Extensive visual training in adulthood significantly reduces the face inversion effect

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The poorer recognition performance for inverted as compared to upright faces is one of the most well-known and robust behavioral effects observed in the field of face perception. Here we investigated whether extensive training at individualizing a large set of inverted faces in adulthood could significantly reduce this inversion effect for novel faces. This issue is important because inverted faces are as complex as upright faces but they are not visually experienced during development. Moreover, inverted faces violate the biological constraints, present at birth, for preferential looking (i.e., a larger number of elements in the top part than the bottom part of the stimulus). Eight adult observers were trained for 2 weeks (16 hr) to individualize 30 inverted face identities presented under different depth-rotated views. Following training, all participants showed a significant reduction of their inversion effect for novel face identities presented in a challenging four-alternatives delayed matching task. This reduction of the face inversion effect was observed in comparison to the magnitude of the same observers' effect before training, and to the magnitude of the face inversion effect of a group of untrained participants. These observations indicate that extensive training in adulthood can lead to a significant reduction of the inversion effect that generalizes to novel faces, suggesting a larger degree of flexibility of the adult face processing system than previously thought.

Keywords: face perception, expertise training, inversion

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Introduction

Faces constitute a special visual category with which human adults show expertise. This expertise in face processing is thought to be based on two major factors: on one hand, biological constraints present in the visual system at birth and, on the other hand, extensive visual experience with faces during development.

Evidence for biological constraints comes from several sources. For instance, newborns look preferentially to faces or to face-like patterns rather than to the same stimuli presented in the inverted orientation, or to other visual control stimuli (Goren, Sarty, & Wu, 1975;

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Johnson, Dziurawiec, Ellis, & Morton, 1991). Whether this face preference is due to face-specific mechanisms organized as such at birth (Farah, Rabinowitz, Quinn, & Liu, 2000; M. Johnson, 1991) or is the result of a more general bias in the newborn's visual system to look at stimuli with a larger number of elements in the top part of the stimulus as compared to the bottom part (Simion, Valenza, Macchi Cassia, Turati, & Umilta, 2002), remains unknown. In any case, such a non-specific bias constrains newborns to orient preferentially to upright rather than to inverted faces (Johnson et al., 1991; Simion et al., 2002). Additional support for the presence of biological constraints that are independent of visual experience has been found in monkeys. When raised without any exposure to faces up to 6 to 24 months of age the non-human primates were found to preferentially look at faces rather than nonface objects immediately following the period of deprivation (Sugita, 2008).

The importance of early visual experience in shaping face recognition abilities is also widely accepted. For instance, dense bilateral cataracts preventing any visual input to the retina from birth until 2 to 19 months of age induce persistent deficits in face perception in adulthood (Geldart, Mondloch, & Maurer, 2002; Le Grand, Mondloch, & Maurer, 2001; Le Grand, Mondloch, Maurer, & Brent, 2003, 2004) to the point where processing of upright faces is only mildly - if at all - better than for inverted faces (Le Grand et al., 2001). These latter studies suggest that there is a sensitive period within the first months of life during which visual stimulation, mainly to the right hemisphere (Le Grand et al., 2003) is crucial to build the neural circuitry responsible for adults' expertise at processing faces. In normally developing infants, early visual experience influences perceptual narrowing of the face perception abilities. Hence, whereas young infants' discrimination abilities up to 6 months of age are broad and extend to faces of other "races" and other species, exposure to a specific subtype of faces will progressively limit these initial discrimination abilities to include only experienced faces, leading to the emergence of the so-called "other-race" (Kelly et al., 2007, 2009,) and "other-species" effects (Pascalis, de Haan, & Nelson, 2002) by the age of 9 months.

Although face recognition abilities emerge and specialize early during development, these abilities maintain a certain degree of plasticity, at least during childhood. Specifically, the other-race effect was reversed (Sangrigoli, Pallier, Argenti, Ventureyra, & de Schonen, 2005) or at least attenuated (de Heering, de Liedekerke, Deboni, & Rossion, 2010) in adult Asian individuals who were exposed to Caucasian faces only in late childhood following adoption by western European families.

In contrast, evidence for a modulation of face recognition abilities in adulthood remains somewhat sparse. For instance, evidence that natural contact with "other-race" individuals decreases the other-race face effect is mixed (Brigham & Barkowitz, 1978; Ng & Lindsay, 1994). More recently, the results of several laboratory training protocols have suggested that the other-race effect can be attenuated when adults are trained for a few hours to individuate faces from an unfamiliar "race" (Lebrecht, Pierce, Tarr, & Tanaka, 2009; McKone, Brewer, MacPherson, Rhodes, & Hayward, 2007; Tanaka & Pierce, 2009). However, these studies suffer from the limitation that they take place in "multi-racial" environments, where other-race effects are known to be weak to start with and could be easily eliminated in an experimental setting even without training (e.g., Hugenberg, Miller, & Claypool, 2007; McKone et al., 2007; Shriver, Young, Hugenberg, Bernstein, & Lanter, 2008; see Rossion & Michel, 2011 for a review of the other-race face effect and a discussion of this issue). Further, most of these studies did not investigate whether or not the effect of the training generalized to new untrained exemplars of other races faces (Lebrecht et al., 2009; McKone et al., 2007; Tanaka & Pierce, 2009), or failed to compare recognition performance of other-race faces to own-race faces (McGugin, Tanaka, Lebrecht, Tarr, & Gauthier, 2011). More convincing evidence for the plasticity of face processes in adulthood comes from a recent study demonstrating that the other-age effect for newborn faces is abolished following individuation training with such faces (Yovel et al., 2012). However, in that study, neonatology nurses exposed naturally to newborn faces do not show a reduction of the other-age effect (but see also Macchi Cassia et al., 2009, who found a marginal effect). Taken as a whole, these latter studies suggest that the plasticity of the adult face processing system is somewhat limited, and may only concern stimuli that fully respect the innate biological constraints of the visual system and that have been previously encountered in the visual environment (such as infant faces). Whether the adult face processing system can be modulated by visual experience acquired *exclusively* in adulthood for visual stimuli that have not been experienced before and violate the biological constraints of the system remains an outstanding question.

