leder, 2005).

Relational-based and featural-based processes have been demonstrated to be independent and parallel processes demonstrated by different experimental manipulations such as stimuli inversion (e.g., Mondloch, Le Grand, & Maurer, 2002; with inversion typically affecting more detection of relational changes than of featural changes), backward masking (Carbon, 2011), or by the analysis of scanpaths of the eyes (Bombari, Mast, & Lobmaier, 2009). Moreover, the capacity to process features seems to develop faster than the capability to discriminate faces on the basis of their relational information (Mondloch, Le Grand, & Maurer, 2003, 2002). From a neuropsychological point of view, the two processes seem to involve, at least partially, different neural circuits (Maurer et al., 2007; Mercure, Dick, & Johnson, 2008; Scott & Nelson, 2006) and there is evidence that featural and configural processing of faces is differently affected in certain conditions such as prosopagnosia (e.g., Lobmaier et al., 2010).

Interestingly, it has been reported that individuals who suffered early visual deprivation due to bilateral congenital cataracts performed normally in a face detection task in which Mooney faces were used as stimuli (Mondloch, Le Grand, & Maurer, 2003), whereas they performed sub-optimally on a relationally manipulated but not a featurally manipulated set of faces, even after several years' recovery (Le Grand et al., 2001, 2004). Hence, a normal earlier visual experience may be necessary to develop the typical shift from featural to configural face processing (e.g., Schwarzer, Zauner, & Jovanovic, 2007) but not to detect that a stimulus is a face. Given that strabismus causes abnormal binocular input, which in turn can lead to amblyopia, we investigated (Experiment 1) the effects of this condition on different aspects of faces processing, and in particular, face detection as measured by the Mooney faces task and relational and featural processing (using the "Jane faces task", see Mondloch, Le Grand, & Maurer, 2002).

Finally, given that participants in our main experiment (Experiment 1) were tested twice on the same task, a second experiment was carried out to assess whether individuals' performance was stable across time (test-retest reliability) in the different experimental tasks we employed. In fact, we are not aware of direct measures of test-retest reliability for the Mooney faces task, although there is evidence that training with the task in the same experimental session leads to increased accuracy (Latinus & Taylor, 2005). In turn, test-retest reliability has been directly investigated earlier for the Jane faces task (Mondloch & Desjarlais, 2010; Mondloch, Maurer, & Ahola, 2006). In particular, Mondloch and Desjarlais (2010) investigated whether performance in the featural and relational set of the Jane faces task was stable over time by

re-testing the same participants on a different version of the same task within a few days after the first testing session. The authors reported that individual differences in sensitivity to spacing between facial elements (relational set) were reliable across days and positively correlated with participants' sensitivity in detecting differences in the spacing of features (doors and windows) in houses (Mondloch & Desjarlais, 2010). In contrast, performance in the featural set was not stable across days. According to the authors, the low internal reliability of the featural task mainly depended on accuracy being very high in that condition with little variation among individuals (Mondloch & Desjarlais, 2010). A previous study by Mondloch and colleagues (Mondloch, Maurer, & Ahola, 2006) also provides a measure of reliability for the spacing task. In particular, study participants were tested within the same experimental session on two different tasks both assessing sensitivity to spacing in faces, but one task used human faces and the other task monkey faces. A positive significant correlation was reported between accuracy of individuals for human faces and their accuracy for monkey faces (Mondloch, Maurer, & Ahola, 2006). Nonetheless, reliability for the Jane faces task using the same set of face stimuli within the same experimental session has not been measured before.

## 2. Experiment 1

### 2.1. Methods

#### 2.1.1. Participants

Ten individuals with strabismic amblyopia (four males; mean age = 34.9 years,  $SD = 10.4$ ; range: 22–48 years) took part in the experiment. All subjects completed an ophthalmologic and binocular examination and review of their ocular history to confirm the diagnosis of amblyopia. All participants were refracted and visual acuity was assessed (with best correction) using a standard Snellen acuity chart (in meters, expressed in LogMAR equivalent in Table 1). Horizontal and vertical angles of deviation were neutralized and quantified using a prism cover test. Pattern of fixation was evaluated using visuoscopy (see Cooper et al., 2005; for test details). For the purposes of this study, participants with an interocular refractive difference of at least 1.5 D spherical equivalent were classified as anisometric. Six participants had amblyopia in the right eye, and four in the left eye. The range in visual acuity of the amblyopic eye was between +0.2logMAR and +0.8logMAR. In seven participants, strabismus was the primary amblyogenic factor and both strabismus and anisometropia were present in three participants. None of the amblyopic participants exhibited nystagmus. Most of the participants had a history of patching treatment during childhood. Any participant with a known or suspected neurological condition was excluded from the study. More details about characteristics of the ten amblyopic participants are reported in Table 1. Ten normally sighted individuals matched for age, sex and educational level (mean age = 35.0 years,  $SD = 10.3$ , range: 21–49 years) were tested as controls. Written informed consent was obtained from all participants and the study was approved by the local ethical committee of the University of Milano-Bicocca. Participants were treated in accordance with the Declaration of Helsinki.

#### 2.1.2. Material and procedure

The experimental tasks consisted of the “Jane faces task” (Mondloch, Le Grand, & Maurer, 2002) and of the “Mooney task” (Mooney, 1957). Participants sat 57 cm from a 17" TFT-computer monitor (1280 × 800 pixels at a refresh rate of 60 Hz). A chin-rest was used to ensure that the eyes of the participants were aligned with the middle of the screen. The software E-prime 2.0 (Psychology Software Tools, Pittsburgh, PA) was used for stimuli presenta-

tion and data collection. Each participant performed each task twice, one viewing the stimuli with two eyes and the other using one eye only (the other eye was covered with a patch). One half of the participants started with the binocular condition and the other half with the monocular condition. Participants performed each task (Jane faces and Mooney task) binocularly and monocularly before being tested in the other task. One half of the participants performed the Jane faces task before the Mooney task, the other half performed the Mooney task first. The two tasks were intermixed by a 15 min break. The same order of tasks and testing condition (binocular and monocular) was used for each amblyopic participant and his/her control. In the monocular condition, amblyopes were tested using their amblyopic eye; control participants were tested using the same eye of the matched amblyopic participant.

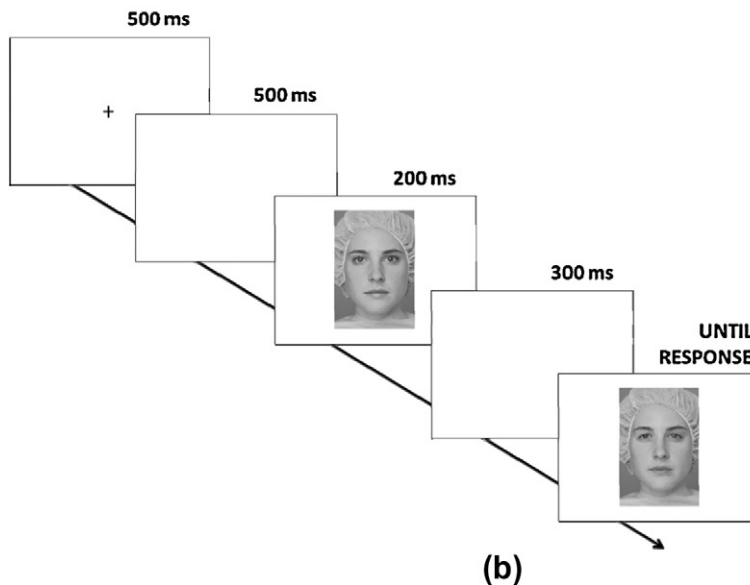
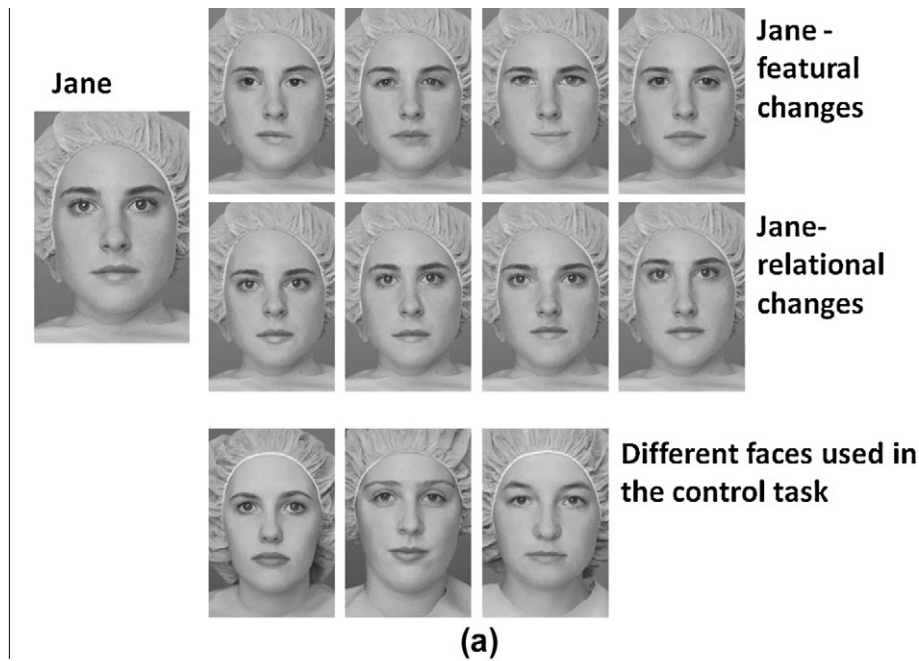
**2.1.2.1. Jane faces task.** Fig. 1 shows the faces used as stimuli (panel A) and the timeline of an experimental trial (panel B). The stimuli used were identical to those created and used by Mondloch and colleagues (Maurer et al., 2007; Mondloch, Le Grand, & Maurer, 2002). Specifically, stimuli consisted of gray scale images of Caucasian female faces that were taken under standard lighting conditions (Geldart, 2000). The photograph of a single face (called “Jane”) was modified by replacing the model's eyes and mouth with the features of the same length from different females (featural set), or by moving the eyes up or down from the original, the eyes closer together or farther apart, and the mouth up or down (relational set). Four new versions of Jane (“Jane's sisters”) were created for the featural set and four for the relational set. The two sets were presented in separate blocks. In each set, all the possible pair-combinations of the five faces were used; in particular, each set consisted of 20 “different” trials plus 10 “same” trials in which the two faces of the pair presented were identical. In the upright condition, all the faces in the set were presented in the upright canonical position. In the inverted condition, all the faces in the set were presented upside-down. A control set was also created in which the original Jane face was presented together with three other females' faces (“Jane's cousins”). All the possible combinations of these faces were used, resulting in 20 trials (in eight of which the faces in the pair were identical). Faces in the control set were only presented in the upright canonical orientation.

Before the experiment, participants were shown Jane and her sisters simultaneously and told that they would see one of the faces flash quickly on the screen followed by another face. They were instructed to press a key with the index finger if the second face matched the first face and to press with the middle finger if the two faces were different (for half the participants the assignments of response keys were reversed). The speed of responding was emphasized in addition to accuracy. Faces were presented in the middle of the screen and subtended a visual angle of approximately 15 deg in height and 10 deg in width. The back color of the screen was in medium gray (R, G, B = 127,127,127). Each trial started with a central fixation cross that was presented for 500 ms followed by a blank screen (500 ms). Hence, the first face was presented for 200 ms, followed by a blank screen showing up for 300 ms and then by the second to be matched face that remained visible until participants responded. Faces-pairs in each set were presented in random order. Before each set presentation, a shorter practice set was presented consisting of 12 trials, in which a combination of three different faces and their modified version (differing for either featural or relational characteristics) were presented in the same orientation as in the following experimental set (in the practice set of the control condition only the three original faces were used in all the possible combinations). In half of the practice trials, the faces were identical.

**Table 1**  
Characteristics of the amblyopic participants.

Subject	Age (years)	Sex	Highest level of education	Hand dominance	Aetiology	Refraction	Amblyopic eye	VA decimal (logMAR)	Fixation	Strabismus	Strabismus onset (years)	Relevant History	Reason for surgery
1	42	F	High school	R	Str	OD PI + 0.75 × 150° OS −0.25 sph	OS	1/10 (+0.8)	Central- Unilateral	Far 4° Eso Near 4° Eso	3	(i) Occlusion therapy between 4 and 6 y.o. (ii) Surgery at 6 y.o. (iii) First Rx at 4 y.o.	Correct esotropia, binocular
2	30	M	Master degree	R	Str + An	OD + 0.50 sph OS −2.00 sph	OD	3/10 (+0.5)	Central- Unilateral	Far 2° Eso Near 3° Eso	3	(i) Occlusion therapy between 5 and 7 y.o. (ii) Unconfirmed age at surgery (iii) First Rx at 5 y.o.	Correct esotropia, binocular
3	35	F	High school	R	Str	OD PI + 2.00 × 90° OS PI + 1.00 × 95°	OD	5/10 (+0.3)	Central- Unilateral	Far 3° Eso Near 3° Eso	3	(i) Occlusion therapy between 4 and 6 y.o. (ii) Surgery at 6 y.o. (iii) First Rx at 4 y.o.	Correct esotropia, binocular
4	30	F	Master degree	R	Str	OD −2.00 sph OS −2.00 sph	OD	6/10 (+0.2)	Central- Unilateral	Far 10° Exo Near 8° Exo	2	(i) Occlusion therapy between 4 and 6 y.o. (ii) No surgery (iii) first Rx at 4 y.o.	na
5	22	M	High school	R	Str	OD + 1.00 sph OS + 0.50 sph	OD	2/10 (+0.7)	Central- Unilateral	Far 3° Eso Near 5° Exo	2	Documented strabismus at infancy (i) Occlusion therapy between 3 and 6 y.o. (ii) No surgery (iii) First Rx at 3 y.o.	na
6	22	M	High school	R	Str	OD −0.50 sph OS −0.50 sph	OS	6/10 (+0.2)	Central- Unilateral	Far 4° DVD Near 4° DVD	3	(i) Occlusion therapy between 3 and 6 y.o. (ii) No surgery (iii) Unconfirmed age of first Rx	na
7	47	F	High school	R	Str	OD −1.25 sph OS −1.00 sph	OS	2/10 (+0.7)	Central- Unilateral	Far 4° Eso Near 4° Eso	2	(i) Occlusion therapy between 2 and 4 y.o. (ii) Surgery at 4 y.o. (iii) Unconfirmed age of first Rx	Correct esotropia, binocular
8	48	F	High school	L	Str + An	OD PI −1.75 × 140° OS PI −3.50 × 30°	OS	2/10 (+0.7)	Central- Unilateral	Far 8° Exo Near 8° Exo	2	Congenital exotropia (i) Occlusion therapy between 2 and 4 y.o. (ii) Surgery at 3 y.o. (iii) Unconfirmed age of first Rx	Correct exotropia, binocular
9	26	M	Master degree	R	Str	OD + 4.00 sph OS + 4.50 sph	OD	6/10 dec (+0.2)	Central- Unilateral	Far 3° Eso Near 4° Eso	2	Documented strabismus at infancy (i) Occlusion therapy between 3 and 6 y.o. (ii) Surgery at 7 y.o. (iii) Unconfirmed age of first Rx	Correct esotropia, binocular
10	47	F	Secondary school	L	Str + An	OD + 2.50 sph OS + 1.00 sph	OD	5/10 (+0.3)	Central- Unilateral	Far 17° Eso Near 17° Eso	2	(i) Occlusion therapy between 4 and 6 y.o. (ii) No surgery (iii) Unconfirmed age of first Rx	na

*Abbreviations:* OS: left eye; OD: right eye; y.o: years old; Str: strabismus; An: anisometropia; DVD = dissociated vertical deviation; VA: visual acuity assessed with a standard Snellen acuity chart (in meters) and expressed in LogMAR equivalent. Note that visual acuity was assessed under best optical correction.