Here, we investigated this question by training adult individuals to recognize inverted faces. Inverted faces constitute a stimulus of choice in this context because despite having more salient elements in the lower part of the stimulus, they share identical low-level visual properties with, and are as complex as upright faces. Unless the stimuli are degraded (as in Mooney stimuli; Mooney, 1957), inverted faces are also perceived as faces and there is evidence from multiple sources that they are handled by the face processing system, albeit not efficiently. For instance, presentation of inverted faces leads to substantial neural activation of face-sensitive areas (Kanwisher, Tong, & Nakayama, 1998; Mazard, Schiltz & Rossion, 2006) and face-sensitive visual evoked potentials such as the N170 (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Rossion et al., 1999). In the non-human primate brain, single neurons that respond to faces but not objects also respond to inverted faces (Perrett et al., 1988). However, and importantly, inverted faces are not visually experienced, and human observers do not develop an expertise at individualizing inverted faces. Indeed, it has long been known that humans' recognition performance is poor for inverted faces (Hochberg & Galper, 1967; Valentine, 1988; Yin, 1969). This face inversion effect (FIE) is already observed in children as young as 3 years of age (Picozzi et al., 2009), and is perhaps the most robust and consistent effect documented in the face perception literature (for recent reviews see Rossion, 2008, 2009).

In line with the putative limitation of the plasticity of the adult face processing system mentioned above, studies that have trained adults to recognize inverted faces have generally been unsuccessful. Robbins and McKone (2003) trained participants to discriminate two pairs of twins (i.e., four faces) in the inverted orientation during 10 hr of training spanning 5 weeks. After training, participants were accurate at recognizing new pictures of the same twins. However, participants were not tested with upright faces before and after training, preventing an assessment of any modulation of the magnitude of the face inversion effect. Moreover, generalization to novel face identities was not tested. Hussain, Sekuler, and Bennett (2009) trained participants in a 1-hr session to discriminate 10 full-front faces in the inverted orientation in a 10-alternative forced choice (AFC) matching task. Participants were tested the next day in four different conditions, namely in the inverted (trained) orientation versus in the upright (untrained) orientation, using the 10 trained exemplars versus 10 novel exemplars. Improvement on inverted faces during training was shown to be only exemplar-specific: there was no reduction of the face inversion effect after training when novel exemplars were used. Finally, Ashworth, Vuong, Rossion, and Tarr (2008) trained participants in two sessions (1 hr each) administered on two consecutive days, to name six target faces in the upright orientation and at a 150° orientation, and six other target faces upright and at a 240° orientation. Participants were tested on the third day using an identical naming task in which learned exemplars and distractors were presented at 12 different orientations from 0 to 360° in steps of 30°. While these authors found learning effects for the trained orientations, generalization to new exemplars was not tested.

Although these observations may not be encouraging, there are reasons to believe that the training and testing protocols used in these studies were not optimal and that this important issue has not been fully explored. First, the duration of the training was relatively short (i.e., 10 hr over 5 weeks in Robbins & McKone, 2003; 2 hr in Ashworth et al., 2008; 1 hr in Hussain et al., 2009). Second, the number of facial identities used for training in these studies was small (i.e., four exemplars in Robbins & McKone, 2003; six exemplars in Ashworth et al., 2008; 10 exemplars in Hussain et al., 2009), a factor that may have limited the possibility for learning to generalize to new exemplars (although note that this was explicitly tested only in Hussain et al., 2009). Most importantly, in Hussain et al. (2009), the number of novel exemplars used to test generalization effects was also small (i.e., 10 exemplars). Because substantial practice effects have been observed in several face processing studies as participants proceed through the experiment (e.g., experiment 1 in Ashworth et al., 2008; Bradshaw & Wallace, 1971), similar practice effects for novel exemplars might be present within the testing session itself, diminishing the possibility to highlight exemplar-generalization properly. Finally, with the exception of the study by Ashworth et al. (2008), correct response times for recognizing upright and inverted faces were not considered. This is unfortunate because the face inversion effect is often found in response times, a critical variable which must be considered in addition to accuracy rates to fully account for the FIE (Rossion, 2008).

In the present study, we trained eight adult observers to individualize a large set (30) of inverted faces over a 2-week extensive training program (16 hr of training). Performance for recognition of upright and inverted faces was measured before and after training using different sets of faces. A challenging four-alternative forced choice (4-AFC) delayed matching task with viewpoint changes between the encoding and target items was used to measure pre- and posttraining performance, for several reasons. First, pilot data collected in our laboratory showed that participants are far from ceiling performance at this task even with upright faces, allowing for the assessment of any potential transfer with learning for inverted faces to upright faces. Second, this task appears to be associated with large inversion effects in accuracy rates (15%–20%), without any trade-off between accuracy rates and correct response times. Third, because of a substantial change of viewpoint (30°) between the stimuli to match and discriminate, the task cannot be performed using a simple image-based matching strategy.