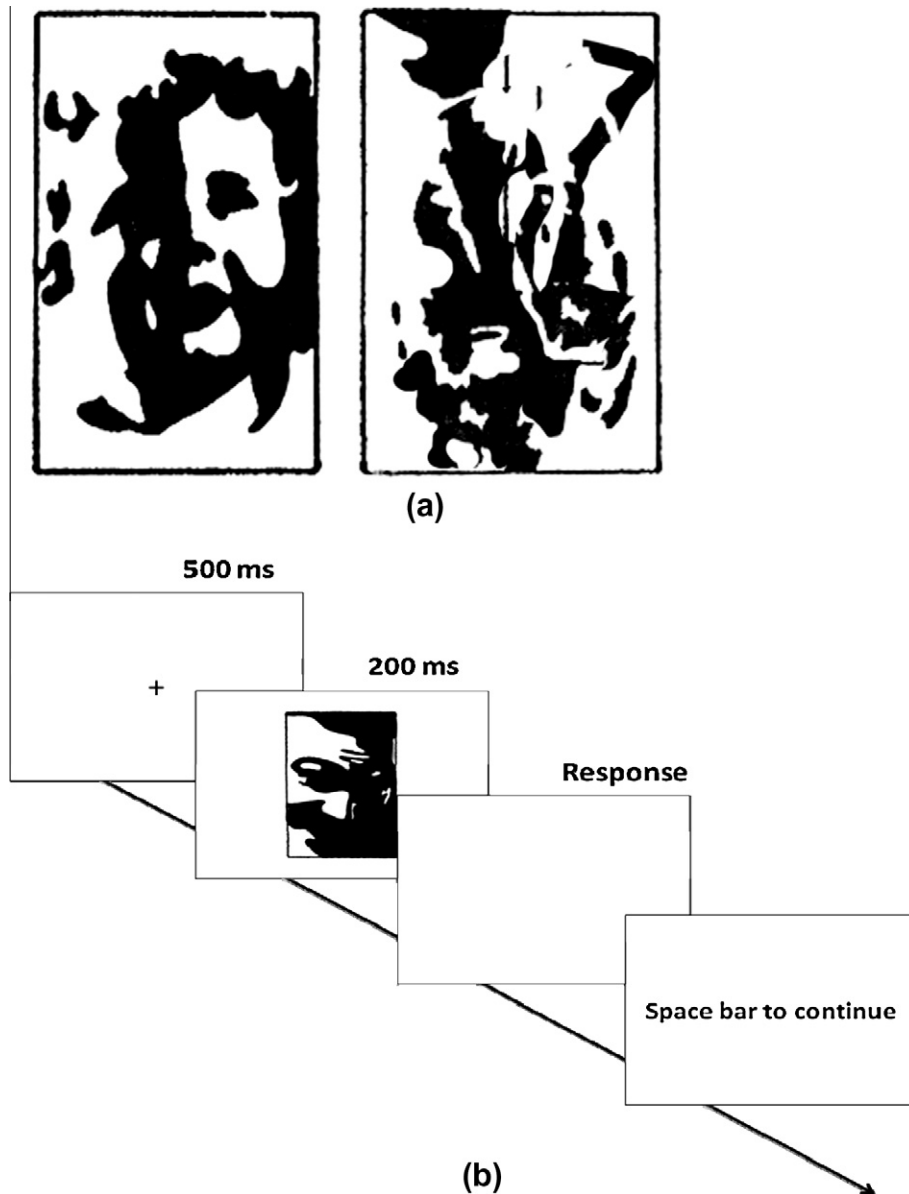
**Fig. 1.** (a) The faces used in the Jane faces task and in the control task. (b) The timeline of an experimental trial.

The experimental sets were presented in two possible orders: (A) (1) featural upright set, (2) featural inverted set, (3) relational upright set (4) relational inverted set, (5) control set (only upright); (B) (1) relational upright set, (2) relational inverted set, (3) featural upright set, (4) featural inverted set, (5) control set (only upright). Half of the amblyopic participants performed the experiment according to order (A) and half according to order (B). The same order assigned to each participant was used in the monocular as well as in the binocular condition. Control participants performed the experiments in the same order as their corresponding amblyopic matches. No feedback was given during the experiment about level of performance. The whole procedure lasted approximately 60 min.

**2.1.2.2. Mooney faces detection task.** The stimuli used in the Mooney task were drawn from the original set of 40 “Mooney faces”

created by Mooney (1957). These two-tone types of face stimuli belong to the standard repertoire of face researchers to test the ability to form a global and coherent perceptual representation on the basis of few details (perceptual closure ability). Additionally, we created 40 new stimuli on the basis of the original set by changing the position of several black areas to generate non-face control stimuli matched for the amount of black and white (see Fig. 2a). The timeline of an experimental trial is shown in Fig. 2b.

Each experimental trial started with a central fixation cross that appeared on a medium grey screen for 500 ms. This was followed by the presentation of one face or one non-face in the middle of the screen (on a grey background) for 200 ms. Each face or non-face stimulus approximately subtended 15 deg in height and 10 deg in width. Hence, the screen was blanked and participants were instructed to press a key with the index finger if the stimulus was recognized as a face and to press with the middle finger if the



**Fig. 2.** (a) Example of a Mooney face (left) and of a non-face (right). (b) The timeline of an experimental trial.

stimulus was classified as a non-face (for half the participants the assignments of the response keys were reversed). By pressing the space bar participants could start the next trial. Both accuracy and speed were encouraged. Stimuli were presented in random order. Before the experiment, participants were presented with a practice task to familiarize themselves with the task. In the practice task 20 Mooney faces and 20 Mooney “non-faces” were presented in random order. The stimuli used in the practice test were additionally created with the same graphic procedure described above preventing the participants to familiarize with the experimental stimuli. No feedback was given during the experiment about level of performance. The whole procedure lasted about 30 min.

## 2.2. Results

Percentages of correct responses and median response times on correct trials were calculated for both the Jane faces task and the Mooney task. Separate analyses were conducted for the binocular

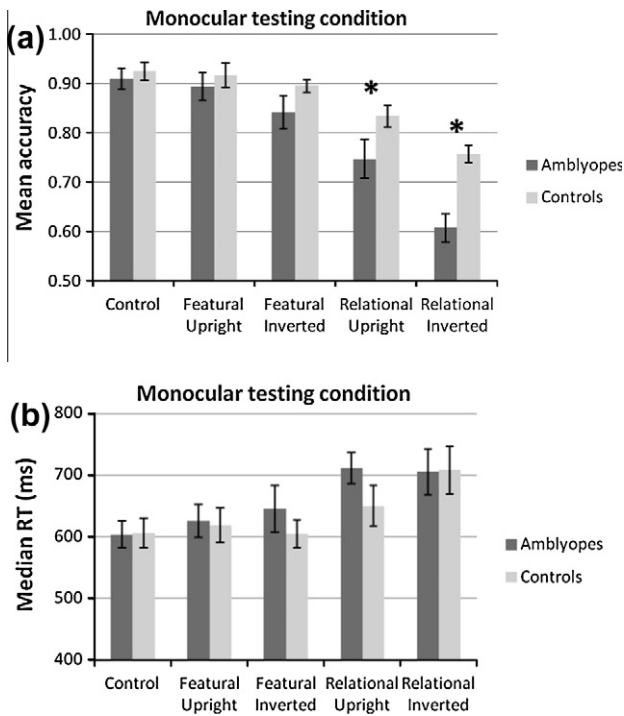
testing and the monocular testing condition. The software SPSS 13.0 for Windows was used for data analysis.

### 2.2.1. Jane faces task

Two separate three-way mixed-design Analysis of Variance (ANOVA) with *set* (relational vs. featural) and *orientation* (upright vs. inverted) as within-subjects variables, and *group* (amblyopes vs. controls) as between-subjects variable were carried out on mean accuracy and on median reaction times for correct responses. The control condition was analyzed separately.

**2.2.1.1. Monocular testing condition.** Mean accuracy and median RT in the monocular testing condition for each experimental condition and for each group are reported in Fig. 3.

*Accuracy:* The ANOVA showed main effects of *set*,  $F(1,18) = 70.16$ ,  $p < .001$ ,  $\eta_p^2 = .80$ , *orientation*,  $F(1,18) = 19.65$ ,  $p < .001$ ,  $\eta_p^2 = .52$ , and *group*,  $F(1,18) = 9.06$ ,  $p = .008$ ,  $\eta_p^2 = .34$ . The main effects were qualified by significant two-way interactions between *set* and *orientation*,  $F(1,18) = 6.44$ ,  $p = .021$ ,  $\eta_p^2 = .26$ , and between



**Fig. 3.** (a) Mean accuracy and (b) median reaction times (RTs) for correct responses of amblyopes and control participants in the different conditions of the Jane faces task for the monocular testing session. Accuracy and RT in the control task are also reported. Error bars represent  $\pm 1$  SEM. Asterisks indicate the presence of a significant difference between the two groups.

set and group,  $F(1, 18) = 5.00$ ,  $p = .038$ ,  $\eta_p^2 = .26$ . Neither the interaction group by orientation ( $p = .17$ ) nor group by set by orientation ( $p = .57$ ) reached significance. The main effect of set was due to performance being overall higher for the featural set ( $M = .89$ ,  $SD = .07$ ) than for the relational set ( $M = .74$ ,  $SD = .09$ ). The main effect of orientation was due to accuracy being higher for upright ( $M = .84$ ,  $SD = .07$ ) than for inverted faces ( $M = .78$ ,  $SD = .09$ ). However, the inversion cost was higher for the relational than for the featural set, as suggested by the significant interaction set by orientation and confirmed by pairwise comparisons,  $t(19) = 1.84$ ,  $p = .08$ ,  $d = .41$  (only approaching significance) for the featural set, and  $t(19) = 4.65$ ,  $p < .001$ ,  $d = 1.04$  (fully significant), for the relational set. The main effect of group was due to amblyopic participants overall performing less accurately than their matched controls,  $M(\text{amblyopes}) = .77$  with  $SD = .08$ ,  $M(\text{controls}) = .85$  with  $SD = .03$ . However, this effect was further modulated by set: in fact, amblyopes performed significantly lower than controls in the relational set,  $t(18) = 3.57$ ,  $p = .002$ ,  $d = .82$ , but not in the featural set,  $t(18) = 1.27$ ,  $p = .22$ , *n.s.*, regardless of orientation.