Methods

Participants

Eight participants (two males) were recruited to take part in the full training study, in exchange of retribution. They were informed that the study required intensive testing and training sessions, over the course of 2 full weeks. In addition, 10 control participants (two males) were tested in only two separate sessions without any training. All participants had normal or corrected-to-normal vision. Three were left-handed (one trained). One control participant showed almost no inversion effect at the pretest session (trade-off between accuracy, lower for inverted faces, and RTs, faster for inverted faces) so that she showed a dramatic increase of face inversion effect from posttest compared to pretest without any training. Her response profile was not only completely opposite to that of the trained participants but also to the other controls. This participant, therefore, was considered as an outlier and was not taken into consideration for the analyses. Note that since we hypothesized a relative decrease of the FIE in trained participants, if anything, removal of this control participant runs counter to our hypotheses.

Stimuli

A total of 118 high-quality photographs of face identities were used in the study. For the tests of inversion effect (pretest and posttest), 64 different face identities were used. Thirty-two face identities were used at pretest (16 females and 16 males) and the remaining 32 face identities (24 females and eight males) were used at posttest. The face photographs were presented in color, cropped off for external features, and displayed on a gray background at a size of 170-200 pixels of width and 250 pixels of height (about 5 cm wide and 7 cm high on the screen). For each face identity, three viewpoints were used: full-front (FF), right (30R) and left (30L) profiles (30° depth rotation). The exact same faces (and combinations of distractor faces for the forced choice) were presented at upright and inverted (vertically flipped) orientations.

Procedure

The participants were trained and/or tested one by one in a dimly illuminated room. They sat 70 cm from the computer screen. A chinrest was used to avoid movement of the head throughout the experiment. The to-be trained participants were tested on day 1 (pretest Friday, week 1), then trained during days 4 to 8 (Monday to Friday, week 2) and days 11 to 13 (Monday to Wednesday, week 3) before being tested again on day 14 (posttest, Thursday, week 3). Control (untrained) participants were tested two times (pretest, posttest) with the exact same delay of 13 days in between sessions, without any training.

Pretest/Posttest

We used the same 4-AFC delayed matching task at testing pre- and posttest. Participants saw a first face presented for 400 ms, followed after a brief delay (500 ms) by four faces arranged in a square around the center of the screen which remained visible until the participant's response (Figure 1). The task was to determine which one of the four faces was presented at encoding. The faces could be presented either in the upright (UP) or in the inverted (INV) orientation, randomly. The first (target) face was always presented in a different depth-rotated view than the four subsequent faces, which were all presented in the same depth-rotated view. Six depths-rotated view combinations between the target and the distractor faces were possible: FF-30R; 30R-FF; FF-30L; 30L-FF; 30L-30R; 30R-30L (FF = full-front; 30L/R = 30° depth rotation on the left/right); in both orientations (UP and INV). There were thus 384 possible combinations (32 faces × 6 combinations × 2 orientations), out of which 280 trials were randomly selected for each participant and session to limit the duration of testing.

Participants were instructed to respond as accurately and rapidly as possible. Responses were made with the two hands using the keyboard keys 1, 3, 4, and 6 on the numeric pad, these keys corresponding to the position on the screen (1 = bottom left, 3 = bottom right, 4 = top left, 6 = top right) of the four faces to discriminate (Figure 1).

Training program

Three sets of 10 faces were used (Set 1, Set 2, Set 3). Faces from the Set 1 were learned first, and faces from the other sets were introduced later during training. Faces from Set 2 and Set 3 were first used as novel faces in an old/new discrimination task following learning of Set 1, and then were learned as well. The training program consisted of four different tasks: exposure/learning, naming, old/new recognition, and forced choice matching, all of which are detailed below. The choice of using several tasks during training rather than solely the 4-AFC task used at pre- and posttest was made in order to ensure maintaining participants' interest and motivation during training. Regarding the tasks, we chose the face-name association task and the old/new task because there is evidence in the literature for the former to be highly effective in

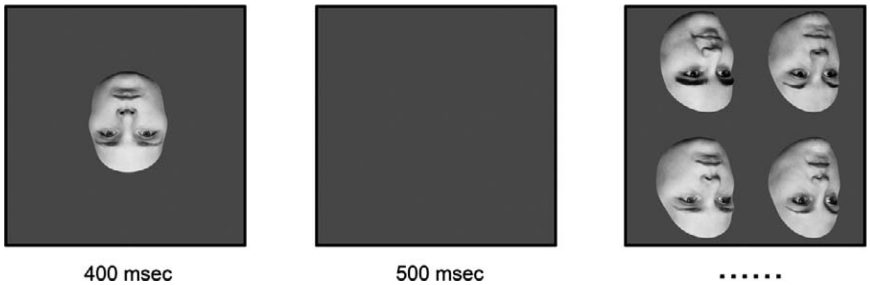

Figure 1. The 4-alternatives forced choice delayed matching task, which was performed for both upright and inverted faces, before and after training (different sets of faces).

individuation learning, and for the latter to be a sensitive measure of individuals' face recognition abilities. Several studies in the field have demonstrated the benefit of individuation over categorization processes in improving performance recognition of inexperienced faces such as other-race faces (Lebrecht et al., 2009; Tanaka & Pierce, 2009), other-age faces (Yovel et al., 2012) or other-species faces (Scott & Monesson, 2009). Among these studies, some have efficiently used naming tasks in order to significantly improve performance recognition, where a specific face is associated to a name (McGugin et al., 2011; Scott & Monesson, 2009) or a letter (Lebrecht et al., 2009; Tanaka & Pierce, 2009) to be learned. Several studies have also documented the sensitivity of old/new tasks in measuring one's ability to individuate specific faces (de Heering et al., 2010; Lebrecht et al., 2009; McGugin et al., 2011; Michel, Caldara, Rossion, 2006; Yovel et al., 2012). Hence, the old/new task administered following the exposure and the naming tasks aimed at monitoring participants' learning of the face sets during training, while progressively introducing the new faces sets to be learned.

During the learning sessions, the different sets of faces to learn were progressively introduced. Participants always started the learning of a set with the exposure/learning task followed by the naming task. The forced choice matching task and the old/new tasks were then introduced (for a detail of the learning program, see Table 1). Each participant of the trained group underwent individual training of approximately 2 hr per day for 8 days, for a total of approximately 16 hr of training. Distributing the training hours this way was done in order to avoid fatigue. The sessions took place in late afternoon or in early evening to facilitate the consolidation of learning (Stickgold, Hobson, Fosse, & Fosse, 2001).

Exposure/learning task

Three identical tasks (E1, E2, E3) were used, one for each set of faces. These tasks were divided into 6 blocks. In the first block, participants were exposed to five inverted full front pictures of faces with the corresponding name. Each inverted face and name combination was presented two times. Participants were asked to learn the face/name association. In the second block, the same five faces were presented but in the other two depth-rotated views (30L, 30R). Each face was presented for 5 s. In the third block, participants were given a visual reminder of the names using a list of names without the associated pictures. Then, in a 30-trials task, participants were instructed to give the name of the previously learned face for each of the three viewpoints, which were each presented twice. The same procedure was used in the three subsequent blocks for the other five faces of the set.

Naming task

Three identical (N1, N2, N3) tasks were used, one for each set of 10 faces to learn. Before the beginning of each naming task, participants were provided with a visual reminder (list) of the names of the faces. In these tasks, a face was presented on the screen until the participant provided the corresponding name. The response was given by pressing the key corresponding to the first letter of the name on the keyboard (note that after the introduction of Set 3, participants were also asked to give the full name of each face orally). A visual feedback was provided following each trial, containing the accuracy ("correct" versus "incorrect") of the response and a reminder of the correct name associated to the face. Each naming task was composed of 30 trials (10 faces * 3 viewpoints). In addition to the naming tasks administered following the exposition to each face set, two more tasks were performed (N4 and N5). The task N4 was composed of Sets 1 and 2 and was introduced after these sets were learned. The task N5 was composed of Sets 1, 2 and 3 and was introduced following learning of the third set. This last task tested all of the 30 learned faces in a random order.

For each naming task, participants had to reach a 100% accuracy rate before they could go on. If this

Learning session	Estimated time
Pre-test, day 1, Week 1 (Friday)	
1 Forced choice matching task Set 0 (32 faces)	
Session 1, day 4, Week 2 (Monday)	
1 exposure/learning task Set 1 (10 faces)	±10 min
2 naming task Set 1	±75 min
3 Forced choice matching task	±25 min
4 naming task Set 1 (only for subject 2)	±/
Session 2, day 5, Week 2 (Tuesday)	
1 exposure/learning task Set 1	±10 min
2 naming task Set 1	±50 min
3 Old/New task Set 1	±5 min
4 exposure/learning task Set 2 (10 faces)	±10 min
5 naming task Set 2	±20 min
6 naming task Set 1+Set 2	±15 min
Session 3, day 6, Week 2 (Wednesday)	
1 exposure/learning task Set 1	±10 min
2 exposure/learning task Set 2	±10 min
3 naming task Set 1+Set 2	±60 min
4 Forced choice matching task	±20 min
5 naming task Set 1+Set 2	±15 min
Session 4, day 7, Week 2 (Thursday)	
1 naming task Set 1+Set 2	±60 min
2 exposure/learning task Set 1	±10 min
3 exposure/learning task Set 2	±10 min
4 Old/New task Set 1+Set 2	±10 min
5 naming task Set 1+Set 2*	±15min
6 Old/New task Set 1+Set 2 (only for subject 2 and 3)	±/
Session 5, day 8, Week 2 (Friday)	
1 Old/New task Set 1+Set 2	±10 min
2 naming task Set 1+Set 2	±30 min
3 exposure/learning task Set 3	±10 min
4 naming task Set 3 (10 faces)	±15 min
5 Forced choice matching task	±15 min
6 naming task Set 3	±25 min
7 naming task Set 1+Set 2+Set 3	±15 min
8 naming task Set 1+Set 2+Set 3 (only for subject 2)*	±/
Session 6, day 11, Week 3 (Monday)	
1 exposure/learning task Set 3	±10 min
2 naming task Set 1+Set 2+Set 3	±40 min
3 Old/New task Set 1+Set 2+Set 3	±15 min
4 Forced choice matching task	±15 min
5 naming task Set 1+Set 2+Set 3*	±40 min
Session 7, day 12, Week 3 (Tuesday)	
1 Old/New task Set 1+Set 2+Set 3	±15 min
2 Forced choice matching task	±15 min
3 naming task Set 1+Set 2+Set 3*	±40 min
4 Old/New task Set 1+Set 2+Set 3	±15 min
5 naming task Set 1+Set 2+Set 3*	±40 min
Session 8, day 13, Week 3 (Wednesday)	
1 Forced choice matching task	±15 min
2 naming task Set 1+Set 2+Set 3*	±40 min
3 Old/New task Set 1+Set 2+Set 3	±15 min
4 naming task Set 1+Set 2+Set 3	±40 min
Post-test, day 14, Week 3 (Thursday)	
1 Forced choice matching task (Set 4)	

Table 1. Training program. *Two successes required.

criterion was not reached, they repeated the entire task. The names of the faces without the associated pictures were provided as a visual reminder to the participants before starting the task each time.

Old/New task

Three Old/New tasks were administered, each following the learning and naming task of each set of 10 faces. In these tasks, a face was presented in three different viewpoints (FF, 30L, 30R). The first task consisted of 60 trials and contained the 10 faces of the first (learned) set and the 10 faces of the second (yet unlearned) set. The second task consisted of 120 trials and contained the 20 faces of the first and second (learned) sets, the 10 faces from the third (yet unlearned) set and 10 new faces. The third task consisted of 180 trials and contained the faces from all (learned) sets as well as 30 new faces.