Importantly, the performance of the two groups did not differ in the control condition,  $t(18) = .54$ ,  $p = .60$ ,  $M(\text{amblyopes}) = .91$ ,  $SD = .07$ ;  $M(\text{controls}) = .93$ ,  $SD = .06$ .

A correlational analysis was run to verify whether the severity of the visual deficit (visual acuity of the amblyopic eye in logMAR) was related to the performance in either the relational or the featural set. Note that a negative correlation would indicate that more severe visual deficits result in lower scores (this because for the logMAR scale higher values indicate worse visual acuity). For the relational set, the correlation was not significant, neither for upright faces,  $r = -.28$ ,  $p = .43$ , nor inverted faces,  $r = -.35$ ,  $p = .33$ . In contrast, in the featural set, we found significant negative correlations for upright,  $r = -.66$ ,  $p = .037$ , as well as inverted faces,  $r = -.85$ ,  $p = .002$ .

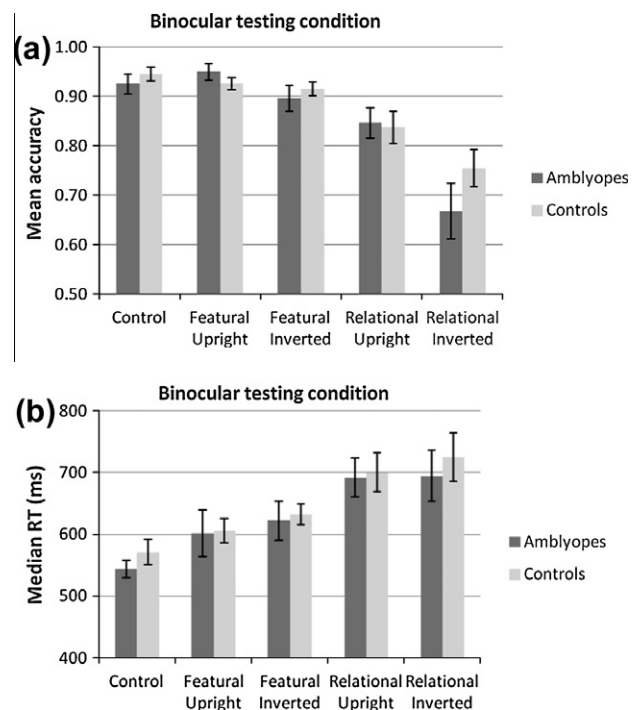
**Reaction times:** The effect of set was significant,  $F(1, 18) = 19.17$ ,  $p < .001$ ,  $\eta_p^2 = .52$ . None of the other main effects or interactions reached significance. The main effect of set was due to participants being overall slower for the relational set ( $M = 694.0$  ms,  $SD = 95.5$ ) than for the featural set ( $M = 623.9$  ms,  $SD = 78.2$ ). Reaction times in the control condition did not differ between the two groups ( $p = .95$ ).

**2.2.1.2. Binocular testing condition.** Mean accuracy and median RT in the binocular testing condition for each experimental condition and for each group are reported in Fig. 4.

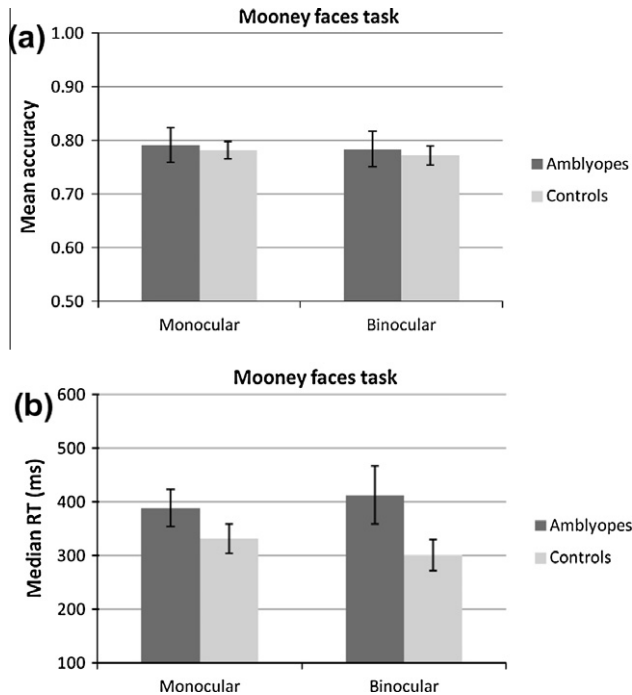
**Accuracy:** The ANOVA revealed a significant effect of set ( $p < .001$ ,  $\eta_p^2 = .72$ ), orientation ( $p < .001$ ,  $\eta_p^2 = .53$ ), and of the interaction set by orientation ( $p = .008$ ,  $\eta_p^2 = .33$ ), indicating overall higher performances for the featural set than for the relational set and for upright than for inverted faces, with the inversion effect being more detrimental for the relational set (see Fig. 5). Group was not significant ( $p = .55$ ), nor did it interact with set ( $p = .36$ ) or orientation ( $p = .07$ ). The performance of the two groups did not differ in the control condition ( $p = .42$ ).

**Reaction times:** The ANOVA showed significant effects of set ( $p = .001$ ,  $\eta_p^2 = .47$ ) and orientation ( $p = .042$ ,  $\eta_p^2 = .21$ ). Participants were overall slower for the relational set than for the featural set and overall slower with inverted faces than with upright faces. Neither the effect of group ( $p = .72$ ) nor any of the interactions were significant. Reaction times in the control condition did not differ between the two groups ( $p = .29$ ).

In order to control for possible effects of unequal number of same/different trials in determining different response biases in amblyopic and control participants, we compared the response bias ("c", see Macmillan & Creelman, 1991) of the two groups in the monocular testing and in the binocular testing condition. Although control participants tended to be liberal overall (i.e., number of false alarms higher than number of missed differences)



**Fig. 4.** (a) Mean accuracy and (b) median correct RTs of amblyopes and control participants in the different conditions of the Jane faces task for the binocular testing session. Accuracy and RT in the control task are also reported. Error bars represent  $\pm 1$  SEM.



**Fig. 5.** (a) Mean accuracy and (b) median correct RTs of amblyopes and control participants in the Mooney faces task for the monocular and binocular testing sessions. Error bars represent  $\pm 1$  SEM.

and amblyopic individuals tended to be conservative overall in both eye-testing conditions, the two groups significantly differed in the monocular testing condition,  $t(18) = 2.93$ ,  $p = .009$ , but not in the binocular testing condition,  $t(18) = 1.55$ ,  $p = .14$ , indicating that amblyopic participants were particular “prudent” when tested with their amblyopic eye. The response criterion was not affected by set or orientation (all tests for significance were  $p > .05$ ).

### 2.2.2. Mooney task

Independent-samples two-tailed  $t$ -tests were carried out to compare the two groups (amblyopes and normally sighted controls) in the Mooney faces task, both for mean accuracy and median reaction times for correct responses. Mean accuracy and median response latencies for correct responses of amblyopes and control subjects in the monocular and binocular testing conditions for the Mooney task are reported in Fig. 5.

In the monocular testing condition, the two groups were found to perform similarly both in terms of accuracy,  $t(18) = .25$ ,  $p = .81$ , and reaction times,  $t(18) = 1.28$ ,  $p = .22$ . A similar pattern was reported in the binocular testing condition, with the two groups performing similarly both in terms of accuracy,  $t(18) = .32$ ,  $p = .75$ , and response latencies,  $t(18) = 1.80$ ,  $p = .09$ . There was no a significant correlation between visual acuity of the amblyopic eye and scores in the monocular viewing condition,  $r = -.24$ ,  $p = .50$ .

## 3. Experiment 2: test-retest reliability

In Experiment 1, the order of binocular/monocular testing was counterbalanced across participants within each of the two experimental groups and between the two groups thus controlling for possible effects of testing order. However, we nonetheless considered it important to provide a measure of test-retest reliability to rule out any possible confounding effect in determining the pattern of results we reported.

### 3.1. Method

#### 3.1.1. Participants

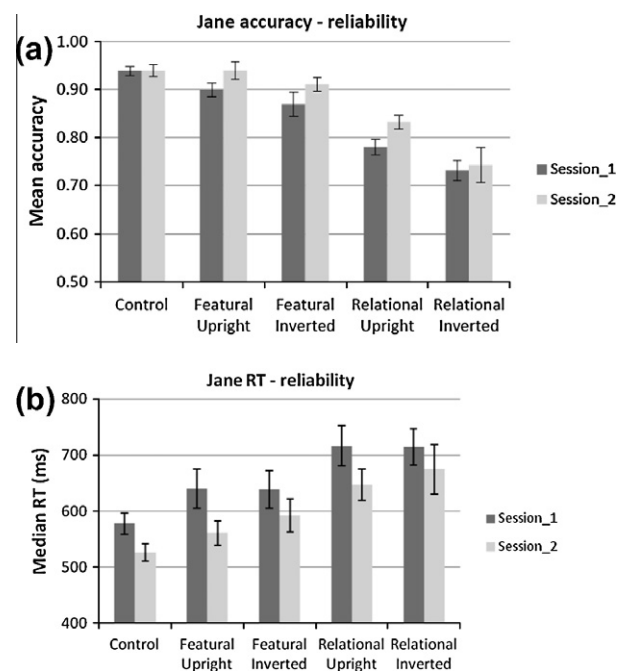
A new group of 18 subjects (7 males; mean age = 28.5 years,  $SD = 4.91$ ; range: 22–38 years), all with normal or corrected-to-normal vision, were tested on the Jane and the Mooney tasks twice in a row during the same experimental session.

#### 3.1.2. Material and procedure

Material and procedure were the same as in the main experiment, but participants performed both sessions using the two eyes. Nine participants performed the Jane task first followed by the Mooney task (session 1) and then again the Jane task and the Mooney task (session 2). The other nine participants performed the tests in the reversed order. Order of sub-conditions of the Jane faces task was counterbalanced as in the main experiment.

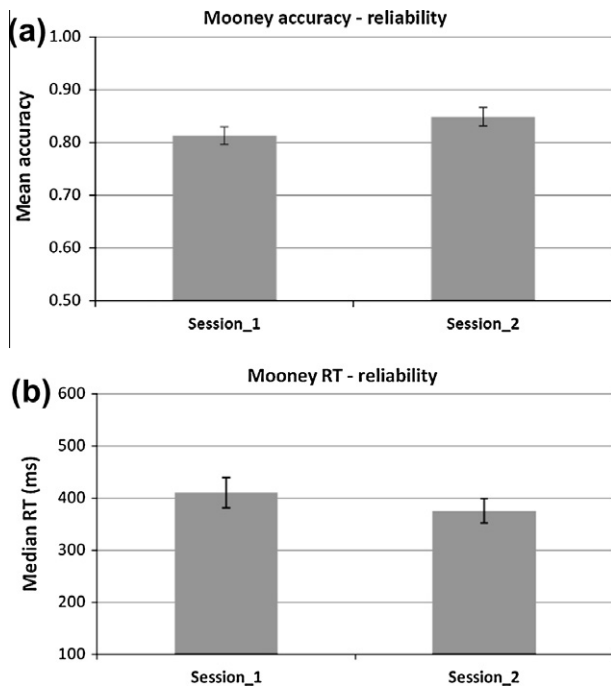
### 3.2. Results

Reliability data for the Jane task are reported in Fig. 6. Correlational analyses (one-tailed Pearson correlation) on mean accuracy showed that for the Jane task, performances across session 1 and 2 were significantly correlated for all the experimental conditions (except for the control Jane task in which correlation only approached statistical significance): featural upright set ( $r = .688$ ,  $p = .001$ ), featural inverted set ( $r = .504$ ,  $p = .016$ ), relational upright set ( $r = .403$ ,  $p = .049$ ), relational inverted set ( $r = .411$ ,  $p = .045$ ), control task ( $r = .334$ ,  $p = .088$ ). A repeated-measures ANOVA with *session* (first presentation vs. second presentation of the task), *set* (relational vs. featural) and *orientation* (upright vs. inverted) as within-subjects variables was carried out to verify possible learning effects between the two sessions. As expected, the effect of session was significant,  $F(1,17) = 5.96$ ,  $p = .026$ ,  $\eta_p^2 = .26$ , with participants' accuracy being overall higher in the second ( $M = .86$ ) than in the first session ( $M = .82$ ). Testing session did not significantly interact with either set ( $p = .67$ ) or orientation ( $p = .33$ ), indicating that learning effects were comparable for the different experimental conditions. No learning effects were



**Fig. 6.** (a) Mean reliability (session 1 and 2) for accuracy and (b) for median RTs in the different conditions of the Jane faces task. Error bars represent  $\pm 1$  SEM.





**Fig. 7.** (a) Mean reliability (session 1 and 2) for accuracy and (b) for median RTs in the different conditions of the Mooney faces task. Error bars represent  $\pm 1$  SEM.

observed for the Jane control task,  $t(17) = .00$ ,  $p = 1.0$ , possibly due to ceiling effects ( $M = .94$  in both session 1 and 2).

The same pattern of significant correlations was also reported when considering median RT: feature upright set ( $r = .729$ ,  $p < .001$ ), featural inverted set ( $r = .894$ ,  $p < .001$ ), relational upright set ( $r = .580$ ,  $p = .006$ ), relational inverted set ( $r = .724$ ,  $p < .001$ ), control task ( $r = .817$ ,  $p < .001$ ). A similar ANOVA was performed for RT as that carried out for Accuracy (see above). The effect of session was significant,  $F(1, 17) = 10.17$ ,  $p = .005$ ,  $\eta_p^2 = .37$ , indicating faster response latencies in the second ( $M = 618.8$  ms) than in the first testing session ( $M = 673.3$  ms). As in case of accuracy, learning effects in RT were comparable across the different experimental conditions, as indicated by the lack of significant interactions between session and either set ( $p = .76$ ) or orientation ( $p = .16$ ). A significant learning effect also emerged in the Jane control task, with participants responding significantly faster in the second than in the first session,  $t(17) = 4.65$ ,  $p < .001$ .

Reliability data for the Mooney task are reported in Fig. 7. Correlational analyses (one-tailed Pearson correlation) showed that performance across session 1 and 2 was significantly positively correlated both when considering mean accuracy ( $r = .892$ ,  $p < .001$ ) and median RT ( $r = .896$ ,  $p < .001$ ). Moreover, participants performed significantly better in session 2 than in session 1, both in terms of accuracy,  $t(17) = 4.31$ ,  $p < .001$ , and in terms of lower reaction times,  $t(17) = 2.65$ ,  $p = .017$ .

### 3.3. General discussion

The goal of the present study was to investigate whether strabismic amblyopia affects face processing and, in particular, whether it selectively affects any of the different sub-processes involved in face detection and discrimination. In our study, a group of strabismic amblyopes were tested both monocularly (using their amblyopic eye) and binocularly in two tasks, one based on a Gestalt representation of a face (the Mooney faces task, see Mooney, 1957) and the other testing featural and relational processing of faces (the Jane faces task, see Mondloch, Le Grand, & Maurer,

2002). We showed that when strabismic amblyopes were tested using their amblyopic eye, a deficit emerged compared to normally sighted participants in discriminating two faces on the basis of second-order relations (i.e., the relational set of the Jane faces task), whether their level of performance was comparable to that of control participants in face detection (recognition of Mooney faces) and in discriminating faces on the basis of their single featural elements (i.e., featural set of the Jane faces task). No significant differences in performance between strabismic amblyopes and normally sighted participants were observed when they were tested using both eyes.

The selective deficit in processing second-order relations in face stimuli found in our strabismic amblyopic participants resembles that reported in previous works with cataract reversal patients (with early visual deprivation due to congenital cataract/s also leading to amblyopia). Specifically, in a pioneering work by Le Grand et al. (2001), it was found that a group of young patients (age 9–21 years) born with bilateral dense central cataracts and undergoing cataract removal within the first 6 months of life were significantly impaired in the relational set of the Jane faces task (with upright faces only) but not in the featural set (see also Mondloch, Robbins, & Maurer, 2010). A following study (Le Grand et al., 2003) clarified that it is the abnormal visual input to the right hemisphere (due to congenital left cataract) but not to the left hemisphere that prevents the development of efficient processing of second-order relations in face stimuli, in line with consistent evidence indicating that the right hemisphere is more specialized for configural/global processing (e.g., Fink et al., 1997; Maurer et al., 2007). In explaining their results, the authors draw attention to poor visual acuity and contrast sensitivity during infancy such that the visual cortex in infants selectively receives inputs of low spatial frequencies that make the infants sensitive to the spatial relations among facial features, but insensitive to the fine details of the features (cf. de Schonen & Mathivet, 1989; Maurer & Lewis, 2001; for a review). Accordingly, the visual system would then be initially biased toward a configural-like kind of processing. When this information is not available (as in case of infants born with dense cataracts, but also in infants born with severe strabismus), the neural circuits responsible for processing configural aspects of face stimuli (but not of other objects, such as houses, see Robbins et al., 2010) would develop sub-optimally (Le Grand et al., 2001). This explanation would also account for the specific relational processing deficit shown by our strabismic amblyopes. In other words, to be critical in determining the observed deficit is not the amblyopic individuals' spatial frequency sensitivity at the time of testing (both deprivation and strabismic induced amblyopia typically leading to a reduction of sensitivity to high spatial frequencies, cf. Hess & Howell, 1977), but rather the amblyogenic influence on the spatial frequency content (i.e., low spatial frequencies for both those treated for congenital cataract or early strabismus) of the normal input in the early stages of development (i.e. prior to the age of 3). As the exact congenital/infant strabismus status of each participant in this study cannot be confirmed with complete certainty, making direct comparisons with studies of congenital cataracts should be done with caution.