Forced choice matching task

This task was identical to the 4-AFC delayed matching task used at pre- and posttest, consisting of 56 faces (32 of which were present at pretest and 24 new faces), which were only presented in the inverted orientation. Each identity was presented two times in a different arrangement for the forced choice for the six viewpoints combinations.

Moreover, after the response of each trial, visual feedback was provided, informing the participant of the accuracy of the response for each particular trial, as well as the overall accuracy rate at that point in the task. Out of 672 possible trials (56 faces $\times$ 6 viewpoints combinations $\times$ 2 repetitions), 336 were randomly selected.

Analyses

Accuracy rates and correct response times (RTs) in the 4-AFC delayed matching task were considered for each participant at pre- and posttest. RTs that were above or below two standard deviations from the mean within each condition were removed, separately in the pre- and the posttest sessions. To take into account speed accuracy trade-offs, we also computed inverse efficiency scores for each participant, by dividing the average response time by the corresponding accuracy within each condition (Townsend & Ashby, 1983).

First, accuracy, correct RTs and inverse efficiency scores in the novice and in the trained group were analyzed by means of an analysis of variance (ANOVA) with the factors *Orientation* (upright vs. inverted) and *Session* (pretest vs. posttest) as within-subjects

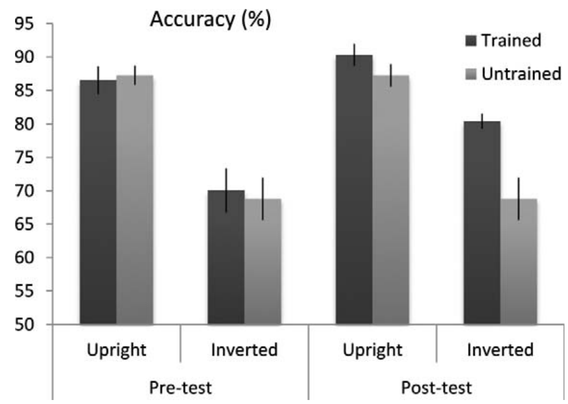

Figure 2. Accuracy rates plotted as a function of orientation and session, separately for the groups of untrained ($N = 9$) and trained ($N = 8$) participants.

variables and the factor *Group* (untrained vs. trained) as a between-subjects variable. Second, accuracy, correct RTs and inverse efficiency scores were analyzed separately in each group using a repeated measure ANOVA with the factors *Orientation* (upright vs. inverted) and *Session* (pretest and posttest) as within-subjects variables.

Results

In the novice group, accuracy rates for the upright orientation condition were relatively high and stable across sessions (pretest: range = 80%–94%; posttest: range = 77%–92%; Figure 2, Table 2). There was a large inversion effect at both sessions. If anything, this effect was even larger in the post- than in the in pretest session in accuracy rates (18.5% vs. 23.8%, Table 2, Figure 3).

For the (to be) trained participants, at the pretest session, the magnitude of the inversion effect was in the normal range (average 17%, range 13%–28%). However, following training, in stark contrast to the data of untrained participants, the inversion effect was largely reduced (average 10%, range 1%–16%) (Table 3a, Figure 2, and Figure 3).

This reduction of the FIE in accuracy was clear for five out of eight trained participants, while there was no such reduction for three participants (Tr1, Tr5 and Tr8) (Table 3a and Figure 3). However, each of these three participants showed a large reduction of the FIE in correct RTs (reduction of 281, 314 and 183 ms respectively at post- relative to pretest, see Table 3b and Figure 3). Considering this observation, it is clear that a full account of the effect of training requires both accuracy rates and correct response times to be taken into consideration in a combined measure. When the data is displayed as inverse efficiency indexes, all

	Pretest		Posttest	
	Upright	**Inverted**	**Upright**	**Inverted**
A. Untrained Participants – Accuracy (%)				
C1	80.00	55.17	82.73	48.94
C2	90.37	80.00	90.97	75.74
C3	90.21	70.80	88.11	61.31
C4	85.51	71.13	86.13	69.93
C5	93.62	71.22	89.29	63.57
C6	88.57	82.14	90.14	73.91
C7	85.00	67.14	76.92	57.66
C8	87.77	60.28	91.67	54.05
C9	84.25	61.19	84.62	60.58
Average	**87.25**	**68.79**	**86.73**	**62.86**
StDev	4.04	8.93	4.74	8.98
B. Untrained Participants – Correct Response Times (ms)				
C1	1525.06	1753.10	1655.45	1558.50
C2	1711.96	2102.61	1708.06	1819.64
C3	1342.46	1519.73	1359.14	1405.43
C4	1254.63	1286.17	1238.62	1315.26
C5	1440.98	1559.03	1326.50	1371.76
C6	1752.70	1872.72	1564.22	1624.88
C7	1480.13	1767.08	1548.72	1852.91
C8	1289.22	1284.96	1300.83	1233.23
C9	1479.56	1528.80	1438.29	1553.57
Average	**1475.19**	**1630.47**	**1459.98**	**1526.13**
StDev	172.34	269.47	166.31	215.97

Table 2. Results (accuracy rates and correct RTs) for untrained participants ($N = 9$).

trained participants show a large reduction of the FIE following training (Figure 4).

The ANOVA performed on accuracy rates revealed a main effect of *Orientation*, $F(1, 15) = 132.172$, $p < 0.001$, and a marginally significant effect of *Group*, $F(1, 15) = 4.442$, $p = 0.052$. Significant two-way interactions were found for the factors *Group* with *Session*, $F(1, 15) = 22.801$, $p < 0.001$, and *Group* with *Orientation*, $F(1, 15) = 6.995$, $p = 0.02$. Most importantly, the three-way interaction was significant, $F(1, 15) = 18.634$, $p = 0.001$, reflecting the decrease of inversion effect at posttest, only for the trained group (Table 3a, Figure 2, and Figure 3). The same analysis performed on correct response times showed a main effect of *Session*, $F(1, 15) = 13.172$, $p = 0.002$, and of *Orientation* $F(1, 15) = 36.593$, $p < 0.001$. Two-way interactions were found for *Group* and *Session*, $F(1, 15) = 5.250$, $p = 0.037$, *Group* and *Orientation*, $F(1, 15) = 7.049$, $p = 0.018$, and *Session* and *Orientation*, $F(1, 15) = 7.091$, $p = 0.018$. The three-way interaction was not significant, $F(1, 15) = 0.13$, $p = 0.723$.

For inverse efficiency scores, there was a main effect of *Session*, $F(1, 15) = 17.782$, $p = 0.001$, and of *Orientation*, $F(1, 15) = 126.419$, $p < 0.001$. The factor *Session* significantly interacted with *Group*, $F(1, 15) =$

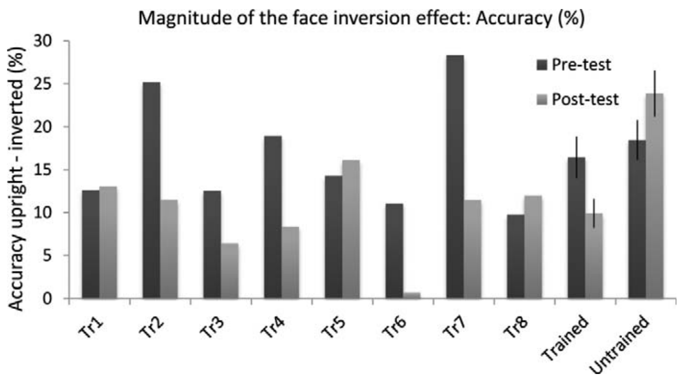

Figure 3. Face inversion effect in accuracy rates computed as the difference in performance for upright and inverted faces, separately plotted for pre- and posttraining session for the groups of untrained participants ($N = 9$), the group of trained participants ($N = 8$) and for each trained individual.

	Pretest		Posttest	
	Upright	Inverted	Upright	Inverted
A. Trained Participants – Accuracy (%)				
Tr1	82.96	70.34	92.20	79.14
Tr2	81.69	56.52	87.41	75.91
Tr3	90.91	78.38	90.97	84.56
Tr4	80.14	61.19	89.93	81.56
Tr5	91.43	77.14	92.41	76.30
Tr6	79.86	68.79	80.71	80.00
Tr7	91.97	63.64	94.12	82.64
Tr8	93.71	83.94	94.96	82.98
Average	**86.58**	**69.99**	**90.34**	**80.39**
StDev	5.93	9.39	4.55	3.14
B. Trained Participants – Correct Response Times (ms)				
Tr1	1819.55	2315.39	1596.77	1811.57
Tr2	1414.87	1438.73	1490.94	1702.60
Tr3	1448.36	1861.51	1197.54	1408.06
Tr4	1374.44	1506.58	1258.55	1464.33
Tr5	1489.58	2148.77	1361.93	1706.99
Tr6	2371.59	2540.01	1774.10	1721.02
Tr7	1288.21	1774.81	1042.45	1533.24
Tr8	1547.45	1907.94	1384.30	1561.70
Average	**1594.26**	**1936.72**	**1388.32**	**1613.69**
StDev	351.24	381.36	231.88	141.95

Table 3. Results (accuracy rates and correct RTs) for trained participants ($N = 8$).

23.371, $p < 0.001$, and *Orientation*, $F(1, 15) = 19.738$, $p < 0.001$, and the three-way interaction was highly significant, $F(1, 15) = 40.106$, $p < 0.001$, reflecting the decrease of inversion effect at posttest, only for the trained group (Figure 4).

We then performed a repeated measure ANOVA on each group separately. In the novice group, this analysis performed on accuracy showed a significant effect of *Session*, $F(1, 8) = 10.456$, $p = 0.012$, *Orientation*, $F(1, 8) = 76.506$, $p < 0.001$, and a significant interaction between the two factors, $F(1, 8) = 18.904$, $p = 0.002$. Importantly, the interaction did not reflect a decrease but rather a small *increase* of the inversion effect in posttest session compared to pretest session (approximately 5% increase, Table 2a, Figure 2, and Figure 3). This increase appeared to reflect at least in part a speed-accuracy trade-off, since untrained participants' FIE in RTs decreased in posttest session as compared to pretest session (Table 2b). However, for correct RTs, there was only a significant effect of *Orientation*, $F(1,8) = 10.671$, $p = 0.01$, due to faster responses for upright as compared to inverted faces (other effects: $p > 0.09$). Because of the speed accuracy trade-off, we performed an analysis on the inverse efficiency scores (Figure 4), for which there was only a significant main effect of *Orientation*, $F(1,8) = 64.212$, $p < 0.001$.