Notably though, in the strabismic amblyopes tested here, the deficit in processing spacing aspects was evident for both upright and inverted faces. This is contrary to reports in cataract reversal patients that were only impaired with upright faces (cf. Le Grand et al., 2001, 2003). These findings are unlikely to depend on spatial frequency tuning since upright and inverted face processing uses similar frequency bands although processing of inverted faces appears less efficient (Gaspar, Sekuler, & Bennett, 2008; Willenbockel et al., 2010). Moreover, for cataract-reversal patients, the deficit also does not extend to spacing differences in monkey faces (whether upright or inverted) or to non-face objects such as houses

(Robbins et al., 2010). This suggests that the deficit following early visual deprivation is specific to upright human faces; the category for which normal adults have especially acute sensitivity. In fact, normally sighted individuals likely rely on a general spacing discrimination mechanism to distinguish among objects (such as houses) or animal faces. This mechanism appears to develop slowly and normally even in early visually deprived patients (Robbins et al., 2010). However, normally sighted adults also make use of an *ad hoc* specific mechanism tuned to human faces from experienced categories (appearing in the standard upright orientation) whose correct development seems to depend on a normal early visual experience (Le Grand et al., 2001, 2003; Robbins et al., 2010, 2012). If strabismic amblyopia selectively affects this specific processing mechanism for standard upright orientation faces, the deficit should not emerge with inverted faces.

Therefore, our finding of a deficit for both upright and inverted human faces in strabismic amblyopes may reflect a more general deficit, beyond the faces category, related to suboptimal functioning of some mid-level visual comparison/alignment skill. In line with this, increasing evidence suggests that the perceptual difficulties experienced by the amblyopes when using their amblyopic eye are due to spatial rather than contrast disturbances. In particular, strabismic amblyopia seems to be associated with positional uncertainty, as demonstrated for instance in paradigms requiring to judge the relative position of a target with respect to a nearby reference, a task in which amblyopes show consistent deficits that appear uncorrelated to either their contrast or acuity loss (see Hess, 2001; for a review). Spatial undersampling has also been found to be affected in amblyopia, with strabismic amblyopes requiring more individual elements to be presented in the pattern to perform at normal level in position discrimination (Wang, Levi, & Klein, 1998) or in pattern perception (Levi, Klein, & Sharma, 1999), even in cases in which the samples are highly visible, suggesting that the samples are not used efficiently by the amblyopic visual system. Notably though, spatial processing deficits do not only pertain to a low level of processing, but also extend to higher levels of processing (Sharma, Levi, & Klein, 2000), suggesting that top-down central mechanisms are also affected. Accordingly, strabismic amblyopes showed a deficit in counting local features (Sharma, Levi, & Klein, 2000) or in integrating local features into a global percept (Simmers & Bex, 2004) even if the single stimuli were stimuli whose spatial frequency and contrast were comfortably within the acuity limit of amblyopic observers and were composed of highly visible and resolvable elements. Recent evidence on the effect of sensory uncertainty due to amblyopia on the planning and execution of visually-guided 3D reaching movements also showed that patients with severe amblyopia had reduced endpoint precision along azimuth and elevation during amblyopic eye viewing (Niechwiej-Szwedo et al., 2012). It might then be the case that the deficit experienced by our strabismic amblyopes in processing relational aspects of faces is related to this high-level spatial deficit rather than being related to low-level limitations (such as blur, visibility, crowding, undersampling or topographical jitter, see Sharma, Levi, & Klein, 2000).

Another aspect to be considered is whether the loss of sensitivity to high spatial frequencies in amblyopes may differentially affect how they use horizontal face information in the discrimination of upright and inverted faces. In fact, a recent paper by Goffaux and Dakin (2010) shows that in visual face processing, normally sighted individuals disproportionately rely on horizontal information. Specifically, when faces are displayed in an upright orientation, there is a robust discrimination advantage in horizontal compared to vertical orientation bands, but the horizontal advantage is eliminated by face inversion (Goffaux & Dakin, 2010). Although contrast sensitivity for horizontal vs. vertical gratings was not directly measured in our amblyopic participants

(given that this test is not part of the routine testing battery of our clinical setting) previous evidence has shown that strabismic amblyopic deficits at threshold are greater for vertical than for horizontal contours (Sireteanu & Singer, 1980). Hence, although future research should properly directly address this issue, it is unlikely that the overall spacing deficit showed by our amblyopes depended on a suboptimal use of the horizontal band of information.

Critically, the strabismic amblyopic participants tested here performed as well as normally sighted controls in the Mooney faces task. Our findings are consistent with previous data showing that patients treated for bilateral cataract performed similarly to normally sighted controls both in terms of accuracy and reaction times in the Mooney task (Mondloch, Le Grand, & Maurer, 2003). In a Mooney face, to perceive any facial feature, such as an eye or a nose, one has first to perceive the image as a face. There is evidence that image segregation is mainly preserved in strabismic amblyopia (Levi, 2007; but see Levi et al., 2007). To perceive a Mooney face one has to somehow segregate the relevant signal from the coextensive noise: the fact that this process was not impaired in our participants is therefore in accordance with previous evidence (Levi, 2007). Our results support Mondloch, Le Grand, and Maurer (2003)'s claim that the eventual development of normal sensitivity to first-order relations (critical for face detection) does not depend upon early normal visual input and that amblyopic patients' poor performance in other aspects of face processing is due to a deficit in processing that occurs after a face is detected (Eimer, 2000; Rossion et al., 2011). In particular, early visual deprivation due to bilateral cataracts (Le Grand et al., 2004) as well as monocular enucleation (Kelly, Gallie, & Steeves, 2011) has been found to cause a deficit in holistic processing tested using the composite-faces task. In this task, the top half of one face is aligned with the bottom half of another, and individuals usually find harder to determine whether the top halves of two faces are identical when they are aligned with different bottom halves; moreover deciding whether two faces are identical is more difficult when the two halves are aligned compared to when they are misaligned (e.g., Young, Hellawell, & Hay, 1987). Although the composite-faces task and the Mooney faces task are both used as measures Gestalt processing of faces, it is likely that they measured partially different mechanisms, the former probably tapping identity recognition that is believed to occur at a later stage than pure face discrimination (Rossion et al., 2011).

The finding of a normal performance of amblyopes when using both eyes is in line with previous evidence finding a limitation in both low and high-level visual functions (e.g., Sharma, Levi, & Klein, 2000; but see Simmers & Bex, 2004) and different cortical responses during face perception (Bankó et al., 2012) only when the amblyopic eye was tested, whereas the fellow eye performs in the normal range and gives rise to normal cortical responses. The binocular viewing condition in our participants is likely to be highly comparable to viewing with the unaffected eye, since there is consistent evidence showing that during dichoptic perception the perceptual input from the amblyopic eye to the visual cortex is usually suppressed (e.g., Farivar et al., 2011). This implies that while during normal binocular viewing the amblyopic eye is open and thus provides neural input to the lateral geniculate and the visual cortex, this input cannot reach awareness, as was demonstrated by a general lack of double vision in strabismic amblyopes. In this regard, it is also worth noting that in strabismic amblyopia, the chronic suppression of the input from the amblyopic eye may cause the loss of perception in the amblyopic eye (Holmes & Clarke, 2006) that may still be subject to residual suppression under monocular viewing conditions.