In the trained group, a repeated measure ANOVA performed on accuracy rates showed a significant effect of *Session*, $F(1, 7) = 12.513$, $p = 0.01$, *Orientation*, $F(1, 7) = 66.478$, $p < 0.001$, and a significant interaction between the two factors, $F(1, 7) = 6.439$, $p = 0.039$. Importantly, this latter result reflected a *reduction* of the face inversion effect in the post- relative to the pretest session (Figure 2 and Figure 3, Table 3a). For correct RTs, there was only a main effect of *Session*, $F(1, 7) = 8.935$, $p = 0.02$, and *Orientation*, $F(1, 7) = 24.054$, $p = 0.002$, because of faster response times in the post- relative to the pretest session and faster response times for upright relative to inverted faces (Table 3b). Here, however, the interaction between the two factors was not significant, $F(1, 7) = 3.305$, $p = 0.112$. Again, because of speed accuracy trade-offs in the individual data, we performed the same analysis on the inverse efficiency scores (Figure 4), which revealed a significant effect of *Session*, $F(1, 7) = 24.254$, $p = 0.002$, *Orientation*, $F(1, 7) = 64.231$, $p < 0.001$, and a highly significant interaction between the two factors, $F(1, 7) = 44.818$, $p < 0.001$, reflecting an important decrease of the inversion effect in the post- relative to the pretest session (Figure 4).

Discussion

Following extensive training at individualizing inverted faces over the course of 2 weeks, eight participants showed substantial improvement at individual recognition of a novel set of inverted faces. This improvement was observed relative to the performance of a group of untrained participants, to the trained participants' pretraining level of performance with inverted faces, and to the trained participants' performance with upright faces. These observations indicate, for the first time to our knowledge, that extensive

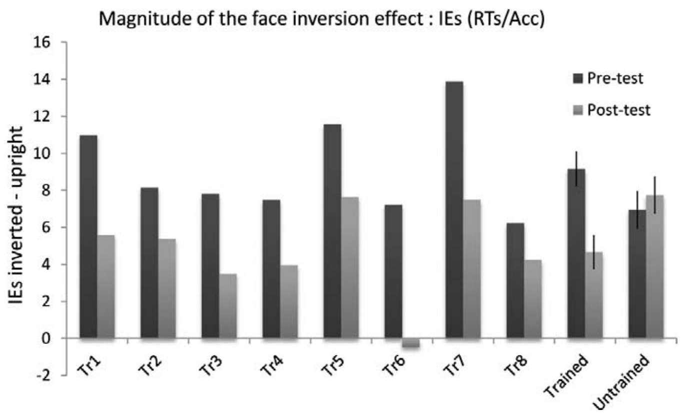

Figure 4. Face inversion effect in inverse efficiency rates (RTs/accuracy) computed as the difference in performance for upright and inverted faces, separately plotted for pre- and posttraining session for the groups of untrained participants ($N = 9$), the group of trained participants ($N = 8$) and for each trained individual.

training in adulthood can significantly reduce the face inversion effect for novel faces. We believe that this observation is interesting because it implies that the adult face processing system remains sufficiently plastic to be able to develop an expertise for a stimulus that is as complex as an upright face, and is neither preferentially attended to at birth, nor visually experienced during development.

The findings were quite clear, since each of the trained participants could be distinguished from the control participants in terms of the change in the magnitude of the inversion effect that took place (Figure 4). This pattern of results was found for accuracy measures and was strengthened when considering both the accuracy rates and correct RTs in the task, showing that a consideration of correct RTs, and a combination of variables as a measure of (inverse) efficiency, are important to fully account for the FIE in a matching/discrimination task (Rossion, 2008). We note also that the improvement at recognizing inverted faces did not come at the expense of the performance for upright faces. Quite the contrary, performance for upright faces slightly improved for the participants who were trained with inverted faces. However, their performance for upright faces was clearly not at ceiling at posttest (average for trained participants: 90%; range: 80%–95%) and thus the reduction of the FIE could not be attributed to a ceiling effect for upright faces.

In contrast to previous studies that attempted to train adults to recognize inverted faces (Ashworth et al., 2008; Hussain et al., 2009; Robbins & McKone, 2003), several characteristics of the training paradigm used in the present study may have contributed to the positive learning effects observed for novel faces. First, our paradigm involved a substantial practice time, spread over 2 weeks. Second, we used a large set of exemplars during training (30 faces to individuate in addition to the 56 faces used in the 4AFC task) as well as during pre- and posttraining tests (64 faces), preventing the emergence of practice effects within the testing sessions (Ashworth et al., 2008; Bradshaw & Wallace, 1971). Third, we used different sets of exemplars when testing performance at recognizing upright and inverted faces before and following training, allowing us to determine the effects of learning generalized to novel exemplars. Fourth, the tasks used at testing and during training required participants to recognize each face under different depth-rotated views, an important aspect for forming robust non-image-based individual face representations and minimizing any possible part-based recognition strategy. Fifth, the use of large sets of exemplars in difficult and challenging tasks prevented participants to perform at ceiling level, even for upright faces, allowing to test for the specificity of learning to the orientation that was trained. Finally, once again, we considered response times as a crucial variable in the measurement of the face inversion effect.

Although previous training studies failed to show an improvement in the recognition of novel inverted faces, one could argue that the improvement we found following extensive training is rather trivial. After all, extensive learning in adulthood at individualizing artificial nonface stimuli appears to improve the processing of such stimuli (e.g., the so-called Greebles in Gauthier & Tarr, 1997; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Gauthier, Williams, Tarr, & Tanaka, 1998; see also Wong, Palmeri, & Gauthier, 2009). However, in such studies, participants are usually tested posttraining with naming or identification tasks of trained stimuli (or of constitutive parts of the trained stimuli), so that there is, in fact, surprisingly scarce evidence that visual expertise training with individual exemplars of such an artificial category of stimuli generalizes to perceptual processing of novel exemplars of that category. Moreover, when hours of expertise training improves individual matching of such Greebles stimuli, the effects are not only very small but appear to be general, for instance transferring completely to the individual matching of the same Greebles presented upside-down (e.g., Figure 3 of Gauthier et al., 1999) or to Greebles split horizontally in two parts (Gauthier & Tarr, 2002). Most importantly, in the present study, we found a performance improvement for visual stimuli that are not only visually inexperienced but (unlike Greebles for instance) violate the biological constraints for preferential looking at birth, are as complex as upright faces, and are handled (inefficiently) by the face processing system in novices.