It is important to note that reaction times of strabismic amblyopes and matched control participants were similar in all experimental conditions, suggesting that amblyopes' impairment in the

relational set of the Jane faces task was not due to a speed-accuracy trade-off (for similar results, see Le Grand et al., 2003). Still, one may object that the deficit shown by our amblyopic participants depended on task difficulty (given the relational set was also the most difficult for normally sighted participants) rather than on the specific type of required processing. However, this possibility appears unlikely when considering the pattern of results obtained in the Mooney faces detection task. Specifically, in this task, patients performed normally even though the control group's accuracy was slightly lower than for Jane relational set (for which amblyopes' performance was abnormal). Moreover, deficit in relational processing cannot be attributed to poor visual acuity *per se* since the magnitude of the deficit in the relational set was not correlated with visual acuity of the amblyopic eye (a similar finding was also reported by Le Grand et al., 2003, who found no correlation between visual acuity of the cataract-reversal eye and accuracy in any of the conditions of the Jane faces task).

In fact, our analyses only revealed a significant correlation between visual acuity in the amblyopic eye and accuracy in the featural set (for both upright and inverted faces). This finding further corroborates the hypothesis that the deficit reported in the relational set cannot be attributed to a mere sensory factor. The correlations we have revealed between acuity in the amblyopic eye and accuracy on the featural task, both upright and inverted, might indicate that strabismic amblyopes with poor acuity will be abnormal for some subtle featural differences. From previous research (Leder & Carbon, 2006), we know that featural information always inherently consists of local plus spacing information as every type of featural change will affect spacing too. It is possible that the subtle and inherent type of spacing information stretches the visual system of amblyopes to their limit. In contrast, when it comes to pure spatial relational information in the spacing condition, it does not depend on the degree of strabismic amblyopia, but amblyopes' visual processing performance just breaks down.

Finally, our results are not likely dependent on possible methodological artifacts due to participants being tested twice in the same task. This is supported by the fact that we also provided evidence from a further group of control participants ( $n = 18$ , Experiment 2) indicating that performance in the Mooney faces detection task and in each condition of the Jane faces task were highly positively correlated across two consecutive sessions when considering accuracy and reaction times as performance outcomes. These findings ensure that the tasks we used were internally reliable, whereas learning effects – consistently reported across the different experimental conditions in Experiment 2 – were controlled for by an accurate counterbalancing of testing conditions order across participants in the main Experiment (Experiment 1). Moreover, our results do not depend on a possible interaction between response bias (i.e., overall participants' tendency to respond "same" or "different") and task condition in the Jane faces task. In fact, although amblyopic participants tended to be more "conservative" overall in their responses (i.e., the number of missed differences were higher than false alarms) compared to control participants (especially when tested with their amblyopic eye), this behavioral strategy did not vary across task conditions (i.e., they were as just as conservative in the featural as in the relational set).

Overall, our findings suggest that strabismic amblyopia leads to a selective deficit in processing second-order relations in faces, whereas processing of single features and mechanisms mediating Gestalt processing of faces are unaffected. These data add to previous reports (e.g., Sharma, Levi, & Klein, 2000) that qualify the deficits induced by strabismic amblyopia also as high-level and not just as low-level. Notably, the deficit in our participants disappeared when they were tested binocularly, indicating that in real-life situation these individuals are able to discriminate among

individuals' faces as efficiently as normally sighted individuals. Finally, our data support the view that distinct functional mechanisms mediate face detection and configural processing of (2nd-order) relational information of faces, with strabismic amblyopia only affecting the latter. From this perspective, the present findings point to the importance of research on disorders of the visual system for obtaining clearer definitions of and distinctions between different visual processes involved in face recognition, also allowing for development of more conclusive theories of vision.

## Acknowledgments

The authors thank Cathy Mondloch and her colleagues for providing the original stimuli of Mondloch, Le Grand, and Maurer (2002) as stimuli for the "Jane Face task". This work was supported by Vigoni/DAAD grants (years 2012–2013) to Z.C. and C.C.C. and by a FIRB grant (RBF12FOBD\_003) to Z.C.

## References

- Avidan, G., Tanzer, M., & Behrmann, M. (2011). Impaired holistic processing in congenital prosopagnosia. *Neuropsychologia*, *49*(9), 2541–2552.
- Bankó, E. M., Körtvélyes, J., Németh, J., Weiss, B., & Vidnyánszky, Z. (2012). Amblyopic deficits in the timing and strength of visual cortical responses to faces. *Cortex*.
- Barnes, G. R., Hess, R. F., Dumoulin, S. O., Achtman, R. L., & Pike, G. B. (2001). The cortical deficit in humans with strabismic amblyopia. *Journal of Physiology*, *533*(Pt. 1), 281–297.
- Bombardi, D., Mast, F. W., & Lobmaier, J. S. (2009). Featural, configural, and holistic face-processing strategies evoke different scan patterns. *Perception*, *38*(10), 1508–1521.
- Bruce, V., & Young, A. (1986). Understanding face recognition. *British Journal of Psychology*, *77*(3), 305–327.
- Carbon, C. C. (2011). The first 100 milliseconds of a face: On the microgenesis of early face processing. *Perceptual and Motor Skills*, *113*(3), 859–874.
- Carbon, C. C., & Leder, H. (2005). When feature information comes first! Early processing of inverted faces. *Perception*, *34*(9), 1117–1134.
- Collishaw, S. M., & Hole, G. J. (2000). Featural and configurational processes in the recognition of faces of different familiarity. *Perception*, *29*, 893–909.
- Cooper, J., Gelfond, I., Carlson, P. E., Campolattaro, B., & Wang, F. (2005). Comparison of eccentric fixation measurements using the streak target of an ophthalmoscope and a traditional visuoscopy target. *Journal of Pediatric Ophthalmology & Strabismus*, *42*(2), 89–96.
- de Schonen, S., & Mathivet, E. (1989). First come first served: a scenario about the development of hemispheric specialization in face processing in infancy. *European Bulletin of Cognitive Psychology*, *9*, 3–44.
- Duchaine, B., & Nakayama, K. (2005). Dissociations of face and object recognition in developmental prosopagnosia. *Journal of Cognitive Neuroscience*, *17*(2), 249–261.
- Eimer, M. (2000). Event-related brain potentials distinguish processing stages involved in face perception and recognition. *Clinical Neurophysiology*, *111*, 694–705.
- Farivar, R., Thompson, B., Mansouri, B., & Hess, R. F. (2011). Interocular suppression in strabismic amblyopia results in an attenuated and delayed hemodynamic response function in early visual cortex. *Journal of Vision*, *11*(14).
- Farzin, F., & Norcia, A. M. (2011). Impaired visual decision-making in individuals with amblyopia. *Journal of Vision*, *11*(14), 6, 1–10.
- Fink, G. R., Halligan, P. W., Marshall, J. C., Frith, C. D., Frackowiak, R. S., & Dolan, R. J. (1997). Neural mechanisms involved in the processing of global and local aspects of hierarchically organized visual stimuli. *Brain*, *120*(Pt 10), 1779–1791.
- Freire, A., Lee, K., & Symons, L. A. (2000). The face-inversion effect as a deficit in the encoding of configural information: Direct evidence. *Perception*, *29*, 159–170.
- Gaspar, C., Sekuler, A. B., & Bennett, P. J. (2008). Spatial frequency tuning of upright and inverted face identification. *Vision Research*, *48*(28), 2817–2826.
- Geldart, S. (2000). *Experiential influences on the development of face perception*. Unpublished Ph.D. thesis. Hamilton, Ontario, Canada: McMaster University.
- Geldart, S., Mondloch, C., Maurer, D., de Schonen, S., & Brent, H. (2002). The effects of early visual deprivation on the development of face processing. *Developmental Science*, *5*, 490–501.
- Goffaux, V., & Dakin, S. C. (2010). Horizontal information drives the specific signatures of face processing. *Frontiers in Perception Science*, *1*(143), 1–14.
- Grill-Spector, K., Knouf, N., & Kanwisher, N. (2004). The fusiform face area subserves face perception, not generic within-category identification. *Nature Neuroscience*, *7*, 555–562.
- Grüter, T., & Carbon, C. C. (2010). Escaping attention. Some cognitive disorders can be overlooked. *Science*, *328*(5977), 435–436.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, *4*, 223–233.
- Hess, R. F. (2001). Amblyopia: Site unseen. *Clinical and Experimental Optometry*, *84*, 321–336.