What are the processes that might account for the improvement at recognizing inverted faces and the reduction of the FIE?

In typical observers, like the untrained participants of the present study, the face inversion effect is generally considered as reflecting the loss of holistic/configural processing for inverted individual faces. That is, inversion apparently disrupts the ability to process the face as an integrated, single, whole representation, leading to the processing of the inverted face in a part-based manner. Evidence for this claim comes from studies showing that behavioral effects considered as hallmarks of holistic processing such as the "whole-part advantage" (Tanaka & Farah, 1993) and the "composite-face effect" (Young, Hellawell & Hay, 1987) disappear or are largely reduced when faces are inverted (Tanaka & Farah, 1993; Young et al., 1987; see also Bartlett & Searcy, 1993; Rhodes, Brake, & Atkinson, 1993; Sergent, 1984; for reviews, see Rossion, 2008; 2009). Moreover, presenting a face upside-down particularly disrupts perceptual sensitivity to relative distances between parts (Freire, Lee, & Symons, 2000; Le Grand et al., 2001), especially vertical long-range distances covering the whole face (e.g., eyes-mouth distance, Goffaux & Rossion, 2007; Sekunova & Barton, 2008). More recent and direct evidence comes from studies using an approach in which face perception is gaze-contingently limited to one fixated face part at a time (i.e., a window condition, forcing analytical processing) or rather prevents the use of the fixated part (i.e., a central mask condition, promoting holistic processing, Van Belle, de Graef, Verfaillie, Busigny, & Rossion, 2010a). In normal observers tested in such conditions, the face inversion effect decreases or increases, respectively (Van Belle, de Graef, Verfaillie, Rossion, & Lefèvre, 2010b). Given these considerations, unless one still argues that even upright faces are processed and represented in a part-based manner (e.g., Gold, Mundy, & Tijan, 2012; Wallis, Siebeck, Swann, Blanz, & Bulthoff, 2008), there may be at least two accounts for the improvement observed for the recognition of inverted faces following training: either the participants experienced an enhancement of the processes that are typically used for the processing of inverted faces (i.e., part-based processing), or they experienced an enhancement of processes similar to the ones typically used for the processing of upright faces (i.e., holistic processing).

On one hand, it could be argued that participants in our study learned to process inverted faces more efficiently without changing the nature of the processing that is typically performed on inverted faces, that is, in a part-based manner. Robbins and McKone (2003) provided convincing evidence for such part-based learning of inverted faces in their study. However, as stated previously, the small set of faces used during training in that study, and the absence of the generalization of learning to novel face identities might have prevented a true expertise for inverted faces from emerging, and might explain why holistic face processing did not increase for inverted faces in that study.

On the other hand, supporting the second view, studies in the face domain performed in naturalistic environments have demonstrated that preschool teachers, who benefit from prolonged visual experience with child faces in their everyday adult life, display similar hallmarks of holistic processing when presented with adult and child faces (de Heering & Rossion, 2008; Kuefner, Macchi Cassia, Picozzi, & Bricolo, 2008). Whereas novices, for instance, show a stronger inversion effect (Kuefner et al., 2008) and a stronger composite effect (de Heering & Rossion, 2008; Kuefner, Macchi Cassia, Vescovo, & Picozzi, 2010) for adult than for children faces, preschool teachers display effects of equal magnitude for both types of faces. Moreover, the magnitude of the composite effect observed for child faces relative to adult faces in the preschool teacher group can be strongly correlated to the number of years of experience with child faces: the longer the experience as a preschool teacher, the larger the composite effect for child faces (de Heering & Rossion, 2008). Similar observations have been reported in a group of maternity-ward nurses when tested with newborn faces (Macchi Cassia et al., 2009). In this vein, it could be argued that participants in the present study developed the capacity to process inverted faces more holistically and became more efficient as a result (e.g., Wang, Li, Fang, Tian, & Liu, 2012).

While the present study cannot provide an answer to this important issue, at least it provides clear evidence for a large improvement of performance at recognizing inverted faces. Moreover, this improvement is largely specific to the inverted orientation, leading to a significant reduction of the FIE. In future studies, one could use a training regime as implemented here to test whether inverted faces are processed qualitatively differently following expertise training. Paradigms measuring the whole-part and composite face effects (Tanaka & Farah, 1993; Young et al., 1987), as well as gaze-contingency manipulations with faces (Van Belle et al., 2010a; 2010b) could be tested, with the hope of showing increases of holistic processing of inverted faces after expertise training. Moreover, one could test whether training with inverted faces would lead to an increase of face-identity adaptation effects in face-sensitive regions of the human brain such as the "fusiform face area" (FFA) or "occipital face area" (OFA; Gilaie-Dotan, Gelbard-Sagiv, & Malach, 2010; Goffaux, Rossion, Sorger, Schiltz, & Goebel, 2009; Mazard et al., 2006; Yovel & Kanwisher, 2005) rather than an increase for inverted faces in more domain-general regions such as the lateral occipital complex (LOC) (Goffaux et al., 2009; Haxby et al., 1999; Yovel & Kanwisher, 2005).

Conclusions

We have shown that extensive visual training in adulthood can lead to a substantial decrease of the face inversion effect, accounting for the idea that the face processing system maintains the capacity to be modulated by visual experience even well into adulthood. Since face recognition is an evolutionarily old function of the brain and is thought to be a particularly good model of a domain-specific system, these observations have important implications for our understanding of the plasticity of the visual system and of the human brain in general.

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