- Hess, R. F., & Howell, E. R. (1977). The threshold contrast sensitivity function in strabismic amblyopia: Evidence for a two type classification. *Vision Research*, 17, 1049–1055.
- Ho, C. S., & Giaschi, D. E. (2006). Deficient maximum motion displacement in amblyopia. *Vision Research*, 46(28), 4595–4603.
- Holmes, J. M., & Clarke, M. P. (2006). Amblyopia. *Lancet*, 367, 1343–1351.
- Imamura, K., Richter, H., Fischer, H., Lennerstrand, G., Franzén, O., Rydberg, A., et al. (1997). Reduced activity in the extrastriate visual cortex of individuals with strabismic amblyopia. *Neuroscience Letters*, 225, 173–176.
- Kelly, K. R., Gallie, B. L., & Steeves, J. K. (2011). Impaired face processing in early monocular deprivation from enucleation. *Optometry & Vision Science*, 89(2), 137–147.
- Latinus, M., & Taylor, M. J. (2005). Holistic processing of faces: Learning effects with Mooney faces. *Journal of Cognitive Neuroscience*, 17, 1316–1327.
- Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. P. (2001). Neuroperception. Early visual experience and face processing. *Nature*, 410, 890 [Erratum: *Nature*, 412, 786].
- Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. (2003). Expert face processing requires visual input to the right hemisphere during infancy. *Nature Neuroscience*, 6(10), 1108–1112 [Erratum: *Nat Neurosci*. 2003, 6(12):1329].
- Le Grand, R., Mondloch, C., Maurer, D., & Brent, H. (2004). Impairment in holistic face processing following early visual deprivation. *Psychological Science*, 15, 762–768.
- Leder, H., & Carbon, C. C. (2005). When context hinders! Learn-test compatibility in face recognition. *Quarterly Journal of Experimental Psychology Section a—Human Experimental Psychology*, 58(2), 235–250.
- Leder, H., & Carbon, C. C. (2006). Face-specific configural processing of relational information. *British Journal of Psychology*, 97, 19–29.
- Levi, D. M. (2007). Image segregation in strabismic amblyopia. *Vision Research*, 47, 1833–1838.
- Levi, D. M., Klein, S. A., & Sharma, V. (1999). Position jitter and undersampling in pattern perception. *Vision Research*, 39(3), 445–465.
- Levi, D. M., Yu, C., Kuai, S. G., & Rislove, E. (2007). Global contour processing in amblyopia. *Vision Research*, 47, 512–524.
- Lobmaier, J. S., Bolte, J., Mast, F. W., & Dobel, C. (2010). Configural and featural processing in humans with congenital prosopagnosia. *Advances in Cognitive Psychology*, 6, 23–34.
- Macmillan, N. A., & Creelman, C. D. (1991). *Detection theory: A user's guide*. New York: Cambridge University Press.
- Maurer, D., Le Grand, R., & Mondloch, C. (2002). The many faces of configural processing. *Trends in Cognitive Sciences*, 6, 255–260.
- Maurer, D., & Lewis, T. L. (2001). Visual acuity: The role of visual input in inducing postnatal change. *Clinical Neuroscience Research*, 1, 239–247.
- Maurer, D., O'Craven, K., Le Grand, R., Mondloch, C., Springer, M., Lewis, T., et al. (2007). Neural correlates of processing facial identity based on features versus their spacing. *Neuropsychologia*, 45, 1438–1451.
- McKee, S. P., Levi, D. M., & Movshon, J. A. (2003). The nature and variety of visual deficits in amblyopia. *Journal of Vision*, 3, 380–405.
- McKone, E. (2004). Isolating the special component of face recognition, peripheral identification and a Mooney face. *Journal of Experimental Psychology: Learning Memory and Cognition*, 30, 181–197.
- Mercure, E., Dick, F., & Johnson, M. H. (2008). Featural and configural face processing differentially modulate ERP components. *Brain Research*, 1239, 162–170.
- Mondloch, C. J., & Desjarlais, M. (2010). The function and specificity of sensitivity to cues to facial identity: An individual-differences approach. *Perception*, 39, 819–829.
- Mondloch, C. J., Le Grand, R., & Maurer, D. (2002). Configural face processing develops more slowly than featural face processing. *Perception*, 31, 553–566.
- Mondloch, C. J., Le Grand, R., & Maurer, D. (2003). Early visual experience drives the development of some (but not all) aspects of face processing. In O. Pascalis & A. Slater (Eds.), *The development of face processing in infancy and early childhood: Current perspectives* (pp. 99–117). New York: Nova Science Publishers.
- Mondloch, C. J., Maurer, D., & Ahola, S. (2006). Becoming a face expert. *Psychological Science*, 17, 930–934.
- Mondloch, C., Robbins, R., & Maurer, D. (2010). Discrimination of facial features by adults, 10-year-olds and cataractreversal patients. *Perception*, 39(2), 184–194.
- Mooney, C. M. (1956). Closure with negative after-images under flickering light. *Canadian Journal of Psychology*, 10, 191–199.
- Mooney, C. M. (1957). Age in the development of closure ability in children. *Canadian Journal of Psychology*, 11, 219–226.
- Muckli, L., Kiess, S., Tonhausen, N., Singer, W., Goebel, R., & Sireteanu, R. (2006). Cerebral correlates of impaired grating perception in individual, psychophysically assessed human amblyopes. *Vision Research*, 46(4), 506–526.
- Niechwiej-Szwedo, E., Kennedy, S. A., Colpa, L., Chandrakumar, M., Goltz, H. C., & Wong, A. M. (2012). Effects of induced monocular blur versus anisometric amblyopia on saccades, reaching, and eye-hand coordination. *Investigative Ophthalmology and Visual Science*, 53(8), 4354–4362.
- Rhodes, G. (1988). Looking at faces: First-order and second order features as determinants of facial appearance. *Perception*, 17, 43–63.
- Robbins, R., Maurer, D., Hatry, A., Anzures, G., & Mondloch, C. (2012). Effects of normal and abnormal visual experience on the development of opposing aftereffects for upright and inverted faces. *Developmental Science*, 10.
- Robbins, R. A., Nishimura, M., Mondloch, C. J., Lewis, T. L., & Maurer, D. (2010). Deficits in sensitivity to spacing after early visual deprivation in humans: A comparison of human faces, monkey faces, and houses. *Developmental Psychobiology*, 52, 775–781.
- Rossion, B., Caldara, R., Seghier, M., Schuller, A. M., Lazeyras, F., & Mayer, E. (2003). A network of occipito-temporal face-sensitive areas besides the right middle fusiform gyrus is necessary for normal face processing. *Brain*, 126, 2381–2395.
- Rossion, B., Dricot, L., Goebel, R., & Busigny, T. (2011). Holistic face categorization in higher-level cortical visual areas of the normal and prosopagnosic brain: Towards a non-hierarchical view of face perception. *Frontiers in Human Neuroscience*, 4, 225.
- Schwarzer, G., Zauner, N., & Jovanovic, B. (2007). Evidence of a shift from featural to configural face processing in infancy. *Developmental Science*, 10(4), 452–463.
- Scott, L. S., & Nelson, C. A. (2006). Featural and configural face processing in adults and infants: A behavioral and electrophysiological investigation. *Perception*, 35(8), 1107–1128.
- Sharma, V., Levi, D. M., & Klein, S. A. (2000). Undercounting features and missing features: Evidence for a high-level deficit in strabismic amblyopia. *Nature Neuroscience*, 3, 496–501.
- Simmers, A. J., & Bex, P. J. (2004). The representation of global spatial structure in amblyopia. *Vision Research*, 44(5), 523–533.
- Simmers, A. J., Ledgeway, T., Mansouri, B., Hutchinson, C. V., & Hess, R. F. (2006). The extent of the dorsal extra-striate deficit in Amblyopia. *Vision Research*, 46, 2571–2580.
- Simmons, D. R., Robertson, A. E., McKay, L. S., Toal, E., McAleer, P., & Pollick, F. E. (2009). Vision in autism spectrum disorders. *Vision Research*, 49(22), 2705–2739.
- Sireteanu, R. (2000). The binocular visual system in amblyopia. *Strabismus*, 8, 39–51.
- Sireteanu, R., & Singer, W. (1980). The 'vertical effect' in human squint amblyopia. *Experimental Brain Research*, 40, 354–357.
- Tanaka, J. W., & Farah, M. J. (1993). Parts and wholes in face recognition. *Quarterly Journal of Experimental Psychology, Human Experimental Psychology*, 46, 225–245.
- Taubert, J., Apthorp, D., Aagten-Murphy, D., & Alais, D. (2011). The role of holistic processing in face perception: Evidence from the face inversion effect. *Vision Research*, 51, 1273–1278.
- Wang, H., Levi, D. M., & Klein, S. A. (1998). Spatial uncertainty and sampling efficiency in amblyopic position acuity. *Vision Research*, 38, 1239–1251.
- Willenbockel, V., Fiset, D., Chauvin, A., Blais, C., Arguin, M., & Tanaka, J. W. (2010). Does face inversion change spatial frequency tuning? *Journal of Experimental Psychology: Human Perception and Performance*, 36, 122–135.
- Young, A. W., Hellawell, D., & Hay, D. C. (1987). Configurational information in face perception. *Perception*, 16, 747–759.